



NEW LATE MIOCENE DROMOMERYCINE ARTIODACTYL FROM THE AMAZON BASIN: IMPLICATIONS FOR INTERCHANGE DYNAMICS

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ABSTRACT—A new dromomerycine palaeomerycid artiodactyl, *Surameryx acrens* new genus new species, from upper Miocene deposits of the Amazon Basin documents the first and only known occurrence of this Northern Hemisphere group in South America. Osteological characters place the new taxon among the earliest known dromomerycine artiodactyls, most similar to *Barbouromeryx trigonocorneus*, which lived in North America during the early to middle Miocene, 20–16 Ma. Although it has long been assumed that the Great American Biotic Interchange (GABI) began with the closure of the Isthmus of Panama in the late Pliocene, or ca. 3.0–2.5 Ma, the presence of this North American immigrant in Amazonia is further evidence that terrestrial connections between North America and South America through Panama existed as early as the early late Miocene, or ca. 9.5 Ma. This early interchange date was previously indicated by approximately coeval specimens of proboscideans, peccaries, and tapirs in South America and ground sloths in North America. Although palaeomerycids apparently never flourished in South America, proboscideans thrived there until the end of the Pleistocene, and peccaries and tapirs diversified and still live there today.

INTRODUCTION

THE GREAT American Biotic Interchange (GABI), wherein components of the North American biota dispersed to South America, and vice versa, after a terrestrial connection was established between the two continents in the late Cenozoic, has long been depicted as a Plio–Pleistocene event, beginning ca. 3.0–2.5 Ma. However, recent discoveries of North American-derived mammals (e.g., proboscideans, peccaries, and tapirs) in upper Miocene deposits of the Amazon Basin (Campbell et al., 2000, 2006; Frailey and Campbell, 2012), as well as a revised chronostratigraphy for deposits in Amazonia (Campbell et al., 2010) and new fossil discoveries in Central America (Carranza-Castañeda and Miller, 2004), indicate that interchange via a terrestrial connection probably began no later than the early late Miocene, ca. 9.5 Ma, and was strong by the early Pliocene, ca. 5.0 Ma (Campbell, in press). The discovery of a close relative of North American palaeomerycid artiodactyls known only from the lower to middle Miocene of North America from upper Miocene deposits of the Amazon Basin (Fig. 1) is further evidence that the first pulse of the GABI occurred no later than the early late Miocene.

It is now widely recognized that a significant North American-derived vertebrate paleofauna was in place in the lowlands of central Panama in the early to middle Miocene (ca. 19.5–14.0 Ma) (Whitmore and Stewart, 1965; MacFadden, 2006). Geological and paleontological data support the hypothesis that southern Central America was a peninsula of North America by the early Miocene (ca. 19.0 Ma) and not an island archipelago (Kirby et al., 2008; Montes et al., 2012a, 2012b). Further, paleofaunas of Central America are increasingly demonstrating that a number of small artiodactyls made their way almost to South America by the early to middle Miocene, including protoceratids (Webb et al., 2003) and floridatraguline camels (Rincon et al., 2012). This is revealing a tendency for

small artiodactyls to be found in greater diversity in this region of tropical forests than previously thought possible.

The presence of this newly recognized North American immigrant in the Amazon Basin provides additional support for a new model of GABI dynamics, the Baudo Pathway hypothesis. This hypothesis incorporates new geotectonic and fossil data pertaining to the formation of the Panamanian isthmus and paleobiogeography of the region and posits an initial pulse of dispersal between the continents in the late Miocene (Campbell et al., 2000; Campbell, in press). Correctly dating the earliest establishment of a terrestrial connection between North America and South America has important implications not only for interpreting terrestrial and marine paleobiogeography, but also changes in the distribution of oceanic currents and, through a redistribution of oceanic waters, potentially patterns of global climate.

The stratigraphy of the Amazon Basin is a contentious issue (Campbell et al., 2006, 2010; Hoorn et al., 2010; Latrubesse et al., 2010). The interpretation followed here is that of Campbell et al. (2001, 2006, 2010), who consider the uppermost deposits within Amazonia to comprise the Madre de Dios Formation (=Içá Formation in Brazil), which is separated from older Tertiary deposits by the basin-wide Ucayali Unconformity. At the base of this formation is the Acre Conglomerate Member (Campbell et al., 1985), from which comes a varied and abundant macro- and microvertebrate paleofauna comprising late Miocene (Chasicuan/Huayquerian SALMA) taxa (Campbell et al., 2006). The best chronostratigraphic data currently available for the Madre de Dios Formation are from southeastern Peru and comprise two ⁴⁰Ar/³⁹Ar ash dates (9.01 ± 0.28 Ma near the base and 3.12 ± 0.02 Ma near the top of the formation [Campbell et al., 2001]) and a paleomagnetic profile of the formation with 18 polarity reversals that correlates quite well with the ash dates (Campbell et al., 2010).



FIGURE 1—Map showing location of the Acre River where the specimen was found, between Cobija, Bolivia (S 11°01', W 68°45') and Assis, Brazil (S 10°56', W 69°34'). The Acre River connects the two towns and represents the international boundary between the two countries.

Based on these data, the Acre Conglomerate and its faunas are interpreted to date from at least 9.5 Ma in age. There are numerous vertebrate fossil-producing localities in the Acre Conglomerate in exposures along the Acre River between Cobija, Bolivia, and Assis, Brazil, but there are no recorded localities underlying the Ucayali Unconformity or overlying the Acre Conglomerate in this part of the river. In addition, the new ruminant specimen shows no sign of recent breakage and its delicate coronoid and articular processes are undamaged, suggesting that it experienced no significant transport since eroding from the bedrock. Its patina and color match that of other specimens from the Acre Conglomerate. In addition, the specimen represents a dromomerycine palaeomerycid, which is a group known only from the Miocene, and never from younger beds, as once thought. This age change was established when the Clarendonian and Hemphillian land mammal ages were moved from the Pliocene to the Miocene in the 1980s (Prothero and Lister, 2007, 2008). This makes it very unlikely that it is a specimen reworked from Pleistocene deposits, from which it would have to be sourced under the classic GABI timing. Thus, the upper Miocene Acre Conglomerate is the presumed source horizon for the palaeomerycid dentary described here.

MATERIALS AND METHODS

The fieldwork that resulted in the recovery of the specimen in 1981 was led by KEC. The specimen was analyzed and compared to fossil collections in the American Museum of Natural History (AMNH), New York, by DRP and BLB, with initial contributions by CDF. Measurements were made with digital calipers. Statistical analyses and plots were performed with Microsoft Excel software.

Abbreviations: LACM=Natural History Museum of Los Angeles County; SALMA=South American Land Mammal Age; UNSM=University of Nebraska State Museum.

SYSTEMATIC PALEONTOLOGY

- Class MAMMALIA Linnaeus, 1758
- Order ARTIODACTYLA Owen, 1848
- Family PALAEOMERYCIDAE Lydekker, 1883
- Subfamily DROMOMERYCINAE Frick, 1937

SURAMERYX new genus

Figures 2–4

Type species.—*Surameryx acrensensis* new species, by monotypy.

Diagnosis.—As for species.

Etymology.—From Spanish “sur” meaning south; and Greek “meryx” meaning ruminant.

Occurrence.—Acre Conglomerate Member of the Madre de Dios Formation; late Miocene (older than ⁴⁰Ar/³⁹Ar date of 9.01 Ma) (Campbell et al., 2001, 2010). LACM locality 5159; Acre River between Cobija, Bolivia (S 11°01', W 68°45') and Assis, Brazil (S 10°56', W 69°34') (Fig. 1).

SURAMERYX ACRENSIS new species

Diagnosis.—Primitive dromomerycine artiodactyl (Prothero and Lister, 2007, 2008) resembling early Miocene *Barbouromeryx trigonocorneus* Barbour and Schultz, 1934 in having unreduced premolar row length compared to molar row length, a “*Palaeomeryx* fold”, and a vertical groove on posterolingual face of P₄. It differs from all other palaeomerycids in having relatively wide lower cheek teeth, a short coronoid process that curves only slightly posteriad, and larger labial stylids.

