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On the Supposed Presence of Miocene Tayassuidae and Dromomerycinae (Mammalia, Cetartiodactyla) in South America

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ABSTRACT

The earliest record of North American mammals in South America is significant for constraining the timing of intercontinental faunal interchange. At present, the oldest securely dated remains of a North American terrestrial mammal in South America pertain to a late Miocene procyonid; a few other North American mammal groups are present in late Miocene and early Pliocene outcrops in South America, but most are not recorded until the late Pliocene or Pleistocene, after the complete emergence of the Panamanian Isthmus. This long-established pattern has recently been called into question by reports of a proboscidean, two tayassuids, and a dromomerycine cervoid in supposed late Miocene deposits of Peruvian Amazon. In this contribution, we analyze the taxonomic identities and stratigraphic provenances of the tayassuid and dromomerycine fossils in detail. We conclude that these specimens are not distinguishable from modern tayassuids (*Tayassu pecari* and *Dicotyles tajacu*) and cervids, and that previous taxonomic identifications are based on misinterpretation of characters or inadequate specimens. In addition, there is insufficient evidence to support a late Miocene age for these terrestrial cetartiodactyl fossils; the stratigraphic provenance of the specimens is highly dubious, and the fossils are likely Quaternary in age.

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INTRODUCTION

South America has a unique mammalian fauna that consists of different faunistic elements that have, at different times, reached the continent. This peculiarity is commonly seen as a consequence of the geographic isolation of South America from other major land masses during much of the Cenozoic (Pascual et al., 1965; Simpson, 1980), with infrequent faunal exchanges until the continent's final connection with North America. Despite some issues related to refinement and classification, it is generally agreed that the mammal fauna of South America can be described as having three basic stages during the Cenozoic: an old phase, with old endemic groups of native mammals, at least some of which arrived from North America during the early Paleogene; an intermediate phase, initiated with the arrival of platyrrhine monkeys and caviomorph rodents from Africa during the middle to late Eocene and/or early Oligocene; and a final phase that ended with the connection of North and South America and the interchange of faunal components between these two continents (Simpson, 1950; Marshall et al., 1982; Poux et al., 2006; Woodburne et al., 2006; Flynn et al., 2007; Woodburne, 2010; Goin et al., 2012; Leigh et al., 2014; Cione et al., 2015; O´Dea et al., 2016; but see Croft, 2012, 2016).

The last of the three phases described above is known as the Great American Biotic Interchange (GABI), and is considered one of the most significant biogeographic events of the Cenozoic (Webb, 1976, 1991; Cione et al., 2015). During the GABI, it is generally agreed that initial and limited exchange occurred during the late Miocene and early Pliocene; procyonid carnivorans and sigmodontine rodents were the first northern immigrants in South America, and two types of ground sloths were the first southern immigrants to Mexico and the southern United States (Woodburne, 2010; Cione et al., 2015; Barbiére et al., 2019; Engelman and Croft, 2019). Procyonid carnivorans, such as *Cyonasua* and *Chapalmalania*, are known from the Huayquerian South American Land-Mammal "Age" (SALMA) of Argentina and Uruguay (late Miocene, 9.0-6.8 Ma) (Reguero and Candela, 2011; Prevosti and Soibelzon, 2012; Prevosti et al., 2013; Engelman and Croft, 2019; Soibelzon et al., 2019). Mustelids have also been reported from the Huayquerian SALMA (Verzi and Montalvo, 2008), but this has been refuted by Prevosti and Pardiñas (2009). The oldest cricetid (sigmodontine) rodent in South America is from the Montehermosan SALMA, but whether it is late Miocene or early Pliocene in age is uncertain (Barbiére et al., 2019). Molecular analyses have suggested an earlier arrival of sigmodontines (Parada et al., 2013; Leite et al., 2014; Maestri et al., 2019), but fossil evidence supporting this is lacking. Cricetid rodents are certainly absent from the La Venta fauna (late middle Miocene) of Colombia, where caviomorph rodents of very small size seem to overlap in size and ecology with cricetids (Walton, 1997).

South American mammals first appeared in North America by the late Miocene, with ground sloths recorded in the Hemphillian North American Land-Mammal "Age" (NALMA; late Miocene, 9.0–8.5 Ma) of Florida and Texas (Marshall, 1988; Morgan, 2008). It is generally agreed that these early immigrants were able to disperse through island hopping (Flynn et al., 2005).

Most of the exchange during the GABI occurred during the late Pliocene, when the fossil record shows a large influx of North American taxa into South America and vice versa (Cione et al., 2015, and references cited therein). Presumably this marked the complete (subaerial) emergence of the Panamanian Isthmus during the late Pliocene (ca. 3.0 Ma), though the timing of the formation and emergence of the Panamanian Isthmus is a contentious issue (Bartoli et al., 2005; Leigh et al., 2014; O'Dea et al., 2016). The GABI continues today, with latecomers such as *Cryptotis* shrews (Tate, 1932).

The description of large North American terrestrial mammals (a proboscidean, two tayassuids, and a dromomerycine ruminant) from supposed late Miocene deposits in western Amazonia (Campbell et al., 2000, 2009; Frailey and Campbell, 2012; Prothero et al., 2014) calls the broad pattern described above into question by implying that a land connection between the Americas existed by the late Miocene. Because these claims have the potential to greatly impact our understanding of the relationship between North and South America during the Neogene, they must be rigorously analyzed. Claims of a Miocene age for the gomphotheriid probocidean "*Amahuacatherium*" have been investigated and refuted in several previous works (Alberdi et al., 2004; Ferretti, 2008; Woodburne, 2010; Lucas, 2013; Mothé and Avilla, 2015). The goals of this paper are: (1) to evaluate the taxonomic identities of the tayassuids *Sylvochoerus woodburnei* Frailey and Campbell, 2012, and *Waldochoerus bassleri* Frailey and Campbell, 2012, and the dromomerycine *Surameryx acrensis* Prothero et al., 2014, in detail; and (2) to critically analyze the stratigraphic provenance of the specimens.

Materials and Methods

The specimens studied in this contribution correspond to those assigned to *Sylvochoerus woodburnei* and *Waldochoerus bassleri* (Tayassuidae) by Frailey and Campbell (2012) and *Surameryx acrensis* (Dromomerycinae cervoid) by Prothero et al. (2014). Most tayassuid specimens are from the Harvey Bassler Collection of Peruvian Fossils (Willard, 1966), which is now housed at the U.S. National Museum of Natural History. Exact geographic and stratigraphic data for these specimens are not available; most are only referred to river valleys in Peru (e.g., Inuya River, Mapuya River). A few specimens of peccaries (only four) are housed at the American Museum of Natural History, Natural History Museum of Los Angeles County, and University of California Museum of Paleontology.

For anatomical comparisons, we followed the unpublished Ph.D. dissertations of two of the authors of the present contribution (Gasparini, 2007; Parisi Dutra, 2016). These are the most current integrative reviews of the South American Tayassuidae. For nomenclatural assignments of collared and white-lipped peccaries, we followed Acosta et al. (2020). The holotype and sole specimen of *Surameryx acrensis* was compared to species of Palaeomerycidae (including Dromomerycinae) and fossil and extant cervid species. Our research was based on the analysis of several mammalogical and palaeontological collections housed at American institutions (Argentina, Bolivia, Brazil, Colombia, Ecuador, Mexico, Paraguay, Peru, Uruguay, United States, and Venezuela).

Abbreviations*:* AMNH, American Museum of Natural History; LACM, Natural History Museum of Los Angeles County, Los Angeles; MCN-M, mammals collection of the Museu de Ciências Naturais, Pontificia Universidade Catolica de Minas Gerais, Brazil;

MLP, Museo de La Plata, Argentina; MN, Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil; UCMP, University of California Museum of Paleontology, Berkeley; UFMG, Universidade Federal de Minas Gerais, Brazil; USNM, United States National Museum of Natural History, Washington, DC.

SYSTEMATIC PALEONTOLOGY

CETARTIODACTYLA Montgelard, Catzeflis and Douzery, 1997

TAYASSUIDAE Palmer, 1897

Referred Material: AMNH 55811 (holotype of *Sylvochoerus woodburnei* Frailey and Campbell, 2012), complete left mandible, lacking i1-3; LACM 150305, right mandibular fragment with p4; UCMP 118779, left mandibular fragment with p4–m1; USNM 205346, palate with complete dentition and portion of left zygomatic arch; USNM 205389, right M3; USNM 513211, left palatal fragment with M1–3; USNM 513212, left palatal fragment with P2–4; USNM 513213, right radio-ulna; USNM 513214, left palatal fragment with M2; USNM 513216, right mandibular fragment with m1–2; USNM 513217, left mandibular fragment with m3; USNM 513218, isolated right m3; USNM 513219, right P3; USNM 513220, left P2 with palatal fragment; USNM 513221, partial left ramus with dp3–m2; USNM 513224, right partial M2.

The identity of *Sylvochoerus woodburnei*: For a better understanding of our analysis, we organize the morphological and morphometric comments of every character considered by Frailey and Campbell (2012) in the following order: (1) diagnosis of the genus; (2) similarities between *Sylvochoerus* and *Tayassu* and differences from *Dicotyles*; (3) differences between *Sylvochoerus* and *Tayassu*; and (4) diagnosis of the species *Sylvochoerus woodburnei* (figs. 1–4).

According to Frailey and Campbell (2012), *Sylvochoerus* has the following diagnostic characters: mandible short and sturdy; postcanine diastema relatively short, deep, and with steep rise to p2; ascending ramus with posterior margin curved in lateral view; high placement of mandibular condyle; forward placement of mandibular condyle; and less procumbent mandibular symphysis.

All these features characterize both extant genera of peccaries, *Tayassu* and *Dicotyles* (Gasparini, 2007; Gasparini et al., 2011, 2014; Parisi Dutra et al., 2017). It is noteworthy that the length of the postcanine diastema measured in this genus allows us to consider it as a short diastema (shorter than 50% and longer than 30% of the length of the toothrow; see Gasparini, 2007). Besides that, a short postcanine diastema represents one of the characters that allow grouping it into Tayassuini. This clade is composed of the three living species, *Dicotyles tajacu* (collared peccary), *Tayassu pecari* (white-lipped peccary), and *Parachoerus wagneri* (Chacoan peccary), in addition to the extinct taxa *Brasiliochoerus stenocephalus, Parachoerus carlesi, Catagonus metropolitanus*, and *Catagonus bonaerensis* (Parisi Dutra et al., 2017).