Description.—The holotype of *Surameryx acrensensis* (LACM 155113) (Figs. 2–4) consists of a left ramus broken at the symphysis just in front of the mental foramen. The P₃–M₃ are preserved, and there are a pair of alveoli for P₂, but no sign of an alveolus for a dP₁ or P₁. The anterior part of the ramus is long and slender, with a diastema that apparently spanned from the canine to the P₂. The rest of the ramus shows minimal breakage or abrasion. The coronoid process of the ramus rises abruptly behind the M₃, with a tall, triangular-pointed dorsal end. The mandibular condyle is large, sits high on the posterior side of the ascending process about three-quarters of the distance up from the plane of the tooth row, and extends posteriad approximately a centimeter posterior to the plane of the coronoid process. The angle of the jaw is slightly abraded, but it has a well-developed convex curvature with no sharp angles or corners, as is seen on the angular processes of some artiodactyl jaws.

The teeth are brachydont, like those in palaeomerycids (Figs. 2–4), and moderately worn. The crests and cristids are well developed, clearly marked, and not so worn as to be merged together. There are no cusps left as would be seen in unworn teeth, even in the M₃, the last tooth to erupt. The total length of the premolars compared to that of the molars is relatively large, as is found only in the most primitive dromomerycines (Fig. 5), such as *Barbouromeryx* Frick, 1937 and *Bouromeryx* Frick, 1937. There is no molarization of the anterior premolars, as is the case with most primitive members of the Palaeomerycidae.

The P₃ consists of a simple, U-shaped crest representing the worn edge of the trigonid, and two additional crests closely appressed where the talonid once formed. The anterior-most of these two talonid crests (the entoconid-protoconid crest) is broad with a rounded lingual termination, whereas the posterior crest, which attaches to the hypoconulid, is narrow and comes to a point on the lingual end. The P₄ is quite similar to the P₃, with a large V-shaped selene formed by the wear of the paraconid-protoconid-metaconid crest of the trigonid. The metaconid-protoconid crest comes to a broad, flat surface on the lingual side. The trigonid fossette in the P₄ is closed lingually, a derived feature of dromomerycines (Figs. 2, 4). As with the P₃, the P₄ has a talonid consisting of a U-shaped crest, with a broadly lobate entoconid crest and a narrow, lingually pointed hypoconulid crest. As in other palaeomerycids, there is a vertical groove on the posterolingual face of P₄ that merges with the notch between the entoconid and hypoconulid. There is also a prominent groove on the labial side that separates the trigonid from the talonid.

The molars have the classic configuration of palaeomerycids (Figs. 2–4). The M₁ is very worn, with no internal crests remaining, leaving only the worn cristids of the trigonid and talonid. The protoconid/protocristid on the lingual side is very highly worn, so there is only a tiny remnant of a fossette

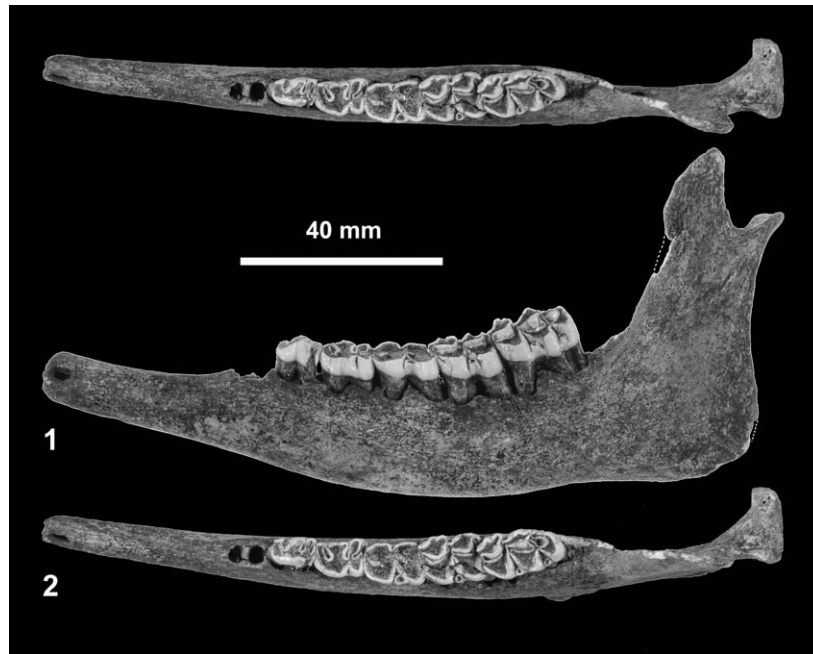


FIGURE 2—1, 2, *Surameryx acrensis* n. gen. n. sp. in lateral and occlusal (stereopair) views, respectively.

separating the protocristid from the metacristid. There is a distinct circular crest representing the tip of the ectostylid in the labial groove between the trigonid and talonid.

The M_2 is considerably less worn, and shows many more diagnostic features. The labial side of the trigonid shows a distinct “*Palaeomeryx* fold” as does the M_3 , but not the M_1 . A “*Palaeomeryx* fold” is a convex fold of enamel that extends from the labial rim of the post-protocristid and lies between it and the ectostylid of lower molars. When worn, it forms a distinct flange of exposed dentine connected to the post-protocristid of the protoconid. It is considered to be a primitive trait of most cervoids (deer and their relatives), including palaeomerycids.

The labial side of M_2 shows a distinct metacristid and entocristid with the classic pattern of a worn selenodont metaconid and entoconid. The hypocristid is also worn down to a lake-shaped depression, but unlike the M_1 , the M_2 has distinct arcuate fossettes remaining between the metacristid and protocristid, and between the entocristid and hypocristid. Like the M_1 , the M_2 has a distinct circular crest present on the tip of a large ectostylid.

The M_3 shows many of the features found in the M_1 and M_2 . The trigonid consists of a well-worn metacristid, with a distinct circular portion representing the worn metaconid, and a selenodont protocristid, with a well-developed fossette between them. A very narrow, pointed cristid is formed where the paracristid and hypocristid converge lingually, and this pointed cristid abuts, but does not merge with, the posterolabial face of the hypoconid/hypocristid. The trigonid consists of three parts: a relatively less worn entoconid/entocristid, a deeply worn selenodont hypocristid, and a large U-shaped hypoconulid. The latter forms a continuous crest posteriorly, but the hypoconulid has a gap at the mouth of the “U” where it faces the hypoconid. It is not clear whether there was once a “double lobe” on the M_3 hypoconulid, as in some dromomerycines, because it is very worn, but it was clearly closed posteriorly as in dromomerycines and unlike the open condition in giraffes. There is also a large, distinct, circular crest representing the tip of the ectostylid, and an

additional circular crest in the intervallum between the hypoconid and hypocristid.

For measurements, see Table 1.

Etymology.—In reference to the Acre River, where the holotypic specimen was found.

Holotype.—LACM 5159/155113, a left ramus with P_3 – M_3 , broken at the symphysis just in front of mental foramen.

Occurrence.—Acre Conglomerate Member of the Madre de Dios Formation; late Miocene (older than $^{40}\text{Ar}/^{39}\text{Ar}$ date of 9.01 Ma) (Campbell et al., 2001, 2010). LACM locality 5159; Acre River between Cobija, Bolivia (S $11^{\circ}01'$, W $68^{\circ}45'$) and Assis, Brazil (S $10^{\circ}56'$, W $69^{\circ}34'$) (Fig. 1).

Remarks.—The “*Palaeomeryx* fold” is typical of most primitive palaeomerycids, and especially primitive dromomerycines, although it is also occasionally found in a few other artiodactyl groups (e.g., some moschids, as well as ruminants like *Eumeryx* Matthew and Granger, 1924 and *Rutitherium* Filhol, 1876 [Janis and Scott, 1987]). The vertical groove on the posterolingual face of P_4 is also typical of nearly all palaeomerycids. The detailed patterns of P_3 and P_4 are almost identical to those seen in the most primitive of the New World Palaeomerycidae, such as the aletomerycine *Aletomeryx* Lull, 1920 and the dromomerycine *Barbouromaryx*. Further, the proportions of the premolars and the lack of premolar reduction relative to the length of the molar row are very similar to those of *Barbouromaryx*, but also similar to the condition in *Aletomeryx* (Fig. 5). LACM 155113 is almost identical in size to *Barbouromaryx*, but it is distinct in that the mediolateral widths of the teeth are broader than in any known palaeomerycid (Figs. 2, 4, 6).

LACM 155113 is clearly a dromomerycine because it possesses numerous synapomorphic features of the group, such as large ectostylids on the molars; a vertical groove on the posterolingual face of P_4 ; and the closed trigonid fossette of P_4 . This taxonomic assignment is corroborated by the presence of primitive palaeomerycid features like the “*Palaeomeryx* fold”, the lack of a large metacristid on the trigonid of P_4 , the primitive condition of M_3 , and the relative brachydonty of the dentition compared to most other ruminants.

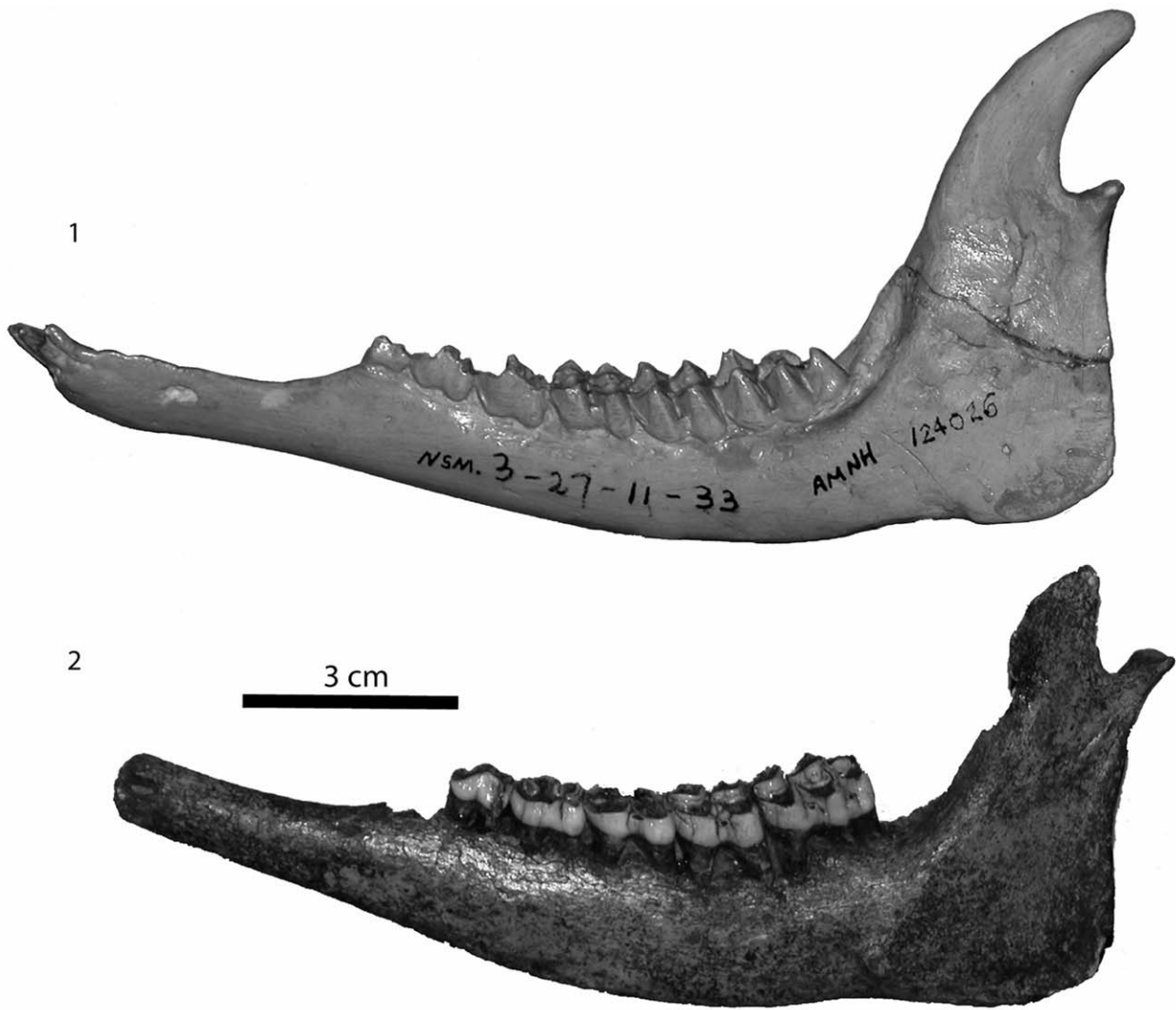


FIGURE 3—1, lateral view of holotypical specimen of *Barbouromeryx trigonocorneus* Barbour and Schultz, 1934, UNSM 3-27-11-33; 2, holotypic specimen of *Surameryx acrensis* n. gen. n. sp. (LACM 155113) for comparison.

LACM 155113 is not referable to the family Cervidae for a number of reasons. Morphologically, the P₄ in LACM 155113 shares little in common with most cervids (Frick, 1937; Webb, 2000). Cervids have a submolariform P₄ with well-developed selenes forming the trigonid and talonid, not the dromomerycine-

like P₄ seen in LACM 155113. In particular, all cervids, and most other ruminants, have a large, well-developed seleniform cusp, the metaacristid, in the paraconid-metaconid portion of the trigonid in P₄, a feature lacking in all palaeomerycids. Cervids never show a “*Palaeomeryx* fold” on the molars, lack ectostylids on the lower molar labial intervalli, and never develop a cusp between the entoconid and hypoconulid on the M₃. Further, true cervids originated in Asia and did not appear in the New World until the latest Hemphillian (ca. 6 Ma) (Webb, 2000), considerably later than the age of LACM 155113 from South America.

LACM 155113 is not referable to hypertragulids because they have an enlarged masseteric fossa and mandibular angle (Frick, 1937). *Hypertragulus* Cope, 1873 has prominent anterior cingula, as well as accessory cuspids (Vislobokova, 1998; Webb, 1998; Metais and Vislobokova, 2007). Another notable difference is that hypertragulids have simpler lower premolars that lack crescentic cusps.

Gelocids, unlike *Surameryx*, are characterized by an anterior cingulum on their lower molars, as in hypertragulids (Janis and Scott, 1987; Metais and Vislobokova, 2007). Also, unlike *Surameryx*, gelocids lack metastylids and have only a remnant of a paraconid present (Metais and Vislobokova, 2007).



FIGURE 4—1, occlusal view of holotypical specimen of *Barbouromeryx trigonocorneus* Barbour and Schultz, 1934, UNSM 3-27-11-33; 2, holotypic specimen of *Surameryx acrensis* n. gen. n. sp. (LACM 155113) for comparison.