According to Frailey and Campbell (2012), the new genus *Sylvochoerus* is a medium- to large-sized peccary with a short snout and a broad cranium. These authors also considered this new taxon to resemble *Tayassu* but to differ from *Dicotyles* in the following characters: man-

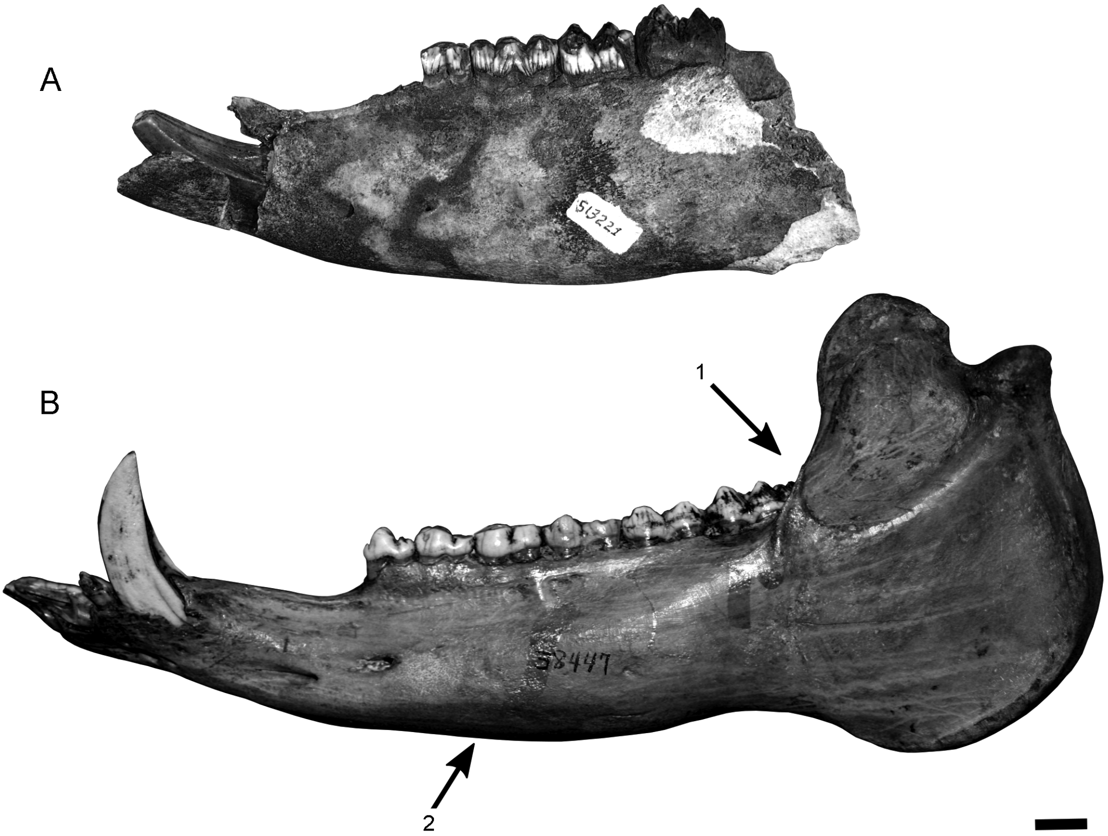

FIG 1. **A,** *Sylvochoerus woodburnei*, USNM 513221, partial left ramus with dp3–m2. **B,** *Tayassu pecari*, USNM 38447, mandible. Arrows: **1,** ascending ramus overlapping part of m3; **2,** difference in depth of the dentary bone below the toothrow. Scale bar = 1 cm.

dibular ramus with postdigastric sulcus shallower and extending anteriorly only to under m2 (as opposed to under m1 in *Dicotyles*); mandibular rami with inferior margin of diastema rounded mediolaterally (broadening laterally under diastema in *Dicotyles*); mandibular condyle higher on ascending ramus; mandibular symphysis recurved anterior to canines (recurved ventral to canines in *Dicotyles*); more complex dental pattern with an abundance of minor cuspids; weak lophodonty with wear (weak selenodonty in *Dicotyles*); more advanced state of molarization of p4; heel of m3 complex (less integrated and more simple in *Dicotyles*).

All these features correspond to those that characterize the genus *Tayassu,* except the tooth crown morphology, which other authors (Gasparini et al., 2011, 2014) have referred to as bunodont for all the species of *Tayassu, Dicotyles*, *Catagonus, Brasiliochoerus* and *Parachoerus* (teeth of *Parachoerus wagneri* are referred to as "zygodont," which is bunodont with relatively high cuspids) (Gasparini et al., 2009, 2011, 2013, 2019; Prothero and Grenader, 2012; Avilla et al., 2013; Parisi Dutra et al., 2017).

According to Frailey and Campbell (2012), *Sylvochoerus* differs from *Tayassu* and can be considered as a different genus, by having: mandibular ramus with nearly consistent

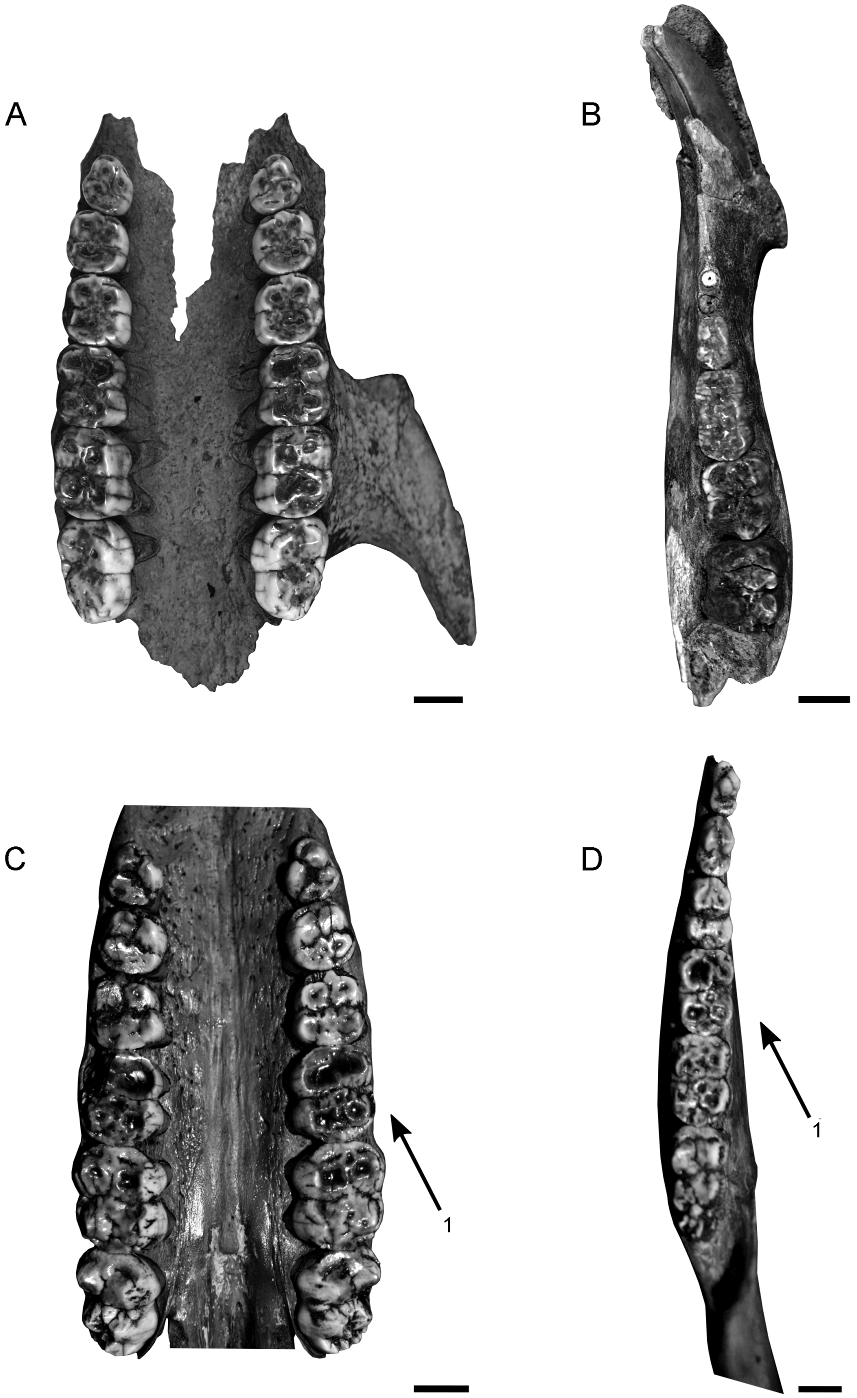

FIG 2. **A,** *Sylvochoerus woodburnei*, USNM 205346, palate with complete dentition and portion of left zygomatic arch; **B,** USNM 513221, partial left ramus with dp3–m2. **C,** *Tayassu pecari*, USNM 38447, upper postcanine dentition (P2–M3), and **D,** lower left p2–m3. Arrows: **1,** bunodont molar morphology described in the text. Scale bars = 1 cm.

depth below the toothrow (i.e., ramus does not lose depth anteriorly; a ramus with reduced depth anteriorly is present in *Tayassu*); ascending ramus with anterior edge overlapping part of m3, in lateral view (m3 more exposed in lateral view in *Tayassu*); angle of mandible gently curving anteriorly into shallow postdigastric sulcus and extending only slightly below lower margin of horizontal ramus (angle of mandible with abrupt change in curvature leading anteriad into deep postdigastric sulcus and extending well below lower margin of horizontal ramus in *Tayassu*); alveoli for incisors more procumbent, directed more anteriad and less dorsad; digastric fossa well differentiated from pterygoid fossa by low, rounded ridge (ridge very low or absent in *Tayassu*); digastric fossa more deeply concave, which is accentuated by medial edge of inferior margin of ramus extending mediad to form a shelf; teeth with lower part of crown taller, more broad based, bulbous, and with major cusps shorter and inclined toward long axis of tooth; alveolar margin of canines lying well below line drawn from alveolar margin of the p2–m1 (lies at or only slightly below line in *Tayassu*); molars with ribbed furrowing on flanks of cusps, resulting in a sculpted appearance (absent in *Tayassu*); dentition with multiple accessory crests and cuspids, producing a more complex occlusal surface than in *Tayassu*. However, all the characters listed by Frailey and Campbell (2012) fall within the variation range of the monotypic genus *Tayassu* (i.e., *Tayassu pecari*), as we describe below (figs. 1, 2, 4).

Mandibular ramus with nearly consistent depth below toothrow: In their description, Frailey and Campbell (2012) point out that *Sylvochoerus* has an almost constant depth below the toothrow and claim that in *Tayassu pecari,* the ramus loses depth anteriorly. In fact, some specimens of *Tayassu pecari* display slight differences in depth from the anterior to the posterior part of the dentary bone below the toothrow (fig. 1B: arrow); however, these differences are minor (almost imperceptible) in some specimens.

Ascending ramus with anterior edge overlapping part of m3 in lateral view: This character probably is the most variable feature in the dentary bone (fig. 1B: arrow). In some specimens of *Tayassu pecari* from Argentina, the anterior part of the ascending ramus overlaps part of m3 as occurs in *Sylvochoerus*, but in several specimens from central and northern Brazil, the ascending ramus does not overlap the m3. Besides that, this character also varies depending on the ontogenetic age of the specimen (see Margarido et al., 2007).

Angle of mandible gently curving anteriad into shallow postdigastric sulcus and extending only slightly below lower margin of horizontal ramus: Frailey and Campbell (2012) suggest that the postdigastric sulcus in *Sylvochoerus* is a gently anteriorly curved structure, whereas in *Tayassu pecari* it is a deep sulcus that abruptly changes the direction of the horizontal ramus of the dentary bone. The holotype of *Sy. woodburnei,* AMNH 55811, and the two paratypes, USNM 513217 and USNM 513221, as stated by Frailey and Campbell (2012), are damaged due to the fossilization process. These features may be a result of this process; however, some living and fossil individuals of *T. pecari* show the same shape of the postdigastric sulcus as *Sy. woodburnei.* This sulcus represents the insertion of the digastric muscle. When contracted, this muscle elevates the hyoid bone and depresses the mandible, a movement involved with opening the mouth. Thus, the shape of the postdigastric sulcus might be related to dietary habits.

Alveoli for incisors more procumbent, directed more anteriad and less dorsad: This character is highly variable in North and South American tayassuid species, so it is not a diagnostic feature useful to differentiate species.