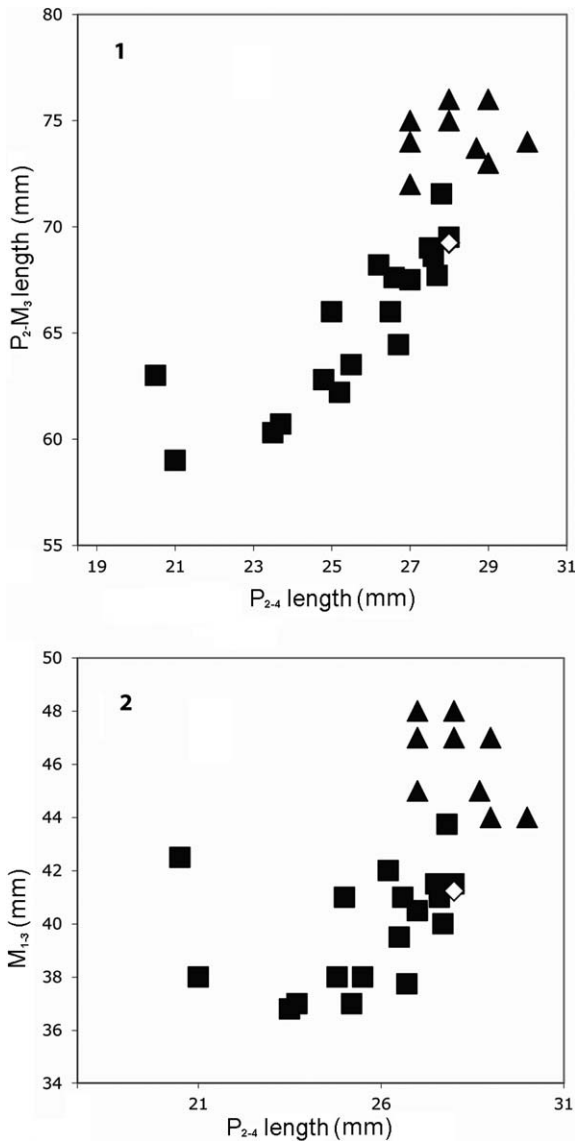


FIGURE 5—1, P₂–M₃ length (postcanine tooth row length) to P₂₋₄ length (premolar tooth row length); 2, M₁₋₃ length (molar tooth row length) to P₂₋₄ length (premolar tooth row length) for *Surameryx acrensis* n. gen. n. sp. (LACM 155113) (open diamond) among the known specimens of *Barbouromeryx trigonocorneus* Barbour and Schultz, 1934 (solid squares) and *Bouromeryx* Skinner et al., 1977 (solid triangles).

Surameryx does not appear to be a member of the Leptomerycidae because the ectostylids in leptomerycids tend to be very small or nearly absent, unlike the large ectostylids of the lower molars of *Surameryx*. Leptomerycids have large metaconids on the P₃ and P₄ (Webb and Taylor, 1980), like *Surameryx*, but those of *Surameryx* are larger. Leptomerycids have a single hypoconulid, unlike the closed double-lophed hypoconulid seen in *Surameryx*.

LACM 155113 is not referable to North American cervoids often assigned to the Moschidae, known as blastomerycines (Prothero, 2007, 2008), because all such “moschids” have much more highly reduced premolars relative to molars than LACM 155113. Blastomerycines do have metastylids like *Surameryx*, though they are all more pronounced and found on all lower molars (Prothero, 2007), not just the M₂ and M₃ as in *Surameryx*. The flattened, loop-like shape of the M₃ hypoconulid in moschids is quite different from the condition seen in LACM 155113.

TABLE 1—Tooth dimensions (mm) of *Surameryx acrensis* n. gen. n. sp. (N=1) and a sample of *Barbouromeryx trigonocorneus* Barbour and Schultz, 1934 (N=27). Abbreviations: OR=observed range; SD=standard deviation; L=length; W=width.

Measurement	<i>Surameryx acrensis</i>	<i>Barbouromeryx trigonocorneus</i>		
		Mean	OR	SD
P ₃ L	9.1	9.3	8.8–9.9	0.6
P ₃ W	4.8	3.8	3.2–4.1	0.5
P ₄ L	9.4	10.9	9.6–12.0	1.2
P ₄ W	7.9	5.4	4.9–5.9	0.5
M ₁ L	10.7	11.8	11.4–12.2	0.4
M ₁ W	8.1	7.4	7.1–7.5	0.3
M ₂ L	12.1	12.1	11.4–12.7	0.6
M ₂ W	10	8.2	8.0–8.3	0.2
M ₃ L	19.1	17.5	16.5–19.4	1.6
M ₃ W	9.8	7.6	7.3–8.1	0.4
M ₁₋₃	41.2	41	37.7–43.7	3
P ₂₋₄	28	27.5	26.7–28.0	0.7
P ₂ –M ₃	68.9	67.2	63.2–70.8	3.8
C ₁ –P ₂	35.8	37.6	35.6–39.7	2.9

We differentiate *Surameryx* from another, similar-sized ruminant, *Delahomeryx* Stevens et al., 1969 on the basis of molar morphology (Stevens et al., 1969). The dentition of *Delahomeryx* is larger (*Delahomeryx* M₂ length=14.4 mm); the protocone has unusual intercolumnar tubercles; and, unlike in *Surameryx*, the entoconid overlaps the hypoconulid (Stevens et al., 1969).

LACM 155113 can be distinguished from all known antilocaprids because the antilocaprid tooth row is much higher-crowned than LACM 155113, or any other dromomerycines, most of which are quite brachydont (Frick, 1937; Prothero and Liter, 2007, 2008). Antilocaprid premolar rows are highly reduced compared to the length of molar rows; their molars have no ectostylids or “*Palaeomeryx* folds”; and the M₃ hypoconulid is a posteriorly stretched lobe, not a closed loop as in many Miocene ruminant groups.

Affinities with the Camelidae are ruled out because all camelids, including the earliest and most primitive forms, are much more hypsodont than LACM 155113 (Honey et al., 1998). Camelids always have completely developed cristids and selenes on their lower premolars and molars, and their lower premolars are much more derived in than those of LACM 155113.

LACM 155113 can be differentiated from the protoceratids, which have a narrow non-looping M₃ hypoconulid and a P₄ that is shaped quite differently from that of LACM 155113 (Prothero, 1998; Prothero and Ludtke, 2007).

The combination of mandibular and dental features listed above is unique to the earliest palaeomerycids, and this combination is not found in any other group of artiodactyls. Thus, there is little doubt that the specimen represents a relic in South America of the early radiation of palaeomerycines in North America.

BIOGEOGRAPHIC IMPLICATIONS

The classic Plio–Pleistocene model of the GABI was first eloquently described in detail by Simpson (1950, 1980), expanded upon by Marshall et al. (1979) and Stehli and Webb (1985), and most recently reviewed by Morgan (2008) and Woodburne (2010). Under this model, a terrestrial connection between North America and South America through the Isthmus of Panama was not achieved until the late Pliocene, or ca. 3.0–2.5 Ma, and the major dispersal events between the two continents occurred during the Pleistocene. Earlier immigrants, such as late Miocene ground sloths in North America ca. 9.5–9.0 Ma and late Miocene procyonids in South America, were thought to have dispersed by island hopping or rafting across an

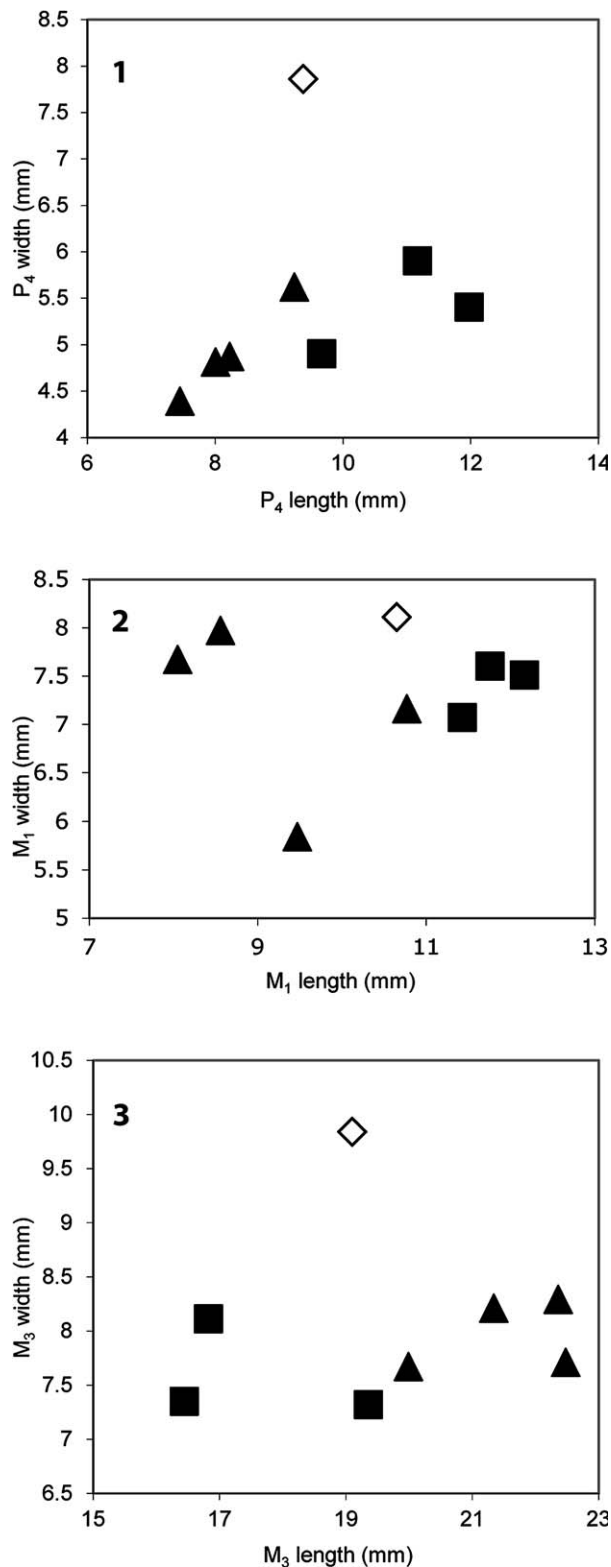


FIGURE 6—1, P₄ length and width; 2, M₁ length and width; 3, M₃ length and width for *Surameryx acrensis* n. gen. n. sp. (LACM 155113) (open diamond) compared to specimens of *Barbouromyx* Barbour and Schultz, 1934 (solid squares) and *Aletomyx* Lull, 1920 (solid triangles) of similar size and wear stage. The cheek teeth of *Surameryx acrensis* n. gen. n. sp. are distinctively wider than any other known palaeomyricid with a similar sized mandibular ramus and wear stage.

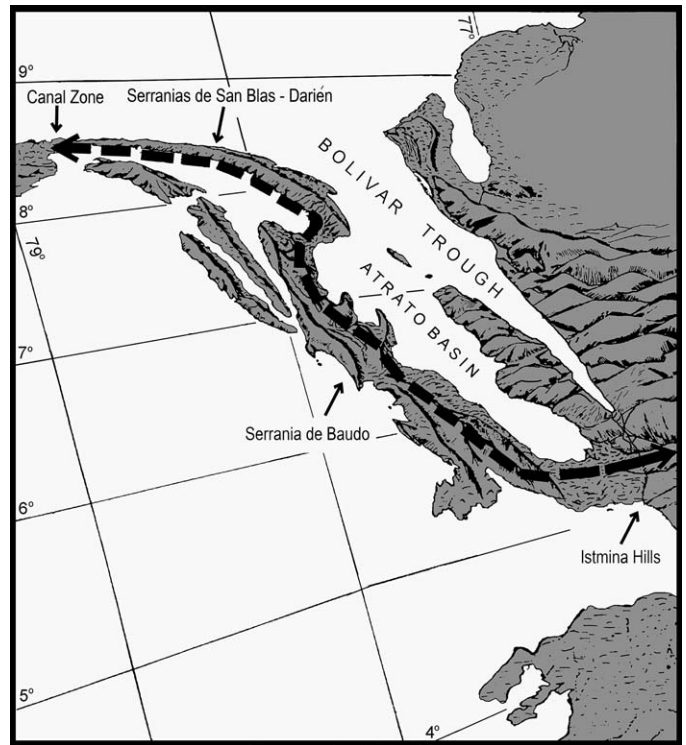


FIGURE 7—The Baudo Pathway hypothesis posits that the earliest interchange of vertebrates in the GABI occurred in the late Miocene, probably no later than ~10.0 Ma, via the Serranías de San Blas-Darién and the Serranía de Baudo as the allochthonous Choco Terrane was being attached to the west coast of what is now Colombia. Early interchange was probably pulsed by sea level fluctuations that interrupted the terrestrial pathway, which probably became permanent by ~5.0 Ma. Modified from Campbell et al. (2000).

oceanic gap between the two continents, the “waifs and strays” model. This model began to break down with the discovery of a late Miocene gomphothere in southeastern Peru (Campbell et al., 2000, 2006) and the recognition that the geologic horizon in southwestern Amazonia producing peccaries and tapirs, both groups being immigrants from North America, was actually an upper Miocene, not Pleistocene, deposit (Campbell et al., 2001, 2006, 2010).

Thus, in recent years, the classic Plio–Pleistocene model of dispersal events has been challenged by a new model that posits an almost continuous land connection across Central America beginning no later than the late Miocene, the Baudo Pathway hypothesis (Fig. 7). This hypothesis proposes that the earliest interchange of vertebrates in the GABI occurred via the Serranías de San Blas-Darién and the Serranía de Baudo as the allochthonous Choco Terrane was being attached to the Isthmia Hills region of southwestern Colombia. As soon as the terrestrial Baudo Pathway opened in the late Miocene, probably no later than ca. 10.0 Ma, vertebrates from both continents began the interchange. The first interchange pulse was possibly facilitated by a sea level lowstand as early as ca. 10.3 Ma (Miller et al., 2005), which is about the time when there was a presumed significant drop in Pacific water flowing into the Caribbean (Newkirk and Martin, 2009). The Baudo Hypothesis is strengthened by the recognition of the new palaeomyricid described here. Although the initial and subsequent Miocene pulses of dispersal might have been relatively short-lived because of sea level fluctuations, it appears that at least by the earliest Pliocene, ca. 5.0 Ma, there was a permanent terrestrial

connection between the continents (Carranza-Castañeda and Miller, 2004; Campbell, in press). This hypothesis is also supported by the findings of Frank et al. (1999), in comparing Atlantic/Pacific records of neodymium and lead isotopes, that water mass exchange across the Panamanian isthmus was essentially complete by 5 Ma.

Most of the reported late Miocene immigrants to South America have come from deposits in southwestern Amazonia, which raises the question as to why they are not found in other late Miocene deposits of South America, such as Urumaco, Venezuela (Sánchez-Villagra et al., 2010). We have no definitive answers to this question at this time, but there are possible explanations.

First, there are still very few specimens of late Miocene North American immigrants, and none of these specimens come from the better known upper Miocene faunal localities of southwestern Amazonia, such as Acre VI of Peru (Frailey, 1986; erroneously referred to as Los Patos by some authors [e.g., Kay and Cozzuol, 2006]). Although these specimens are usually found as isolated individuals, some have good stratigraphic control. Further, there are very few upper Miocene sites in northern South America that produce numerous fossil terrestrial vertebrates. For example, although well-known as “rich” vertebrate fossil producing beds, the Urumaco sequence of Venezuela has produced only 23 different terrestrial mammals, only 12 of which are referred to named species and five of which are referred to family only (Sánchez-Villagra et al., 2010; table 3.2). Given the rarity of both specimens and fossil producing localities, the absence of late Miocene North American immigrants from the better known fossil producing localities is perhaps to be expected.

Second, although tropical dry habitats existed in Central America in the Miocene (Retallack and Kirby, 2007), it is probably safe to say that the first mammals to traverse between the Americas were lowland tropical forest forms. As a consequence, their dispersal most likely would have been limited to those habitats, which could have affected their dispersal in the following ways. Entering South America via the Baudo Pathway would place them in the lowlands of southern coastal Pacific Colombia. Dispersing north and east would have been improbable because the Cordillera Occidental and Cordillera Central were in place as formidable barriers, and even the Cordillera Oriental was being elevated by that time (Guerrero, 1997). Dispersing south along the coast into Ecuador would have brought them to the “Pacific Portal”, or the opening to the Pacific from Amazonia that apparently existed up until ca. 9 Mya, when the Ecuadorian Andes began a rapid ascent (Steinmann et al., 1999). Once in Amazonia, the immigrants could have dispersed in many directions, but the existence of the vast Miocene Lake Pebas (Wesselingh, 2006) might have been sufficient to prevent them from dispersing eastward or northward into eastern Colombia and Venezuela.

Unlike northern hemisphere continents, South America did not have continent-wide habitat belts that would facilitate west to east, or vice versa, dispersal. Likewise, although there are no data to support any given hypothesis, if general climatic conditions of South America were similar to today, ecotonal transitions to tropical wet, grassland savannas and semi-arid chaco south of Amazonia and east of the Andes would have prevented dispersal to well-known late Miocene sites of southern South America. Similarly, the Urumaco sequence of Venezuela, which has produced marine as well as terrestrial mammals (Sánchez-Villagra et al., 2010; table 3.2), is described as a strandplain-deltaic sequence with marine influences via multiple transgressions (Quiroz and Jaramillo, 2010), a habitat

unlikely to be suited to tropical forest species. In summary, habitat restrictions and physical barriers were probably major deciding factors in the dispersal of the earliest North American immigrants.