Digastric fossa well differentiated from pterygoid fossa by low, rounded ridge: In *Tayassu pecari*, this ridge is quite variable (low, very low, or absent), and thus is a nondiagnostic character. This feature, as developed in *Sy. woodburnei*, is also commonly observed in *T. pecari*.

Digastric fossa more deeply concave, accentuated by medial edge of inferior margin of ramus extending mediad to form a shelf: The digastric fossa is also deeply concave in *Tayassu pecari*. The development of a medial edge of the inferior margin of the ramus is variable in specimens of *T. pecari*.

Teeth with lower part of crown taller, more broad based, bulbous, and with major cusps shorter and inclined toward long axis of tooth: These characters are also observed in *Tayassu pecari* (fig. 2D).

Alveolar margin of canines lying well below line drawn from alveolar margin of p2–m1 (lies at or only slightly below line in *Tayassu*): This feature is developed in tayassuids in general.

Dentition with multiple accessory crests and cuspids, giving a more complex occlusal surface than in *Tayassu*: Teeth of *Sy. woodburnei* have the same crown morphology, dental pattern (e.g., placement of major cusps and accessory cuspids and multiplicity of minor crown features), and tooth size observed in *Tayassu pecari* (fig. 2).

Features listed in the diagnosis of *Sylvochoerus woodburnei* given by Frailey and Campbell (2012: 854–857) correspond in fact to diagnostic features of *Tayassu pecari*, such as: medium to large-sized peccary, with a short snout and a broad cranium, p4 molariform, molars multicuspidate with minor cuspids between major cusps (Gasparini, 2007; Gasparini et al., 2011, 2014). Instead of "indications of lophation resulting from wear in teeth," we note that the bunodont crown morphology developed in the specimens of *Sy. woodburnei* shows a transversely oval surface due to wear. Frailey and Campbell also mention as a diagnostic character of *Sy. woodburnei* the presence of lower premolars with a trigonid much taller than the talonid. It is true that the trigonid is taller than the talonid; however, the height of the trigonid represents a nondiagnostic morphometric feature because it varies in tayassuids with bunodont tooth morphology.

The monotypic genus *Tayassu* is widely distributed across the Neotropical region from northern Argentina to southern Mexico (Gasparini, 2013; Gasparini et al., 2014), occupying several types of habitats along this distribution. This species has a great ecological tolerance, but it is generally associated with bodies of water. Some authors (Beck, 2006; Reyna-Hurtado et al., 2009; Sicuro et al., 2011; Hendges et al., 2016, 2019) have pointed out that this animal has a large range of morphological variability due to food habit, sexual dimorphism and ontogenetic age factors.

Taking into account the morphological and morphometric characters observed in specimens described in Frailey and Campbell (2012) and comparing them with other fossil and living Tayassuidae specimens, we conclude *Sy. woodburnei* is based on specimens of *Tayassu pecari*. Therefore, we consider *Sy. woodburnei* a junior subjective synonym of *T. pecari*.

CETARTIODACTYLA Montgelard, Catzeflis and Douzery, 1997

TAYASSUIDAE Palmer, 1897

Referred material: LACM 154877 (holotype of *Waldochoerus bassleri* Frailey and Campbell, 2012), partial left mandibular ramus with p3–m3; USNM 513215, partial right mandible with p4, m2–3; USNM 513222, isolated right m1; USNM 513223, partial right mandible with m1–m3; USNM 515225, right palatal fragment, with P4–M3 (M2 damaged).

Identity of *Waldochoerus bassleri*: For a better understanding of our analysis, we organize the morphological and morphometric remarks on every character considered by Frailey and Campbell (2012) in the following order: (1) diagnosis of the genus; (2) similarities of *Waldochoerus* to *Dicotyles* and differences from *Tayassu*; (3) differences of *Waldochoerus* from *Dicotyles*; and (4) diagnosis of the species *Waldochoerus bassleri* (figs. 3, 4).

According to these authors, *Waldochoerus* has the following diagnostic characters: mandible short and sturdy; high placement of mandibular condyle; and forward placement of mandibular condyle. All of these features characterize both extant genera of peccaries, *Tayassu* and *Dicotyles* (Gasparini, 2007; Gasparini et al., 2011, 2014; Parisi Dutra et al., 2017). It is notable that mandibles in *Dicotyles* are smaller than those observed in *Tayassu* (see measurements in Gasparini, 2007; Gasparini et al., 2011, 2014).

According to Frailey and Campbell (2012), the new genus *Waldochoerus* is a medium- to small-sized peccary with a short snout that resembles *Dicotyles* and differs from *Tayassu* in having: posterior margin of ascending ramus below mandibular condyle straight or only slightly curved; dental crown pattern simple; labial conids with weak selenodonty; metaconid and hypoconid with reduced lophate connection; and quadrangular molar outline interrupted by deep indentations at transverse valleys.

In both genera, *Dicotyles* and *Tayassu,* the posterior margin of the vertical ramus extends posteriorly beyond the mandibular condyle, usually describing a pronounced curve in both genera. However, this outline is variable in both genera, and the posterior margin of the ascending ramus below the mandibular condyle can be a pronounced curve or slightly curved or even a straight line, as is present in *W. bassleri.*

The tooth crown morphology observed in the specimens from Peru is typically bunodont (fig. 3); the metaconid and hypoconid are well defined and contact each other via minor cuspids, as occurs in the bunodont morphology (the lophate connection mentioned by Frailey and Campbell does not correspond to this morphology). Lower molar teeth, in fact, have a rectangular outline in *Waldochoerus bassleri* as well as in *Tayassu* and *Dicotyles* (instead of a quadrangular molar outline referred to by these authors).

According to Frailey and Campbell (2012), *Waldochoerus* differs from *Dicotyles* and can be considered a distinct genus by having: temporal and digastric fossae deeper; coronoid process with central axis close to vertical and mandibular notch wide (versus coronoid process with anterior tilt to vertical axis and mandibular notch narrow in *Dicotyles*); higher placement of mandibular condyle; posterior margin of ascending ramus below condyle straight for more than half the height of the ramus before curving smoothly anteriad (posterior margin smoothly

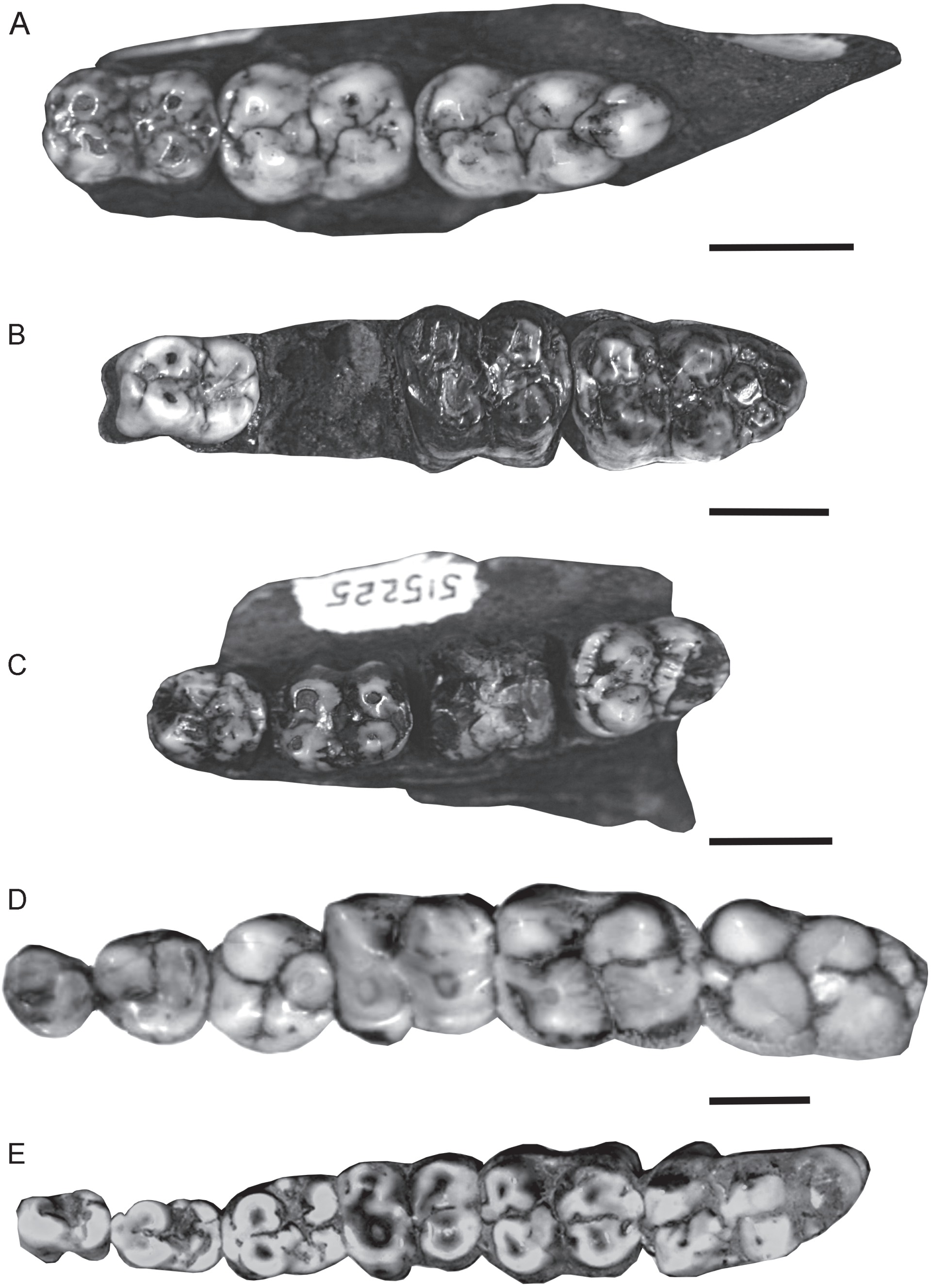

FIG 3. *Waldochoerus bassleri*: **A,** USNM 513223, partial right mandible with m1–m3; **B,** USNM 513215, partial right mandible with p4, m2–3; **C,** USNM 515225, right palatal fragment with P4–M3 (M2 damaged). *Dicotyles tajacu*: **D,** MACN zool 8-X-97-4, left P2–M3, and **E,** right p2-m3. Scale bars = 1 cm.