Given the lack of good stratigraphic control (i.e., the holotypic specimen was found as riverine float), the assignment of a late Miocene age to *Surameryx acrensis*, as opposed to a Pleistocene age assignment, can be questioned. Indeed, as noted above, the stratigraphy of the Amazon Basin is a very controversial issue. We follow here the model proposed by Campbell et al. (2006) wherein the uppermost stratigraphic horizons of Amazonia are upper Miocene to Pliocene in age, and Pleistocene deposits, if they occur at all, are found only as riverine terrace deposits. Although the models of sediment accumulation in Amazonia presented by others (e.g., Latrubesse et al., 2010; Hoorn et al., 2010) conflict with this model, the former models would also restrict any Pleistocene deposits to riverine terraces, although this consequence is not specifically recognized by those authors.

Multiple field excursions by two of us (KEC and CDF) in southwestern Amazonia have provided both $^{40}\text{Ar}/^{39}\text{Ar}$ dates and magnetostratigraphic data to support our stratigraphic age assignments (Campbell et al., 2001, 2010). We have encountered no Pleistocene stratigraphic horizons in any outcrops of the region, except as riverine terrace deposits, and given the available dating data, the earlier interpretations by Campbell et al. (1985) that Pleistocene horizons did exist in southwestern Amazonia are now seen as having been erroneous. Although some authors have argued that all North American immigrants found in southwestern Amazonia came from Pleistocene deposits (e.g., Webb and Rancy, 1996), because these age assignments are not supported by any independent dating techniques, they were presumably proposed because the deposits produced North American mammals that were not supposed to be in South America before the Pleistocene.

Further, the specimen in question is clearly a primitive dromomerycine artiodactyl, the closest relatives of which were extinct in North America by the late Miocene. If *Surameryx acrensis*, or its ancestors, did not enter South America until ca. 3.0–2.5 Mya, or the classic GABI paradigm timing, why have no traces of it, or any close relatives, been found in North America after the late Miocene? Also, the late Miocene North American immigrants to South America that have been described (i.e., the gomphothere *Amahuacatherium* Romero-Pittman, 1996 and the peccaries [Frailey and Campbell, 2012]) are clearly more primitive morphologically than their Pleistocene relatives and they simply cannot be referred to Pleistocene taxa. If other “Pleistocene” specimens were carefully examined, many would probably likewise be seen to be morphologically distinct from true Pleistocene taxa.

It should also be noted that salt-intolerant freshwater fish (Birmingham and Martin, 1998) and frogs (Weigt et al., 2005) of presumed South American origins are reported to have been in Central America since the late Miocene. Other than having their eggs attached to the feet of wading or swimming birds, the only way these taxa could have dispersed northward is via an emergent terrestrial connection providing a source of freshwater. These and other extensive data that support a late Miocene connection between the Americas are reviewed in Campbell (in press).

The movement of vertebrates between North America and South America in the late Miocene, and the probable establishment of a permanent terrestrial connection between the continents by ca. 5.0 Ma, has important implications for several fields of science in addition to vertebrate

paleobiogeography. For example, the classic late Plio–Pleistocene dating of the GABI has been used to explain changes in ocean current circulation patterns, which, in turn, have been invoked as triggering the onset of Pleistocene glaciations (Haug and Tiedemann, 2008; Bartoli et al., 2005, but see Molnar [2008] for a contrasting view heavily dependent on classic GABI dating). The classic dating also has been used extensively as a vicariant event for the calibration of molecular clocks. For example, Lessios (2008) pointed out that 251 studies had used the date of ca. 2.8 Ma to calibrate the timing of phylogenetic events elsewhere. This has resulted in numerous complicated hypothetical scenarios to explain molecular data results. A late Miocene date for initial dispersal via a terrestrial pathway, followed by pulsed events until the earliest Pliocene, has the potential of eliminating many of these complications. For example, in one recent study (Fritz et al., 2012) molecular data indicated that at least two successive colonization events were required to explain the phylogeny of slider turtles (*Trachemys* spp.). The authors suggested that their data place the mean divergence time for the first dispersal at ~6 Ma. Another molecular study (Duarte et al., 2008) suggested that at least eight separate invasions were required to explain the molecular phylogeny of South American deer. Although these authors suggested that dispersal of eight lineages took place after ca. 2.5 Ma, in light of new data an earlier dispersal by one or two lineages at ca. 5.0 Ma or earlier, followed by radiation in South America, is a more parsimonious scenario. Recognizing that terrestrial pathways connecting North America and South America were in place by the late Miocene, albeit probably intermittently closed by sea level fluctuations until the earliest Pliocene, provides a new perspective for evaluating associated phenomena.

The presence in the early Miocene (19.3 Ma) Gaillard Cut local fauna in Panama of fossils of boid snakes, which originated in South America, was interpreted as resulting from overwater dispersal (Head et al., 2012), which is distinct from the terrestrial routes needed by land animals. Boids are also found in the early Miocene Thomas Farm local fauna, in Florida, North America (Head et al., 2012). When members of the lineage leading to *Surameryx acrensis* dispersed to South America is unknown but it is interesting to note that the holotypic specimen most closely matches North American specimens from the early Miocene (23–19 Ma), the same time that boids crossed from South America to Panama. But, at this time, there are no data supporting a terrestrial connection between Central America and South America in the early or middle Miocene. Dromomerycines were surely one of the earliest to make the passage along a terrestrial route in the early late Miocene.

CONCLUSIONS

The new taxon described herein is the first and so far only record of palaeomerycid artiodactyls in South America. It is anageographic and anachronistic, representing an early Hemphillian (10.3–4.9 Ma) or earlier arrival to South America of a close relative of Hemingfordian (20.6–16.3 Ma) taxa from North America, such as *Aletomeryx*, *Barbouromeryx*, *Sinclairiomeryx* Frick, 1937 and *Diabolocornis* Beatty, 2010. Though *Surameryx* is most similar to *Barbouromeryx* among palaeomerycids, it also bears similarities to contemporary aletomerycines. Even though some aletomerycines (e.g., *Aletomeryx* and *Diabolocornis*) clearly ranged as far south as Florida (Simpson, 1932; Lull, 1920; Beatty, 2010) and California (Whistler, 1984) in the early Miocene, there is no record of them anywhere south of these areas in the Miocene. The youngest and southernmost record of

aletomerycines is a possible specimen of *Sinclairiomeryx* sp. from the early Barstovian (16.3–13.6 Ma) Echo Quarry (Olcott Formation) of Nebraska (Skinner et al., 1977) (originally called *Blastomeryx elegans* Matthew and Cook, 1909, but questionably referred to this species). All other specimens of *Sinclairiomeryx* are known from more northern localities, including the Hemingfordian of Nebraska (Skinner et al., 1977; Galusha, 1975) and some possible remains from Saskatchewan (Skwara, 1988). There are no records of dromomerycines in southernmost North America from any period. *Surameryx* is truly unique, not only in reaching South America in the Miocene, but in retaining into the late Miocene characters of the most primitive of the New World palaeomerycids. To date, no fossils linking North American dromomerycines to *Surameryx* have been found, but new excavations in Panama (MacFadden, 2006; Rincon et al., 2012) give us renewed hope of finding such fossils.

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REFERENCES

- BARBOUR, H. AND C. B. SCHULTZ. 1934. A new antilocaprid and a new cervid from the late Tertiary of Nebraska. *American Museum Novitates*, 734:1–4.
- BARTOLI, G., M. SARNTHEIN, M. WEINELT, H. ERLKENUSER, D. GARBE-SCHÖNBERG, AND D. W. LEA. 2005. Final closure of Panama and the onset of Northern Hemisphere glaciation. *Earth and Planetary Sciences Letters*, 237:33–44.
- BEATTY, B. L. 2010. A new aletomerycine (Artiodactyla, Palaeomerycidae) from the early Miocene of Florida. *Journal of Vertebrate Paleontology*, 30: 613–617.
- BERMINGHAM, E. AND A. P. MARTIN. 1998. Comparative mtDNA phylogeography of neotropical freshwater fishes: testing shared history to infer the evolutionary landscape of lower Central America. *Molecular Ecology*, 7: 499–517.
- CAMPBELL, K. E., JR. In press. The Great American Faunal Interchange: the first phase, p. 00–00. In A. L. Rosenberger and M. F. Tejedor (eds.), *Origins and Evolution of Cenozoic South American Mammals*. Springer, New York.
- CAMPBELL, K. E., JR., C. D. FRAILEY, AND L. J. ARELLANO. 1985. The geology of the Rio Beni: further evidence for Holocene flooding in Amazonia. *Contributions in Science, Natural History Museum of Los Angeles County*, 364:1–18.
- CAMPBELL, K. E., JR., C. D. FRAILEY, AND L. ROMERO-PITTMAN. 2000. The late Miocene gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: implications for the Great American Faunal Interchange. *Instituto de Geológico Minero y Metalúrgico, Serie D: Estudios Regionales, Boletín*, 23:1–152.
- CAMPBELL, K. E., JR., C. D. FRAILEY, AND L. ROMERO-PITTMAN. 2006. The Pan-Amazonian Ucayali Peneplain, late Neogene sedimentation in Amazonia, and the birth of the modern Amazon River system. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 239:166–219.
- CAMPBELL, K. E., JR., M. HEIZLER, C. D. FRAILEY, L. ROMERO-PITTMAN, AND D. R. PROTHERO. 2001. Upper Cenozoic chronostratigraphy of the southwestern Amazon Basin. *Geology* 29:595–598.
- CAMPBELL, K. E., JR., D. R. PROTHERO, L. ROMERO-PITTMAN, F. HERTEL, AND N. RIVERA. 2010. Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. *Journal of South American Earth Sciences*, 29:619–626.
- CARRANZA-CASTAÑEDA, O. AND W. E. MILLER. 2004. Late Tertiary terrestrial mammals from Central Mexico and their relationship to South American dispersants. *Revista Brasileira de Paleontologia*, 7:249–261.
- COPE, E. D. 1873. On *Menotherium lemurinum*, *Hypisodus minimus*, *Hypertragulus calcaratus*, *Hypertragulus tricostatus*, *Prothippus*, and

- Procamelus occidentalis*. Proceedings of the Philadelphia Academy of Natural Sciences, 25:410–420.
- DUARTE, J. M. B., S. GONZALEZ, AND J. E. MALDONADO. 2008. The surprising evolutionary history of South American deer. *Molecular Phylogeny and Evolution*, 49:17–22.
- FILHOL, H. 1876. Recherches sur le phosphorites du Quercy etude des fossils qu'on y rencontre et spécialement des mammifères, *Annales des sciences géologiques*, 7:1–220.
- FRAILEY, C. D. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Rio Acre region, western Amazonia. *Contributions in Science*, Natural History Museum of Los Angeles County, 374:1–46.
- FRAILEY, C. D. AND K. E. CAMPBELL, JR. 2012. Two new genera of peccaries (Mammalia, Artiodactyla, Tayassuidae) from upper Miocene deposits of the Amazon Basin. *Journal of Paleontology*, 86:852–877.
- FRANK, M., B. C. REYNOLDS, AND R. K. O'NIIONS. 1999. Nd and Pb isotopes in Atlantic and Pacific water masses before and after closure of the Panama gateway. *Geology*, 27:1147–1150.
- FRICK, C. 1937. Horned ruminants of North America. *Bulletin of the American Museum of Natural History*, 69:1–669.
- FRITZ, U., H. STUCKAS, M. VARGAS-RAMIREZ, A. K. HUNSDÖRFER, J. MARAN, AND M. PACKERT. 2012. Molecular phylogeny of Central and South American slider turtles: implications for biogeography and systematics (Testudines: Emydidae: *Trachemys*). *Journal of Zoological Systematics and Evolutionary Research*, 50:125–136.
- GALUSHA, T. 1975. Stratigraphy of the Box Butte Formation, Nebraska. *Bulletin of the American Museum of Natural History*, 156:1–68.
- GUERRERO, J. 1997. Stratigraphy, sedimentary environments, and the Miocene uplift of the Colombian Andes, p. 15–43. *In* R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington.
- HAUG, G. H. AND R. TIEDEMANN. 1998. Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. *Nature*, 393:673–676.
- HEAD, J. J., A. F. RINCON, C. SUAREZ, C. MONTES, AND C. JARAMILLO. 2012. Fossil evidence for earliest Neogene American faunal interchange: *Boa* (Serpentes, Boinae) from the early Miocene of Panama. *Journal of Vertebrate Paleontology*, 32:1,328–1,334.
- HONEY, J., J. A. HARRISON, D. R. PROTHERO, AND M. S. STEVENS. 1998. Camelidae, p. 439–462. *In* C. Janis, K. M. Scott, and L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America*. Cambridge University Press, Cambridge.
- HOORN, C., ET AL. (17 additional authors). 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, 330:927–931.
- JANIS, C. AND K. M. SCOTT. 1987. The interrelationships of higher ruminant families with special emphasis on the members of the Cervioidea. *American Museum Novitates*, 2893:1–85.
- KAY, R. F. AND M. A. COZZUOL. 2006. New platyrrhine monkeys from the Solimões Formation (late Miocene, Acre State, Brazil). *Journal of Human Evolution*, 50:673–686.
- KIRBY, M. X., D. J. JONES, AND B. J. MACFADDEN. 2008. Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central American Peninsula. *PLoS One* 3(7):e2791. doi:10.1371/journal.pone.0002791.
- LATRUBESSE, E. M., M. COZZUOL, C. RIGSBY, S. SILVA, M. L. ABSY, AND C. JARAMILLO. 2010. The late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. *Earth Sciences Reviews*, 99: 99–124.
- LESSIOS, H. A. 2008. The Great American schism: divergence of marine organisms after the rise of the Central American Isthmus. *Annual Reviews of Ecology, Evolution, and Systematics*, 39:63–91.
- LINNAEUS, C. 1758. *Systema Naturae. I. Regnum animale*. Editio decimal, Stockholm, Laurentii Salvii.
- LULL, R. S. 1920. New Tertiary Artiodactyls. *American Journal of Science*, 200:83–130.
- LYDEKKER, R. 1883. Indian Tertiary and post-Tertiary vertebrata. Siwalik selenodont Suina, etc. *Geological Survey of India Memoirs, Palaeontologia Indica*, 10:142–177.
- MACFADDEN, B. J. 2006. North American Miocene land mammals from Panama. *Journal of Vertebrate Paleontology*, 26:720–734.
- MARSHALL, L. G., R. F. BUTLER, R. E. DRAKE, G. H. CURTIS, AND R. H. TEDFORD. 1979. Calibration of the Great American Interchange. *Science*, 204:272–279.
- MATTHEW, W. D. AND H. J. COOK. 1909. A Pliocene fauna from western Nebraska. *Bulletin of the American Museum of Natural History*, 26:361–414.
- MATTHEW, W. D. AND W. GRANGER. 1924. New insectivores and ruminants from the Tertiary of Mongolia, with remarks on the correlation. *American Museum Novitates*, 105:1–7.
- MÉTAIS, G. AND I. A. VISLOBOKOVA. 2007. Basal ruminants, p. 227–240. *In* D. R. Prothero and S. E. Foss (eds.), *The Evolution of Artiodactyls*. The Johns Hopkins University Press, Baltimore.
- MILLER, K. G., M. A. KOMINZ, J. V. BROWNING, J. D. WRIGHT, G. S. MOUNTAIN, M. E. KATZ, P. J. SUGARMAN, B. S. CRAMER, N. CHRISTIE-BLICK, AND S. F. PEKAR. 2005. The Phanerozoic record of global sea-level change. *Science*, 310:1,293–1,298.
- MOLNAR, P. 2008. Closing of the Central American Seaway and the Ice Ages: a critical review. *Paleoceanography*, 23:PA2,201.
- MONTES, C., A. CARDONA, R. MCFADDEN, S. E. MORON, C. A. SILVA, S. RESTREPO-MORENO, D. A. RAMIREZ, N. HOYOS, J. WILSON, D. FARRIS, G. A. BAYONA, C. A. JARAMILLO, V. VALENCIA, J. BRYAN, AND J. A. FLORES. 2012a. Evidence for middle Eocene and younger land emergence in central Panama: implications for Isthmus closure. *Geological Society of America Bulletin*, 124:780–799.
- MONTES, C., G. BAYONA, A. CARDONA, D. M. BUCHS, C. A. SILVA, S. MORON, N. HOYOS, D. A. RAMIREZ, C. JARAMILLO, AND V. VALENCIA. 2012b. Arc-continent collision and orocline formation: the closure of the Central American seaway. *Journal of Geophysical Research*, 117:B04105.
- MORGAN, G. 2008. Vertebrate fauna and geochronology of the Great American Biotic Interchange in North America. *New Mexico Museum of Natural History Bulletin*, 44:93–140.
- NEWKIRK, D. R. AND E. E. MARTIN. 2009. Circulation through the Central American Seaway during the Miocene carbonate crash. *Geology*, 37:87–90.
- OWEN, R. 1848. Description of teeth and portions of jaws of two extinct Anthracotheriid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the NW coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the Classification of Pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, 4:103–141.
- PROTHERO, D. R. 1998. Protoceratidae, p. 431–438. *In* C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America*. Cambridge University Press, Cambridge.
- PROTHERO, D. R. 2007. Moschidae, p. 221–226. *In* D. R. Prothero and S. E. Foss (eds.), *The Evolution of Artiodactyls*. The Johns Hopkins University Press, Baltimore.
- PROTHERO, D. R. 2008. Systematics of the musk deer (Artiodactyla: Moschidae: Blastomerycinae) from the Miocene of North America. *New Mexico Museum of Natural History Bulletin*, 44:207–225.
- PROTHERO, D. R. AND M. LITER. 2007. Palaeomerycidae, p. 248–248. *In* D. R. Prothero and S. E. Foss (eds.), *The Evolution of Artiodactyls*. The Johns Hopkins University Press, Baltimore.
- PROTHERO, D. R. AND M. LITER. 2008. Systematics of the dromomerycines and alatomerycines (Artiodactyla: Palaeomerycidae) from the Miocene and Pliocene of North America. *New Mexico Museum of Natural History Bulletin*, 44:273–298.
- PROTHERO, D. R. AND J. LUDTKE. 2007. Protoceratidae, p. 169–176. *In* D. R. Prothero and S. E. Foss (eds.), *The Evolution of Artiodactyls*. The Johns Hopkins University Press, Baltimore.
- QUIROZ, L. I. AND C. A. JARAMILLO. 2010. Stratigraphy and sedimentary environments of Miocene shallow to marginal marine deposits in the Urumaco Trough, Falcón Basin, Western Venezuela, p. 153–172. *In* M. R. Sánchez-Villagra, O. A. Aguilera, and A. A. Carlini (eds.), *Urumaco and Venezuelan Paleontology*. Indiana University Press, Bloomington.
- RESTALLACK, G. J. AND M. X. KIRBY. 2007. Middle Miocene global change and paleogeography of Panama. *Palaeos*, 22:667–679.
- RINCON, A. F., J. I. BLOCH, C. SUAREZ, B. J. MACFADDEN, AND C. A. JARAMILLO. 2012. New floridatragulines (Mammalia, Camelidae) from the early Miocene Las Cascadas Formation, Panama. *Journal of Vertebrate Paleontology*, 32:456–475.
- ROMERO-PITTMAN, L. 1996. *Paleontología de Vertebrados*. Instituto Geológico Minero y Metalúrgico, Carta Geológica Nacional, Boletín, Serie A, No. 81: 171–178.
- SÁNCHEZ-VILLAGRA, M. R., O. A. AGUILERA, AND A. A. CARLINI (eds.). 2010. Urumaco and Venezuelan Paleontology. Indiana University Press, Bloomington.
- SÁNCHEZ-VILLAGRA, M. R., O. A. AGUILERA, R. SÁNCHEZ, AND A. A. CARLINI. 2010. The fossil vertebrate record of Venezuela of the last 65 million years, p. 19–51. *In* M. R. Sánchez-Villagra, O. A. Aguilera, and A. A. Carlini (eds.), *Urumaco and Venezuelan Paleontology*. Indiana University Press, Bloomington.
- SIMPSON, G. G. 1932. Miocene land mammals from Florida. *Florida State Geological Survey Bulletin*, 10:7–41.
- SIMPSON, G. G. 1950. History of the fauna of Latin America. *American Scientist*, 38:361–389.
- SIMPSON, G. G. 1980. *Splendid Isolation: The Curious History of South American Mammals*. Yale University Press, New Haven.
- SKINNER, M. F., S. M. SKINNER, AND R. J. GOORIS. 1977. Stratigraphy and biostratigraphy of late Cenozoic deposits in central Sioux County, western