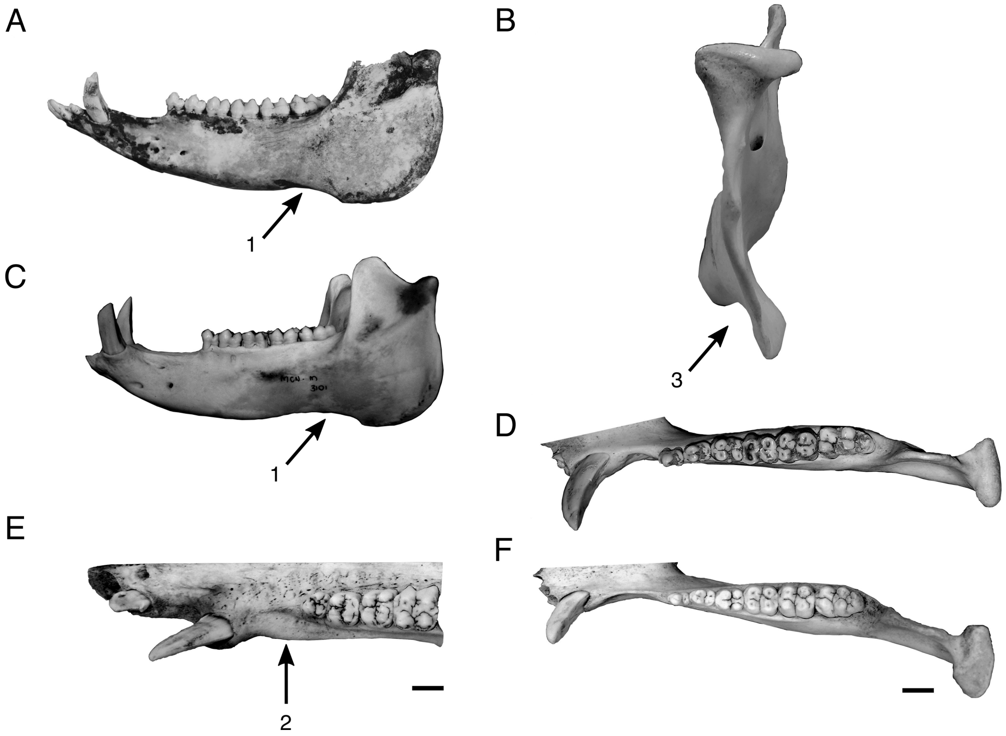

FIG 4. **A,** Lateral view of the mandible of *Tayassu pecari* (MCN-M 2663). **B,** Posterior view of the left dentary of *Dicotyles tajacu* (MCN-M 3101). **C,** Lateral view of mandible of *Dicotyles tajacu* (MCN-M 3101). **D.** Occlusal view of the left side of the mandible of *Tayassu pecari* (MCN-M 2663); **E,** Occlusal view of the right side of the palate of *Tayassu pecari* (MCN-M 2663). **F,** Occlusal view of the left side of the mandible of *Dicotyles tajacu* (MCN-M 3101). Arrows: **1,** the shallow post digastric sulcus; **2,** the buccinator crest; and **3,** the medially inflected angular process. Scale bars = 1 cm.

curved, beginning at base of condyle in *Dicotyles*); mandibular angle without ventral extension below ramus (significant ventral extension in *Dicotyles*); extremely shallow postdigastric sulcus (ventral extension of mandibular angle results in deep postdigastric sulcus in *Dicotyles*); ascending ramus and angle strongly curved medially, in posterior view (comparatively straight in *Dicotyles*); ascending rami diverge sharply laterad from vertical plane of horizontal rami posterior to m3, in superior view (little or no divergence in *Dicotyles*); smooth lateral surface of horizontal ramus (horizontal ramus bulges laterad at m2–3 in *Dicotyles*); slight medial rotation of m3 (versus greater rotation involving m1–3 in *Dicotyles*); and teeth with taller bases and rounded, bulbous conids. Nevertheless, all the characters listed by Frailey and Campbell (2012) fall within the variation range of *Dicotyles tajacu*, as we describe below (figs. 3, 4).

Higher placement of mandibular condyle: This feature is commonly observed in both *Tayassu* and *Dicotyles*.

Posterior margin of ascending ramus below condyle straight for more than half height of ramus before curving smoothly anteriad (posterior margin smoothly curved beginning at base of condyle in *Dicotyles*): This character is quite different from most specimens of *Dicotyles*; however, some Brazilian specimens of this genus have this characteristic.

Ascending ramus and angle strongly curved medially, in posterior view (comparatively straight in *Dicotyles*): The ascending ramus and angle are also strongly curved medially in both *Tayassu* and *Dicotyles* (fig. 4B).

Ascending rami diverge sharply laterad from vertical plane of horizontal rami posterior to m3, in superior view (little or no divergence in *Dicotyles*): This feature observed in *Waldochoerus bassleri* is similarly developed in both *Tayassu* and *Dicotyles.*

Slight medial rotation of m3 (versus greater rotation involving m1–3 in *Dicotyles*): This character is not clear. However, it is noteworthy that the tooth series observed in *Waldochoerus bassleri* are quite similar to those observed in both extant peccaries.

Teeth with taller bases and rounded, bulbous conids: This feature is the same as observed in *Dicotyles.* However, taking into account the variability of this feature in both *Tayassu* and *Dicotyles*, we consider it a nondiagnostic character and therefore not useful to differentiate taxa.

Features of the diagnosis of *Waldochoerus bassleri* given by Frailey and Campbell (2012: 866–869) correspond in fact to diagnostic features of the species *Dicotyles tajacu,* such as: short to medium-sized peccary, short snout, p4 submolariform and lower molars multicuspidate with minor cuspids (Gasparini, 2007). The teeth observed in the specimens from Peru are typically bunodont instead of the selenodont crown morphology referred to by Frailey and Campbell (2012). These authors also mention as a diagnostic character the presence of lower premolars with trigonids only slightly taller than talonids, but, as already stated, the height of the trigonid is variable in tayassuids with bunodont teeth.

The species *Dicotyles tajacu* has the largest geographic distribution of any living tayassuid, recorded from north-central Argentina to the southwestern United States (Gasparini et al., 2006; Gasparini, 2013), and occupies diverse habitats (forests and woodlands, savannas, and deserts) throughout this distribution. Taking into account the morphological and morphometric characters observed in the Peruvian specimens and comparing them with other fossil and living Tayassuidae specimens, we conclude *Waldochoerus bassleri* is based on specimens of *Dicotyles tajacu.* Therefore, we consider *W. bassleri* a junior subjective synonym of *D. tajacu.*

CETARTIODACTYLA Montgelard, Catzeflis and Douzery, 1997

RUMINANTIA Scopoli, 1777

CERVOIDEA Batsch, 1788

Referred material: LACM 5159/155113, left ramus with p3–m3, broken at the symphysis just in front of mental foramen (holotype of *Surameryx acrensis* Prothero et al., 2014) (figs. 5–7).

Identity of *Surameryx acrensis*: Dromomerycinae is a group of deerlike ruminants that share some affinities with true deer, as both groups are part of the superfamily Cervoidea. They are usually included in the family Palaeomerycidae (Janis and Manning, 1998; Prothero and

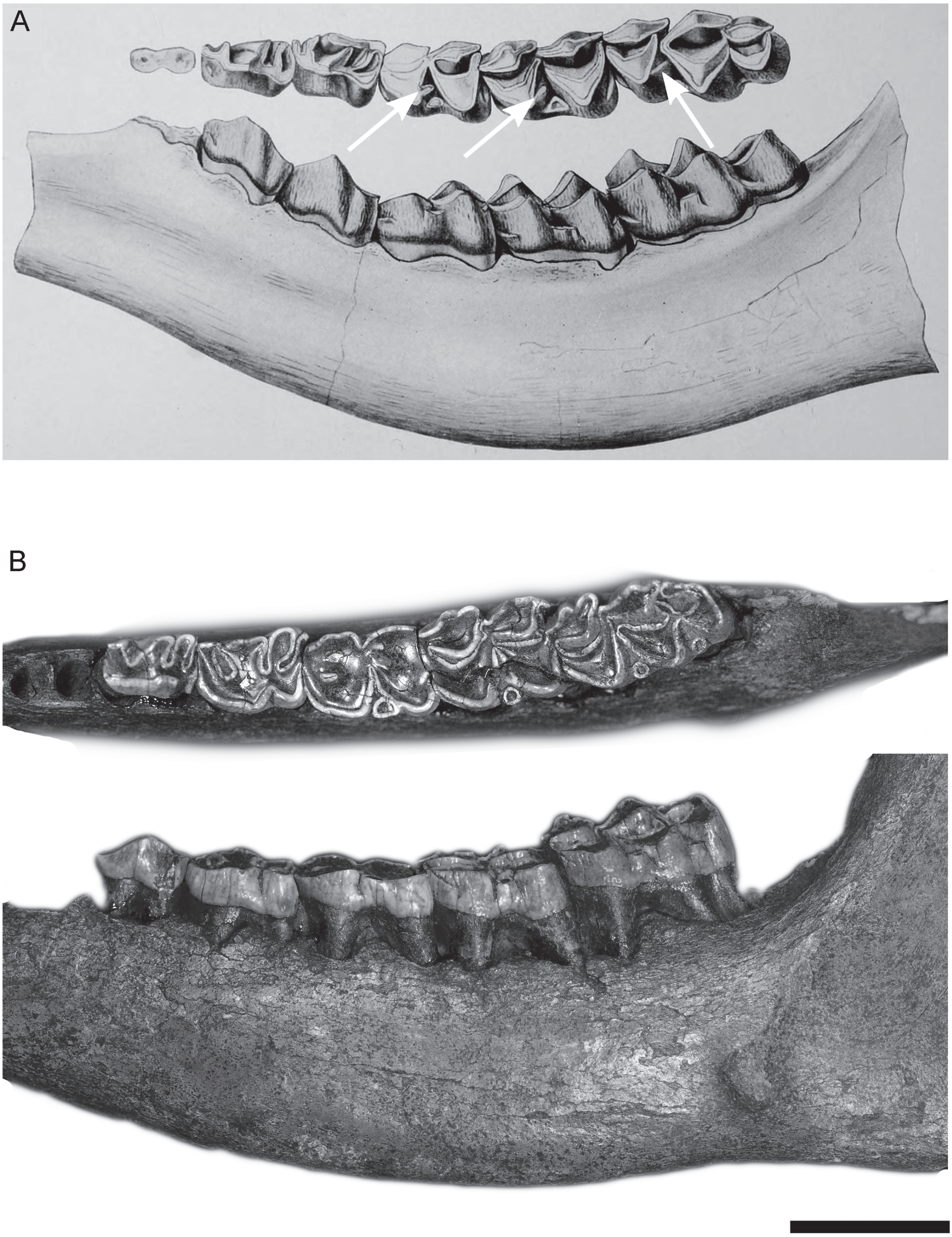

FIG 5. **A,** Plate depicting *Dromomeryx* from Douglass (1909) with white arrows indicating the *Palaeomeryx* fold. **B,** LACM 155113, the holotype of *Surameryx acrensis* in occlusal (above) and left lateral (below) views, showing the absence of the *Palaeomeryx* fold in this specimen. Scale bar = 1 cm.

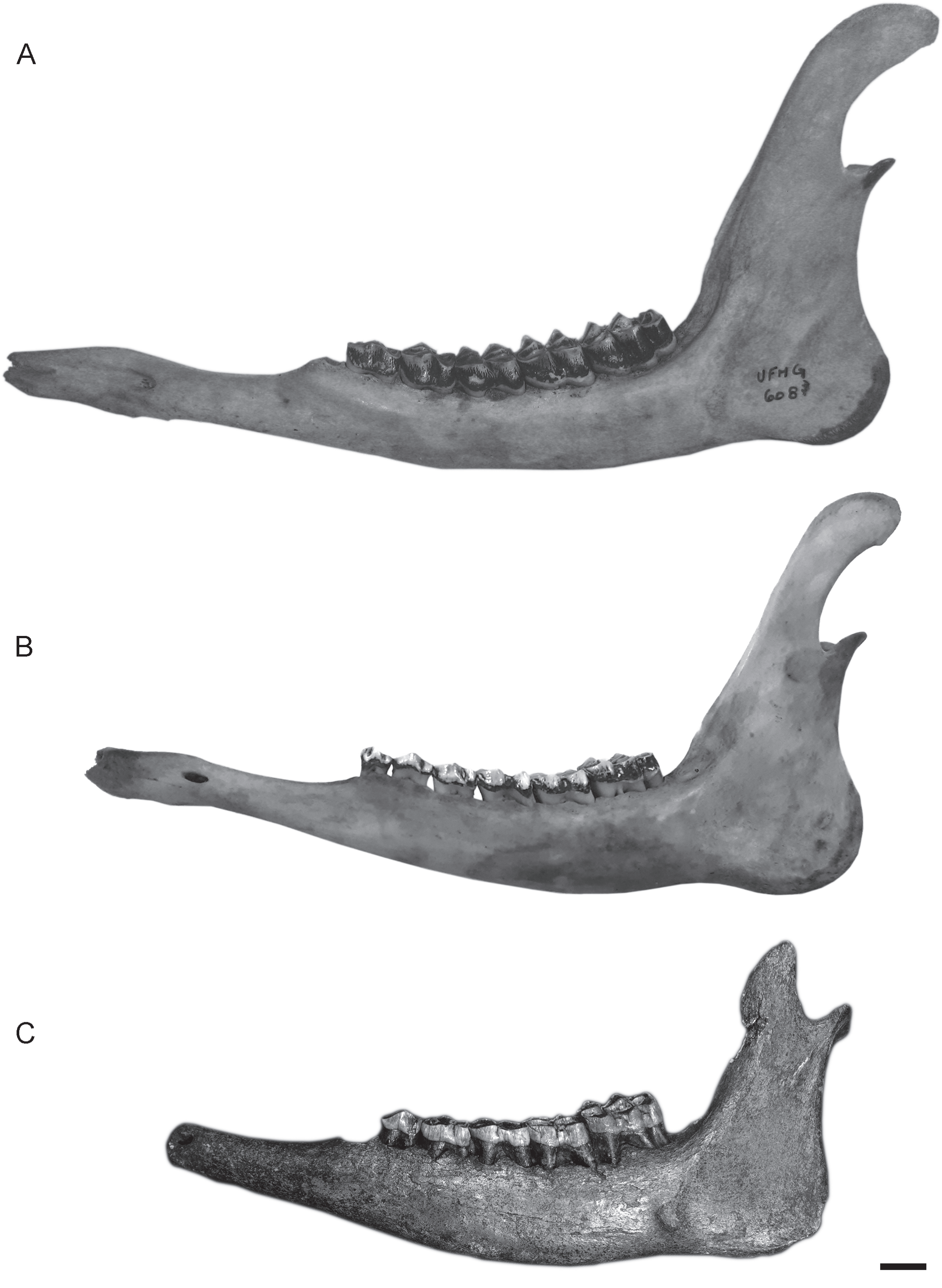

FIG 6. Left dentaries in lateral view: **A,** UFMG 6087, *Odocoileus virginianus* from Roraima, Brazil; **B,** unnumbered specimen (teaching collections of UFMG) of *Mazama americana* from Brazil; **C,** LACM 155113, the holotype of *Surameryx acrensis.* Scale bar = 1 cm.

Liter, 2008) but are sometimes considered to constitute a distinct family (Dromomerycidae) that is not particularly closely related to the former (Sánchez et al., 2015). Dromomerycines are restricted to the Miocene and early Pliocene of North America, and were moderately diverse during the middle Miocene, especially in the early Barstovian NALMA (Janis and Manning, 1998; Prothero and Liter, 2008). They are characterized by the presence of unbranched, nondeciduous cranial appendages on the frontal bone and some dental features, including large and nonmolariform premolars, no permanent first premolar, and the "*Palaeomeryx* fold," a short enamel ridge that extends posteromedially from the protoconid on the labial face of the lower molars. Many species also possess a double posterior lobe on m3 that is closed posteriorly (Janis and Manning, 1998; Prothero and Liter, 2008).

Prothero et al. (2014) compared *Surameryx acrensis* to an extensive list of ruminants, including Antilocapridae, Blastomerycinae (Moschidae), Hypertragulidae, Gelocidae, Leptomerycidae, Protoceratidae, and Camelidae, but we will restrict our discussion to the Palaeomerycidae (Dromomerycinae) and Cervidae because: (1) we agree with the features noted by Prothero et al. (2014) that preclude referral of LACM 5159/155113 to these other families; and (2) these groups are unlikely candidates for referral of the specimen. We will, therefore, address the reasons given for identifying *Su. acrensis* as a member of the Dromomerycinae and why a cervid identity was discarded. Only dental characters were used to assign the specimen to Dromomerycinae and, although dental characters in cervoid artiodactyls are highly homoplastic, some are in fact diagnostic. However, this is not the case for the characters used by Prothero et al. (2014).

The "*Palaeomeryx* fold" occurs in primitive Palaeomerycidae and other groups of noncetacean cetartiodactyls such as some Moschidae, some ruminants like *Eumeryx* (Prothero et al., 2014), and in some Miocene Cervidae (Janis and Scott, 1987). This structure, common in primitive Palaeomerycinae, is absent in most later Dromomerycinae (Solounias, 2007). The "*Palaeomeryx* fold" is not present on molars of the holotype of *Surameryx acrensis*, despite the authors (Prothero et al., 2014) describing it as the worn shape of a flange of exposed dentine connected to the postprotocristid of the protoconid, which is simply not visible on the specimen (fig. 5). The teeth of the specimen are very worn and, as befits an old individual, the heavy wear has played a part in confounding and obscuring some of the dental features. The protoconid and hypoconid region is broken in m2, which may have been mistaken for a "*Palaeomeryx* fold," but the assertion that it is present in m3 is puzzling. Prothero et al. (2014) also state that the molars "have the classic configuration of palaeomerycids," although most of the features described subsequently also agree with the molars of a cervid.

Another character mentioned is a vertical groove on the posterolingual face of p4 that divides the trigonid from the talonid. It divides the tooth into a posterior third separated from the anterior two-thirds by a lingual waist and is known to occur in giraffids, the palaeomerycid *Amphitragulus*, the bovid *Eotragus*, the ruminant *Prolibytherium*, dromomerycids, and blastomerycids (Janis and Scott 1987). The authors (Prothero et al., 2014) consider it typical of "nearly all palaeomerycids," but it is also present in large South American cervids (e.g., *Odocoileus*, *Ozotoceros*; fig. 7). They consider the "detailed pattern of pm3 and pm4 are almost identical to those seen in most primitive New World Palaeomerycidae" (Prothero et al., 2014: 436).

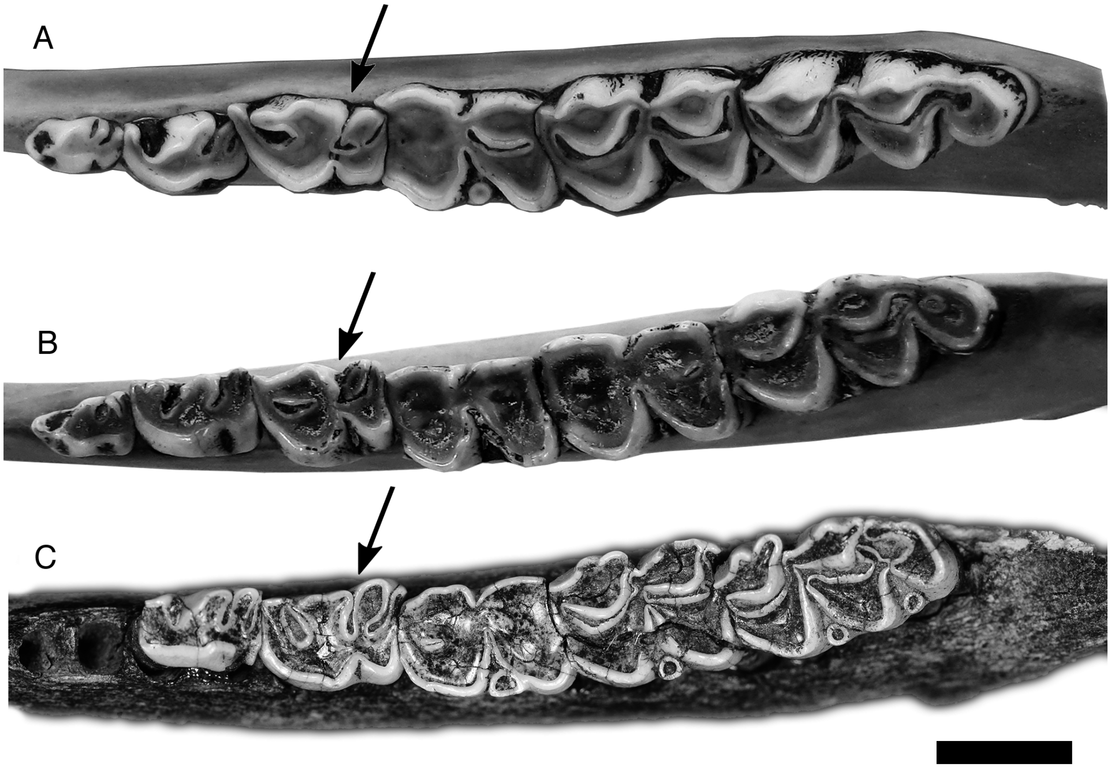

FIG 7. Left lower tooth series in occlusal view with arrows indicating the vertical groove on the posterolingual face of p4 that divides the trigonid from the talonid: **A,** MN 206, *Ozotoceros bezoarticus* from Brazil; **B,** unnumbered specimen (teaching collections of UFMG) of *Mazama americana* from Brazil; **C,** LACM 155113, the holotype of *Surameryx acrensis*. Scale bar = 1 cm.

The holotype of *Surameryx acrensis* presents a significantly worn premolar series and a nonmolariform p4, interpreted by Prothero et al. (2014) as a dromomerycine-like feature. *Barbourumeryx trigonocorneus*, a dromomerycine used for comparison, shows a nonmolariform p4, but it is developed in a different way (Prothero et al., 2014). Prothero et al. (2014) also consider a closed fossette in the p4 trigonid as “a derived feature of dromomerycines,” but it also occurs in cervids (Heckeberg, 2020). In addition, with wear the premolars lose the cusps and expose the dentine, and the fossettes may be entirely enclosed by wear. The shape of the p4 is highly variable in cervids, ranging from relatively simple to molariform (Heckeberg, 2020). In *Su. acrensis,* the p4 is similar to the worn corresponding tooth of South American cervids (fig. 7), being particularly similar to a highly worn p4 of *Odocoileus virginianus* (Severinghau, 1949; Cooper et al., 2013).

It is also noteworthy that no records of Dromomerycinae are known from Central America, including the rich early Miocene deposits of Panama (MacFadden, 2006; Kirby et al., 2008). Despite a great diversity of both browsing and grazing ungulates, including extinct cetartiodactyls such as Protoceratidae, Oreodontidae, and Anthracotheriidae, as well as camels (Floridatragulinae), musk deer (Moschidae), horses (Equidae), and rhinoceros (Rhinocerotidae)

(MacFadden, 2006, 2009; Rincon et al., 2015), to date, not a single fossil from Central America can be attributed to Dromomerycinae. At present, the southernmost record of this group is the southern United States (Janis and Manning, 1998; Prothero and Liter, 2008). If LACM 5159/155113 is indeed a Dromomerycinae, it would imply a huge geographic gap in dromomerycine distribution that cannot reasonably be attributed to a lack of sampling.

We believe that the interpretation of the holotype specimen of *Surameryx acrensis* as a dromomerycine Palaeomerycidae was heavily influenced by its supposed late Miocene age; at that time, cervids are unknown in North America (Webb, 1998; Prothero et al., 2014: 437). If the preserved morphology is the only information considered, the identity of the material becomes clearer, and we attribute LACM 5159/155113 to Cervidae, likely an old individual with a dental age greater than seven years (Cooper et al., 2013). Given the uniformity usually found in the teeth of cervids, a specific identity may be difficult to reach. The size of the specimen agrees with small members of the genus *Mazama* and South American populations of *O. virginianus*, but the horizontal ramus is taller in lateral view. The possible taxonomic significance of this latter characteristic is not known.