- Nebraska. Bulletin of the American Museum of Natural History, 158(5): 263–370.
- SKWARA, T. 1988. Mammals of the Topham Local Fauna: early Miocene (Hemingfordian), Cypress Hills Formation, Saskatchewan. Natural History Museum of Saskatchewan Contributions, 9:1–169.
- STEHLI, F. G. AND S. D. WEBB (eds). 1985. The Great American Biotic Interchange. Plenum, New York.
- STEVENS, M. S., J. B. STEVENS, AND M. R. DAWSON. 1969. New early Miocene formation and vertebrate local fauna, Big Bend National Park, Brewster County, Texas. Pearce-Sellards Series, Texas Memorial Museum, 15:1–53.
- STEINMANN, M., D. HUNGERBÜHLER, D. SEWARD, AND W. WINKLER. 1999. Neogene tectonic evolution and exhumation of the southern Ecuadorian Andes; a combined stratigraphy and fission-track approach. Tectonophysics, 307:255–276.
- VISLOBOKOVA, I. A. 1998. A new representative of the Hypertraguloidea (Tragulina, Ruminantia) from the Khoer-Dzan locality in Mongolia, with remarks on the relationship of the Hypertragulidae. American Museum Novitates, 3225:1–24.
- WEBB, S. D. 1998. Hornless ruminants, p. 463–476. In C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Cambridge University Press, Cambridge.
- WEBB, S. D. 2000. Evolutionary History of the New World Cervidae, p. 38–64. In E. S. Vrba and G. B. Schaller (eds.), Antelopes, Deer, and Relatives: Fossil Record, Behavioral Ecology, Systematics, and Conservation. Yale University Press, New Haven.
- WEBB, S. D., B. L. BEATTY, AND G. POINAR. 2003. New evidence of Miocene Protoceratidae including a new species from Chiapas, Mexico. Bulletin of the American Museum of Natural History, 279:348–367.
- WEBB, S. D. AND A. RANCY. 1996. Quaternary Environmental history and forest diversity in the Neotropics, p. 335–358. In J. B. C. Jackson, A. F. Budd, and A. G. Coates (eds.), Evolution and Environment in Tropical America. The University of Chicago Press, Chicago.
- WEBB, S. D. AND B. E. TAYLOR. 1980. The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. Bulletin of the American Museum of Natural History, 167:121–157.
- WEIGT, L. A., A. J. CRAWFORD, A. S. RAND, AND M. J. RYAN. 2005. Biogeography of the túngara frog, *Physalaemus pustulosus*: A molecular perspective. Molecular Ecology, 14:3,857–3,876.
- WESSELINGH, F. 2006. Miocene long-lived Lake Pebas as a stage of mollusk radiations, with implications for landscape evolution in western Amazonia. Scripta Geologica, 133:1–17.
- WHISTLER, D. P. 1984. An early Hemingfordian (early Miocene) vertebrate fauna from Boron, western Mojave Desert, California. Contributions in Science, Natural History Museum of Los Angeles County, 355:1–36.
- WHITMORE, F. C., JR., AND R. H. STEWART. 1965. Miocene mammals and Central American seaways. Science, 148:180–185.
- WOODBURNE, M. O. 2010. The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. Journal of Mammalian Evolution, 17:245–264.

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