SPECIMEN PROVENANCE AND AGE

The authors of the alleged Dromomerycine and Miocene tayassuids from Peru considered them about 9.01 million years old (Frailey and Campbell, 2012; Prothero et al., 2014), but current concepts of the stratigraphy of Cenozoic deposits in Amazonia, as recognized by Frailey and Campbell (2012), are highly contentious (Campbell et al., 2001, 2006; Latrubesse et al., 2007, 2010). Prothero et al. (2014) refer to Carranza-Castañeda and Miller (2004) as support for the revised age of the GABI, citing "new discoveries in Central America," but this fauna is from central Mexico, near the southern tip of North America; it is dated to the Hemphillian/Blancan boundary (ca. 4.5 Ma; early Pliocene), half the reputed age of the Amazonian Miocene artiodactyls, and refers mainly to ground sloths, which are known in North America since the early Hemphillian (Marshall, 1988; McDonald and Naples, 2008). Frailey and Campbell (2012) and Prothero et al. (2014) see the putative Peruvian tayassuids and dromomerycine as part of an immigration of these and other mammals from North to South America during the late Miocene, about 10 Ma. However, similar claims of a Miocene age for the gomphotheriid proboscidean "*Amahuacatherium*" from Peru (Campbell et al., 2000, 2009), a supposed element in this immigration, have been refuted in previous works (Alberdi et al., 2004; Ferretti, 2008; Woodburne, 2010; Lucas, 2013; Mothé and Avilla, 2015).

The stratigraphic origin of the Peruvian tayassuid specimens is also unclear. Only four of the Tayassuidae specimens have stratigraphic information (Frailey and Campbell, 2012). Two of them, including the holotype of *Waldochoerus bassleri*, were collected "from surface deposits" (Frailey and Campbell, 2012: 853), but it was assumed that they came from the "Acre Conglomerate" (a unit discussed in the stratigraphy section below) because they were collected during the rainy season. However, the conglomerate is under the high-water line during that season (Campbell et al., 1985: fig. 22; 2000: fig. 3; 2001: figs. 1, 11; 2006: fig. 6), which has been confirmed by personal observation by one of us (M.A.C.).

The holotype of *Sylvochoerus woodburnei* was collected by G.G. Simpson (1953) at the upper Jurua River, Acre State, Brazil. Simpson and Paula-Couto (1981: 47) described the specimen as "indistinguishable from the homologous parts of the Recent white lipped peccary, still living in the same region" (i.e., *Tayassu pecari*) and concluded its age was "probably Recent." At the same locality (Locality 3, Gastão), numerous specimens of Pleistocene mammals were found (Simpson and Paula-Couto, 1981: 21, figs. 2, 3), which suggests the specimen could be Pleistocene in age.

The remaining specimens attributed to Tayassuidae lack precise geographic or stratigraphic data (Frailey and Campbell, 2012: 852). Most of them come from the Harvey Bassler Collection of Peruvian Fossils, which were collected during the 1920s by an American petroleum geologist in Peru (Willard, 1962, 1966) and derive from three broadly assigned "localities": (1) Inuya River; (2) eastern end of Pongo de Manseriche (Puerto Beatrix); and (3) Mapuya. Given that Bassler had no access to detailed topographic maps in the 1920s, these names are the only geographic provenance provided, and there is no explicit lithostratigraphic context associated with his collections (Willard, 1962, 1966). Indeed, Willard (1962) drew attention to the mixed nature of the vertebrate fossil "assemblages" collected by Bassler, which include disarticulated and scattered elements of marine and nonmarine taxa (see below), many of which are abraded by transport or erosion. Further, as is clear from Frailey and Campbell (2012), at least the Inuya River locality likely consists of more than a single assemblage; it includes fossils collected at the Inuya River in 1922 (including specimens of *Sylvochoerus woodburnei* and *Waldochoerus bassleri*), specimens from a beach on the Inuya River (perhaps a distinct locality?) collected in 1922 (including a specimen of *Sylvochoerus woodburnei*), and many specimens with no date of collection indicated, including most of the USNM peccary specimens. An ulna collected in 1929 from the Pongo de Manseriche locality was referred to *Sylvochoerus woodburnei* by Frailey and Campbell (2012), and a specimen collected in 1929 at Mapuya is one of the paratype specimens of *Waldochoerus bassleri*.

Willard (1966: 75) lists the collective Inuya River fossils as those of fishes, turtle, crocodile, peccary, toxodont, marsupial, glyptodont, astrapothere, and possibly bird. Willard (1966) lists the collective assemblage from Pongo de Manseriche as fish (including sharks), turtle, reptile, peccary and mammal, associated with "Pliocene Mollusca," but the basis for assigning the molluscs a Pliocene age is not clear. The Mapuya River fossils, according to Willard (1966: 76), are similar to those from the Inuya River and also include an astrapothere. The astrapothere is the only possible evidence of a Miocene age. However, the geologically youngest astrapotheres are middle Miocene in age rather than late Miocene (Goillot et al., 2011; Croft et al., 2020a, 2020b) and therefore provide no support for a late Miocene age for the peccaries. Additionally, given that Pleistocene mammal-bearing strata rest (with evident unconformity) directly on Miocene mammal-bearing strata in upper Amazonia, these "assemblages" are surely mixed, as first suggested by Willard (1962). Thus, there is no basis for directly assigning a late Miocene age to the peccary fossils in the Bassler collection. The provenance and age of the only known specimen of *Surameryx acrensis* is equally dubious. It was collected "as riverine float" (Prothero et al., 2014: 440), and, although the possibility of a Pleistocene age was mentioned, it was dismissed.

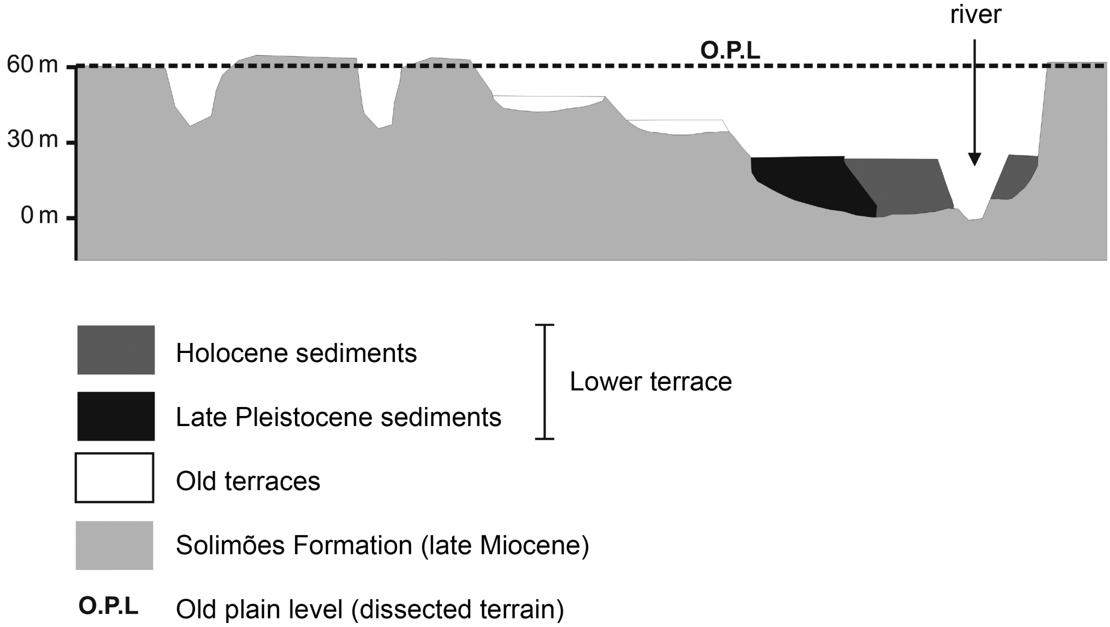

FIG 8. Schematic section showing the characteristic main elements of the landscape in southwestern Brazilian Amazonia (lowlands). Modified from Latrubesse et al. (2010).

STRATIGRAPHY AND AGE OF AMAZONIAN DEPOSITS

Interpretation of Amazonian stratigraphy is central to this discussion. The authors follow Campbell et al. (2006) in assuming the existence of the "Ucayali unconformity," an alleged regional tectonic feature found across the Amazon as a consequence of Quechua I and II phases of Andean tectonism. Above this peneplain, according to them, is a conglomerate, often called the "Acre conglomerate," the source of many of the vertebrate fossils recovered from the outcrops along the Acre and Jurua rivers, in southwestern Amazonia. Along the upper Acre River, this conglomerate is intraformational and composed of clay-pebble balls formed from the underlying clays of the Solimões Formation (Frailey, 1986; Cozzuol, 2006). Along the Jurua River, the pebbles are composed of hard concretions and quartzite, 10–15 cm in diameter, and the matrix is sandy to clayey-sandy, made of indurated sediment (Latrubesse and Rancy, 1998). Occasionally, in the upper Jurua River, conglomerates may occur also at other stratigraphic levels, but in all cases they are of the same nature (Latrubesse and Rancy, 1998: fig. 3).

These coarse sediments are channel lithofacies that represent channel reactivation of a gradational fluvial system during subsidence, which flowed and eroded into a muddy riverbed, cutting floodplain or lake deposits. Mud balls were eroded and transported short distances by processes like erosion of a muddy channel bottom, the entrance of a channel into muddy sediments such as a saturated floodplain/lake, the generation of a new fluvial belt by avulsion that cut the fine-grained sediments of the floodplain, and mass movements along the banks that introduced sediments into the channel. Consequently, they are discontinuous and not a continuous layer of conglomerate (Latrubesse et al., 2007, 2010).

The underlying Solimões Formation, also called the Pebas or Ipururo Formation in Peru, is the result of a fluvio-tidal mega wetland (palustrine) environment that developed in western Amazonia from 11–7 Ma (Latrubesse and Rancy, 1998) in a subsiding basin. As in the present-day Pantanal, rivers had no fixed courses and migrated laterally, producing a variety of environments such as swamps, lakes, grasslands, and localized forests in which a diverse fauna flourished (Cozzuol, 2006; Latrubesse et al., 2007, 2010; Antoine et al., 2016). By the end of this period, the subsidence and sedimentation virtually stopped, so the rivers were set to stable courses, and an erosive phase started in the west while sedimentation increased in eastern Amazonia, originating the modern Amazon fluvial system (Latrubesse and Rancy, 1998). This produced a sedimentation gap in western Amazonia that lasted until the late Pleistocene, reflected by a dramatic drop in the fossil record (Antoine et al., 2016). Deposits representing this interval may be found locally as older riverine terraces, such as those along the Acre, Jurua, Beni, and Madre de Dios rivers (Simpson and Paula-Couto, 1981; Frailey, 1986; Latrubesse and Rancy, 1998; Cozzuol, 2006; Latrubesse et al., 2007, 2010).

The composite section that is illustrated in several papers by Campbell, Frailey, and coworkers since 1985 (Campbell et al., 1985, 2000, 2001, 2006; Frailey, 1986) has remained the same over the years, but the age changed from Holocene, with Miocene strata just at the base, to an entirely Tertiary succession. Figure 8 shows the sections at the river bank as fluvial terraces deposited as the river excavated its channel, producing an incised, reversed-in-time sequence, with younger deposits topographically lower than the older ones (Latrubesse et al., 2007, 2010). This explains the late Pliocene age (3.12 Ma) obtained at the Piedras locality (Campbell et al., 2001) from the older and higher terraces.

The late Miocene age (9.01 Ma) obtained from what they called Unit A apparently is not compatible with this interpretation. The problem with this age is its provenance. Campbell et al. (2000: 77) said “The outcrop is heavily vegetated, however, so it was not possible to observe directly its relationships to other horizons of Unit ‘A’ exposed just upriver.” However, it may even not be in this “horizon.” It should be noted that the paleorelief on top of the Solimões Formation (also known as Pebas, Ipuro, and other names) is variable, making it possible that the ashes from which the late Miocene dates of the Cocama locality were obtained (Campbell et al., 2000, 2001) may have come from outcrops of the Solimões/Ipuro Formation.

Similar terrace sequences are observed along the Mamoré-Madeira River, but since it runs on the border of the Brazilian craton instead of on Tertiary sediments, only Quaternary fauna has been recovered from them. These are the same taxa found at other localities, especially those from the upper Jurua River (Simpson and Paula-Couto, 1981; Latrubesse and Rancy, 1998; Latrubesse et al., 2007, 2010) where they are often mixed with reworked late Miocene taxa.

CONCLUSION

There is no convincing evidence for the presence of terrestrial cetartiodactyls in the Miocene of South America. Our morphological analyses of the holotype and only specimen of *Surameryx acrensis,* a supposed Miocene dromomerycine, indicate that it represents a cervid rather than a dromomerycine. Similarly, the supposed late Miocene tayassuid taxa *Sylvochoerus woodburnei* and *Waldochoerus bassleri* are based on materials that fall within the range of variation observed in *T. pecari* and *D. tajacu* respectively, and thus are synonymous with these species. The lack of precise geographic and/or stratigraphic provenance for these specimens precludes independently constraining their ages. As a result, the most parsimonious conclusion is that these remains pertain to Quaternary representatives of modern species rather than late Miocene species. The stratigraphic scheme advocated as supporting a late Miocene age for certain outcrops in the area does not take into consideration the fluvial activity in the region and does not support a late Miocene age for these specimens.

It is noteworthy that all three of these alleged late Miocene species represent endemic genera; this suggests a relatively long time of local isolation, which implies that their ancestors must have arrived even earlier. However, no mammals of North American affinities have been found at older localities in northern South America, some of which are close to the areas where the specimens were collected. Accepting the idea that these species are late Miocene endemics requires making unreasonable assumptions about the incompleteness of the fossil record of both the northern tropics and other parts of South America. Taken together, morphological, geological, and paleontological data do not support the idea that terrestrial cetartiodactyls immigrated from North to South America during the late Miocene.

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REFERENCES

Acosta, E.L., G.T. Garbino, G.M. Gasparini, and R. Parisi Dutra. 2020. Unraveling the nomenclatural puzzle of the collared and white-lipped peccaries (Mammalia, Cetartiodactyla, Tayassuidae). Zootaxa 4851: 60–80.

Alberdi, M.T., J.L. Prado, and R. Salas. 2004. The Pleistocene Gomphotheriidae (Proboscidea) from Peru. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 231: 423–452.

Antoine, P.O., R. Salas-Gismondi, F. Pujos, M. Ganerød, and L. Marivaux. 2016. Western Amazonia as a hotspot of mammalian biodiversity throughout the Cenozoic. Journal of Mammalian Evolution. [doi:10.1007/s10914-016-9333-1]

Avilla, L.S., et al. 2013. The northernmost record of *Catagonus stenocephalus* (Lund in Reinhardt, 1880) (Mammalia, Cetartiodactyla) and its palaeoenvironmental and palaeobiogeographical significance. Journal of South American Earth Sciences 42: 39–46.

Barbiére, F., P.E. Ortiz, and U.F.J. Pardiñas. 2019. The oldest sigmodontine rodent revisited and the age of the first South American cricetids. Journal of Paleontology 93: 368–384.

Bartoli, G., et al. 2005. Final closure of Panama and the onset of northern hemisphere glaciation. Earth and Planetary Science Letters 237: 33–44.

Batsch, A.J.G.C. 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien, für akademische Vorlesungen entworfen, und mit den nöthigsten Abbildungen versehen. Erster Theil. Allgemeine Geschichte der Natur; besonder der Säugthiere, Vögel, Amphibien und Fische, 1–528, Tab. I–V. Jena: (Akademische Buchhandlung).

Beck, H. 2006. A review of peccary-palm interactions and their ecological ramifications across the Neotropics. Journal of Mammalogy 87: 519–530

Campbell, K.E., 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., C.D. Frailey, and L. Romero-Pittman. 2000. The Late Miocene gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: implications for the Great American Faunal Interchange. Instituto Geológico Minero y Metalúrgico, Série D, Estudios Regionale 23: 1–152.

Campbell, K.E., M. Heiizler, 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., 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., C.D. Frailey, and L. Romero-Pittman. 2009. In defense of *Amahuacatherium* (Proboscidea: Gomphotheriidae). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 252: 113–128.

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.

Cione, A.L., G.M. Gasparini, E. Soibelzon, L.H. Soibelzon, and E.P. Tonni. 2015. The Great American Biotic Interchange: a South American perspective. Springer Briefs in Earth System Sciences. South America and the Southern Hemisphere. Springer Verlag, London: Springer, 97 pp.

Cooper, S.M., S.S. Sieckenius, and A.L. Silva. 2013. Dentine method: aging white-tailed deer by tooth measurements. Wildlife Society Bulletin 37: 451–457.

Cozzuol, M. 2006. The Acre vertebrate fauna: diversity, geography and time. Journal of South American Earth Sciences 21: 185–203.

Croft, D.A. 2012. Punctuated isolation: the making and mixing of South America's mammals. *In* B.D. Patterson and L.P. Costa (editors), Bones, clones, and biomes: the history and geography of Recent Neotropical mammals: 9–19. Chicago: University of Chicago Press.

Croft, D.A. 2016. Horned armadillos and rafting monkeys: the fascinating fossil mammals of South America. Bloomington: Indiana University Press, 320 pp.

Croft, D.A., J.N. Gelfo, and G.M. López. 2020a. Splendid innovation: the South American native ungulates. Annual Review of Earth and Planetary Sciences 48: 259–290.

Croft, D.A., J.-N. Martinez, and P.M. Tapia. 2020b. The first record of a Miocene terrestrial mammal (Astrapotheria: Uruguaytheriinae) from northern coastal Peru. Ameghiniana 57: 146–158.

Douglass, E. 1909. *Dromomeryx*, a new genus of American ruminants. Annals of Carnegie Museum 5 (11): 457-479.

Engelman, R.K., and D.A. Croft. 2019. Strangers in a strange land: ecological dissimilarity to metatherian carnivores may partly explain early colonization of South America by *Cyonasua*-group procyonids (Carnivora). Paleobiology 45: 598–611.

Ferretti, M.P. 2008. A review of South American gomphotheres. New Mexico Museum of Natural History and Science Bulletin 44: 381–391.

Flynn, J.J., et al. 2005. Geochronology of Hemphillian-Blancan aged strata, Guanajuato, Mexico, and implications for timing of the Great American Biotic Interchange. Journal of Geology 113: 287–307.

Flynn, J.J., A.R. Wyss, and R. Charrier. 2007. South America's missing mammals. Scientific American 296: 68–75.

Frailey, C.D. 1986. Late Miocene and Holocene mammals, exclusive of the Notoungulata, of the Río Acre region, Western Amazonia. Contribution in Science, Natural History Museum of Los Angeles County 374: 1–46.

Frailey, C.D., and K.E. Campbell. 2012. Two new genera of peccaries (Mammalia, Artiodactyla, Tayassuidae) from upper Miocene deposits of the Amazon Basin. Journal of Paleontology 86: 852–877.

Gasparini, G.M. 2007. Sistemática, biogeografía, ecología y bioestratigrafía de los Tayassuidae (Mammalia, Artiodactyla) fósiles y actuales de América del Sur, con especial énfasis en las especies fósiles de la provincia de Buenos Aires. Ph.D. dissertation, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina.

Gasparini, G.M. 2013. Records and stratigraphical ranges of South American Tayassuidae (Mammalia, Artiodactyla). Journal of Mammalian Evolution 20: 57–68.

Gasparini, G.M., E. Ortiz Jaureguizar, and A.A. Carlini. 2006. Familia Tayassuidae. *In* R.M. Bárquez, M.M. Díaz, and R.A. Ojeda (editors), Los mamíferos de Argentina: sistemática y distribución: 114–115. Tucumán: Sociedad Argentina para el Estudio de los Mamíferos (SAREM).

Gasparini, G.M., L. Kerber, and E. Oliveira. 2009. *Catagonus stenocephalus* (Lund in Reinhardt, 1880) (Mammalia, Tayassuidae) in the Touro Passo Formation (Late Pleistocene), Rio Grande do Sul, Brazil. Taxonomic and palaeoenvironmental comments. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 254: 261–273.

Gasparini, G.M., B. Ferrero, R. Vezzosi, and E. Brunetto. 2011. El registro de *Tayassu pecari* (Link, 1795) (Artiodactyla, Tayassuidae) en el Pleistoceno Tardío de la provincia de Santa Fe, Argentina. Aspectos biogeográficos y de distribución de una especie en retracción. Revista Mexicana de Ciencias Geológicas 28: 203–211.

Gasparini, G.M., E. Soibelzon, E.P. Tonni, and M. Ubilla. 2011. The "living fossil" peccary, *Catagonus wagneri* (Tayassuidae) and its climatic significance during the Pleistocene and Holocene. Current Research in the Pleistocene 28: 157–159.

Gasparini, G.M., M. Ubilla, and E.P. Tonni. 2013. The Chacoan peccary, *Catagonus wagneri* (Mammalia, Tayassuidae), in the late Pleistocene (northern Uruguay, South America): paleoecological and paleobiogeographic considerations. Historical Biology: an International Journal of Paleobiology 25 (5–6): 679– 690.

Gasparini, G.M., et al. 2014. *Tayassu pecari* (Link, 1795) (Mammalia, Cetartiodactyla): comments on its South American fossil record, taxonomy and paleobiogeography. Historical Biology: an International Journal of Paleobiology 26: 785–800.

Gasparini, G.M., R. Parisi Dutra, G.N. Lamenza, E.P. Tonni, and A. Ruella. 2019. *Parachoerus carlesi* (Mammalia, Tayassuidae) in the Late Pleistocene (northern Argentina, South America): paleoecological and palaeobiogeographic considerations. Historical Biology: an International Journal of Paleobiology 31: 1082–1088.

Goillot, C., P.O. Antoine, J. Tejada, F. Pujos, and R. Salas-Gismondi. 2011. Middle Miocene Uruguaytheriinae (Mammalia, Astrapotheria) from Peruvian Amazonia and a review of the astrapotheriid fossil record in northern South America. Geodiversitas 33: 331–345.

Goin, F.J., J.N. Gelfo, L. Chornogubsky, M.O. Woodburne, and T. Martin. 2012. Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds. *In* B.D. Patterson and L.P. Costa (editors), Bones, clones, and biomes: the history and geography of Recent Neotropical mammals: 20–50. Chicago: University of Chicago Press.

Heckeberg, N.S. 2020. The systematics of the Cervidae: a total evidence approach. PeerJ 8: e8114.

Hendges, C.D., J. Moura Bubadué, and N.C. Cáceres. 2016. Environment and space as drivers of variation in skull shape in two widely distributed South American Tayassuidae, *Pecari tajacu* and *Tayassu pecari* (Mammalia: Artiodactyla). Biological Journal of the Linnean Society 119: 785–798.

Hendges, C.D., B.D. Patterson, N.C. Cáceres, G.M. Gasparini, and C.F. Ross. 2019. Skull shape and the demands of feeding: a biomechanical study of peccaries (Mammalia, Cetartiodactyla). Journal of Mammalogy 100: 475–486.

Janis, C.M., and E. Manning. 1998. Dromomerycidae. *In* C. M. Janis, K.M. Scott, and L.L. Jacobs (editors), Evolution of Tertiary mammals of North America, vol. 1. Terrestrial carnivores, ungulates, and ungulate like mammals: 477–490. Cambridge: Cambridge University Press.

Janis, C.M., and K.M. Scott. 1987. The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. American Museum Novitates 2893: 1–85.

Kirby, M.X., D.S. Jones, and B.J. MacFadden. 2008. Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central America Peninsula. PLoS One 3: e2791

Latrubesse, E., and A. Rancy. 1998. The Late Quaternary of the Upper Jurua River, southwestern Amazonia, Brazil: Geology and Vertebrate Paleontology. Quaternary of South America and Antarctic Peninsula 11: 27–46.

Latrubesse, E.M., S.A.F. Silva, M.A. Cozzuol, and M.L. Absy. 2007. Late Miocene continental sedimentation in southwestern Amazônia and its regional significance: biotic and geological evidence. Journal of South American Earth Sciences 23: 61–80.

Latrubesse, E.M., et al. 2010. The late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. Earth-Science Reviews 99: 99–124.

Leigh, E.G., A. O'Dea, and G.J. Vermeij. 2014. Historical biogeography of the Isthmus of Panama. Biological Reviews 89: 148– 172.

Leite, R.N., et al. 2014. In the wake of invasion: tracing the historical biogeography of the South American cricetid radiation (Rodentia, Sigmodontinae). PLoS One 9: e100687.

Lucas, S.G. 2013. The palaeobiogeography of South American gomphotheres. Journal of Palaeogeography 2: 19–40.

MacFadden, B.J. 2006. North American Miocene mammals from Panama. Journal of Vertebrate Paleontology 26: 720–734.

MacFadden, B.J. 2009. Three-toed browsing horse *Anchitherium* (Equidae) from the Miocene of Panama. Journal of Paleontology 83: 489–492.

Maestri, R., N.S. Upham, and B.D. Patterson. 2019. Tracing the diversification history of a Neogene rodent invasion into South America. Ecography 42: 683–695.

Margarido, T.C., V. Abilhoa, and E.L. Monteiro-Filho. 2007. Age in *Tayassu pecari* according to dental eruption. Acta Theriologica 52: 189–196

Marshall, L.G. 1988. Land mammals and the Great American Interchange. American Scientist 76: 380–388.

Marshall, L.G., S.D. Webb, J.J. Sepkoski, and D.M. Raup. 1982. Mammalian evolution and the Great American Interchange. Science 215: 1351–1357.

McDonald, H.G., and V.L. Naples. 2008. Xenarthra. *In* C. M. Janis, G.F. Gunnell, and M.D. Uhen (editors), Evolution of Tertiary mammals of North America, vol. 2: Small mammals, xenarthrans, and marine mammals: 147–160. Cambridge: Cambridge University Press.

Montgelard, C., F. Catzeflis, and E. Douzery. 1997. Phylogenetic relationships of artiodactyls and cetaceans as deduced from the comparison of cytochrome *b* and 12S rRNA mitochondrial sequences. Molecular Biology and Evolution 14: 550–559.

Morgan, G. 2008. Vertebrate fauna and geochronology of the Great American Biotic Interchange in North America. *In* S. Lucas, G. Morgan, J. Spielmann, and D. Prothero (editors), Neogene mammals. New Mexico Museum of Natural History and Science Bulletin: 93–140.

Mothé, D., and L. Avilla. 2015. Mythbusting evolutionary issues on South American Gomphotheriidae (Mammalia: Proboscidea). Quaternary Science Reviews 110: 23–35.

O´Dea, A., et al. 2016. Formation of the Isthmus of Panama. Science Advances 2 (8): 1-1. Published by the American Association for the Advancement of Science. [doi: http://dx.doi.org/10.1126/sciadv.1600883]

Palmer, T.S. 1897. Notes on the nomenclature of four genera of tropical American mammals. Proceedings of the Biological Society of Washington 11: 173–174.

Parada, A., U.F. Pardiñas, J. Salazar-Bravo, G. D’Elía, and R.E. Palma. 2013. Dating an impressive Neotropical radiation: molecular time estimates for the Sigmodontinae (Rodentia) provide insights into its historical biogeography. Molecular Phylogenetics and Evolution 66: 960–968.

Parisi Dutra. R. 2016. Filogenia, sistemática, taxonomía e biogeografía da familia Tayassuidae (Mammalia, Artiodactyla). Ph.D. dissertation, Pós-graduacão Zoología, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Brazil.

Parisi Dutra, R., et al. 2017. Phylogenetic systematics of peccaries (Tayassuidae: Artiodactyla) and a classification of South American tayassuids. Journal of Mammalian Evolution 24: 345–358.

Pascual, R., E.J. Ortega Hinojosa, D. Gondar, and E.P. Tonni. 1965. Las edades del Cenozoico mamalífero de Argentina con especial atención a aquellas del territorio bonaerense. Anales de la Comisión de Investigación Científica de la provincia de Buenos Aires 6: 165–193.

Poux, C., P. Chevret, D. Huchon, W.W. De Jong, and E.J. Douzery. 2006. Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. Systematic Biology 55: 228–244.

Prevosti, F.J., and U.J.F. Pardiñas. 2009. Comment on “The oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora): late Miocene faunal turnover in central Argentina and the Great American Biotic Interchange” by D.H. Verzi and C.I. Montalvo [Palaeogeography, Palaeoclimatology, Palaeoecology 267 (2008): 284–291]. Palaeogeography, Palaeoclimatology, Palaeoecology 280: 543–554.

Prevosti, F., and L.H. Soibelzon. 2012. Evolution of the South American carnivores (Mammalia, Carnivora): a paleontological perspective. *In* B.D. Patterson and L.P. Costa (editors), Bones, clones, and biomes: the history and geography of Recent Neotropical mammals: 120–122. Chicago: University of Chicago Press.

Prevosti, F.J., A.M. Forasiepi, and N. Zimicz. 2013. The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? Journal of Mammalian Evolution 20: 3–21.

Prothero, D.R., and J. Grenader. 2012. A new primitive species of the flat-headed peccary *Platygonus* (Tayassuidae, Artiodactyla, Mammalia) from the Late Miocene of the High Plains. Journal of Paleontology 86: 1021–1031

Prothero, D.R., and M.R. Liter. 2008. Systematics of the dromomerycines and aletomerycines (Artiodactyla: Palaeomerycidae) from the Miocene and Pliocene of North America. New Mexico Museum of Natural History and Science Bulletin 44: 273–298.

Prothero, D.R., K.E. Campbell, B.L. Beatty, and C.D. Frailey. 2014. New late Miocene dromomerycine artiodactyl from the Amazon Basin: implications for interchange dynamics. Journal of Paleontology 88: 423–443.

Reguero, M.A., and A.M. Candela. 2011. Late Cenozoic mammals from the northwest of Argentina. *In* J.A. Salfity and R.A. Marquillas (editors), Cenozoic geology of the central Andes of Argentina: 411–426. Salta, Argentina: SCS Publisher.

Reyna-Hurtado, R., E. Rojas-Flores, and G.W. Tanner. 2009. Home range and habitat preferences of white-lipped peccaries (*Tayassu pecari*) in Calakmul, Campeche, Mexico. Journal of Mammalogy 90: 1199–1209.

Rincon, A.F., J.I. Bloch, B.J. MacFadden, and C.A. Jaramillo. 2015. New early Miocene protoceratids (Mammalia, Artiodactyla) from Panama. Journal of Vertebrate Paleontology 35: e970688.

Sánchez, I.M., J.L. Cantalapiedra, M. Rios, V. Quiralte, and J. Morales. 2015. Systematics and evolution of the Miocene three-horned palaeomerycid ruminants (Mammalia, Cetartiodactyla). PLoS One 10: e0143034.

Scopoli, G.A. 1777. Introductio ad historiam naturalem sistens genera lapidum, plantarum et animalium hactenus detecta, characteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. Prague: Gerie, 506 pp.

Severinghau, C.W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13: 195–216.

Sicuro, F.L., L.F. Neves, and L.F.B. Oliveira. 2011. Sex-and age-related morphofunctional differences in skulls of *Tayassu pecari* and *Pecari tajacu* (Artiodactyla: Tayassuidae). Journal of Mammalogy 92: 828–839.

Simpson, G.G. 1950. History of the fauna of Latin America. American Scientist 38: 261–389.

Simpson, G.G. 1953. The major features of evolution. New York: Columbia University Press.

Simpson, G.G. 1980. Splendid isolation: the curious history of South American mammals. New Haven: Yale University Press, 266 pp.

Simpson, G.G., and C. de Paula-Couto. 1981. Fossil mammals from the Cenozoic of Acre, Brazil. III. Pleistocene Edentata Pilosa, Proboscidea, Sirenia, Perissodactyla and Artiodactyla. Iheringia, Série Geológica 6: 11–73.

Soibelzon, L.H., A. Rinderknecht, J. Tarquini, and R. Ugalde 2019. First record of fossil procyonid (Mammalia, Carnivora) from Uruguay. Journal of South American Earth Sciences: 92: 368–373.

Solounias, N. 2007. Family Giraffidae. *In* D.R. Prothero and S.E. Foss (editors), The evolution of Artiodactyls: 257–277. Baltimore: Johns Hopkins University Press.

Tate, G.H.H. 1932. Distribution of the South American shrews. Journal of Mammalogy 13: 223–228.

Verzi, D.H., and C.I. Montalvo. 2008. The oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora): Late Miocene faunal turnover in central Argentina and the Great American Biotic interchange. Palaeogeography, Palaeoclimatology, Palaeoecology 267: 84–291.

Walton, A.H. 1997. Rodents. *In* R.F. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn (editors), Vertebrate paleontology in the Neotropics – the Miocene fauna of La Venta, Colombia: 392–409. Washington: Smithsonian Institution Press.

Webb, S.D. 1976. Mammalian faunal dynamics and the Great American Interchange. Paleobiology 2: 220–234.

Webb, S.D. 1991. Ecogeography and the Great American Interchange. Paleobiology 17: 266–280.

Webb, S.D. 1998. Hornless ruminants. *In* C.M. Janis, K.M. Scott, and L.L. Jacobs (editors), Evolution of Tertiary Mammals of North America: 463–476. Cambridge: Cambridge University Press.

Willard, B. 1962. Paleoenvironment of fossil vertebrates from the Bassler Peruvian collection. Proceedings of the Pennsylvania Academy of Science 36: 255–259.

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

Woodburne, M.O. 2010. The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. Journal of Mammalian Evolution 17: 245–264.

Woodburne, M.O., A.L. Cione, and E.P. Tonni. 2006. Central American provincialism and the Great American Biotic Interchange. *In* O. Carranza-CastaZeda and E.H. Lindsay (editors), Advances in late Tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange, 4: 73–101. Mexico City: Universidad Nacional Autónoma de México, Insitituto Geología and Centro de Geosciencias.

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