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ABSTRACT

The Honda Group of La Venta, Colombia, has yielded a wide array of crown platyrrhine primates, documenting the late Middle Miocene epoch (ca. 13.1–12.6 Ma, Laventan South American Land Mammal Age). Although exceptional, this record represents only a snapshot of the evolutionary history of New World monkeys because virtually none of the primate taxa recorded at La Venta had so far been found elsewhere. We describe here few dental remains of a cebine platyrrhine discovered from Laventan deposits in the San Martín Department of Peru (Peruvian Amazonia). The primate dental specimens from that new fossil-bearing locality (TAR-31) are strongly reminiscent morphologically of the teeth of *Neosaimiri fieldsi* from La Venta. However, given that several aspects of the dental variability from TAR-31 are unknown, we prefer to provide an assignment with open nomenclature (i.e., *Neosaimiri* cf. *fieldsi*), instead of formally referring these remains to *N. fieldsi*, pending the discovery of additional specimens. The occurrence of *Neosaimiri* in Peru, in coeval deposits of La Venta, thus represents a second and southernmost record of that low-latitude genus in the Neotropics, thereby demonstrating its wide distribution along the northwestern edge of the Pebas Mega-Wetland System, in tropical western South America.

Keywords: Primates; Tropical South America; Peru; Neogene; Laventan; Paleobiogeography.

1. Introduction

The fossil record of primates from tropical South America is primarily documented by the famous late Middle Miocene outcrops of La Venta (Honda Group) in Colombia, which have yielded a wide array of crown platyrrhines (e.g., Stirton and Savage, 1950; Stirton, 1951; Setoguchi, 1985; Setoguchi and Rosenberger, 1985, 1987; Luchterhand et al., 1986; Kay et al., 1987; Rosenberger et al., 1991; Kay, 1994; Takai, 1994; Fleagle et al., 1997; Kay and Meldrum, 1997; Meldrum and Kay, 1997; Takai et al., 2001; for recent summaries, see Rosenberger and Hartwig, 2013; Kay, 2015). Apart from this exceptional past diversity, fossil primates from low latitudes of South America are rare and limited, notably in Amazonia s.l.[1] (Kay and Frailey, 1993; Kay and Cozzuol, 2006; Marivaux et al., 2012, 2016a, b; Bond et al., 2015; Kay et al., 2019), although this vast land shelters today the most diversified platyrrhine communities of the Americas (e.g., Garber et al., 2009). Because archetypical traits of a modern tropical rainforest seem to have been present in this region of South America for most parts of the Cenozoic (Jaramillo et al., 2010, 2017), an equally large fossil primate diversity is expected to have existed there. However, due to extensive recent alluvial deposition, dense vegetation cover and harsh field conditions, scientists have long been reluctant to explore Amazonia s.l. from a paleobiological perspective. Recent field efforts in Peruvian Amazonia have proven that the Andean foothills had great paleontological potential for highlighting the evolutionary history of New World monkeys. Although very fragmentary, the paleontological evidence recently gathered in this area of Western Amazonia has shed new light on the origin, emergence, and subsequent evolution of platyrrhines (Marivaux et al., 2012, 2016a, b; Bond et al., 2015; Kay et al., 2019; Seiffert et al., 2020).

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[1] Amazonia sensu latissimo (s.l.) includes the Amazonian Basin (the immense watershed of the Amazon River and its tributaries) and the Guiana Shield plus the subregions such as the Planalto, Gurupí and the low eastern part of Andes (see Eva and Hubert, 2005).

1.1. *A new primate-bearing locality from Peruvian Amazonia*

In the framework of an ongoing paleontological program in the Cenozoic of Peruvian Amazonia, following our works in the Atalaya region (Madre de Dios Department; e.g., Marivaux et al., 2012; Antoine et al., 2013), the Fitzcarrald arch area (Ucayali Department, e.g., Antoine et al., 2007; Tejada-Lara et al., 2015) and in Contamana (Loreto Department; e.g., Antoine et al., 2016, 2017), we have recently enlarged our survey area and started new paleontological investigations in the San Martín Department of Peru (Fig. 1A). In this region, close to the western Amazonian/Sub-Andean transition, southeast of the Tarapoto city (TAR), a recent road cut of several kilometers (Shapaja road; Fig. 1B) offers a unique access to a well-exposed Cenozoic stratigraphic section documenting the Eocene–Miocene interval (e.g., Hermoza et al., 2005; Roddaz et al., 2010; Klaus et al., 2017; Boivin et al., 2018). Miocene fluvial deposits are accessible in the Juan Guerra area, notably along the Río Mayo (Fig. 1B). These outcrops have been assigned to the lower member of the Ipururo Formation (Sánchez-Fernández et al., 1997; Hermoza et al., 2005). Our survey of these deposits has resulted in the discovery of a 10–15 cm thick fossil-bearing microconglomerate (TAR-31; Figs. 1B and 2A). The sediment of this layer has yielded a diverse assemblage of aquatic and terrestrial vertebrates, including fishes, anurans, turtles, crocodiles, a small passerine bird, and mammals such as marsupials, hoofed mammals, xenarthrans, a sirenian, bats, rodents, and a primate. In this paper, we describe the few recovered primate dental specimens. Although meager, the primate material documents a small-bodied cebine cebid assigned to *Neosaimiri*. This monotypic genus is well documented in late Middle Miocene deposits of La Venta, Colombia (Laventan South American Land Mammal Age [SALMA]; Fig. 1A), by the species *Neosaimiri fieldsi* Stirton, 1951 (see also Takai, 1994). Here we describe and compare these new dental remains from Peruvian Amazonia, and discuss the paleobiogeographic implications of that discovery.

1.2. *Stratigraphic and biochronological context*

The 10–15 cm-thick lens which yielded the TAR-31 assemblage consists of a yellowish microconglomerate interbedded within a gray cross-stratified and sandstone-dominated fluvial unit (Fig. 2A). The latter is intercalated between thick violet-gray variegated paleosols pointing to the existence of a meandering river with sustainable floodplain. This unit can be assigned unambiguously to the lower member of the Ipururo Formation, Middle Miocene in age in the Huallaga basin (Hermoza et al., 2005; Feussom Tcheumeleu et al., 2019). Among the mammal remains (Fig. 2B), we have preliminarily identified an argyrolagid marsupial, the didelphid marsupial *Marmosa* (*Micoureus*) sp., the interatheriine notoungulate *Miocochilius* sp., the didolodontid *Megadolodus* sp., as well as a cohort of rodents including among others the adelphomyine octodontoid *Ricardomys longidens* sensu Walton, 1997, an erethizontoid (cf. *Microsteiromys* sp.), and the chinchilloids *Microscleromys* sp. and "*Scleromys*" sp. (sensu Walton, 1997). This assemblage strongly recalls that of the lower part of the Villavieja Formation, including the Monkey Beds, in the La Venta area in Colombia (13.1–12.6 Ma; e.g., Kay et al., 1997; geomagnetic ages as revised in Hilgen et al., 2012) and, to a lesser extent, that of the Quebrada Honda locality in Bolivia (12.5–12.2 Ma; e.g., Croft, 2007; Brandoni et al., 2018) and the Fitzcarrald local fauna in SE Peru (Tejada-Lara et al., 2015). All these localities are Laventan in age (Serravallian; Hilgen et al., 2012). Accordingly, the new TAR-31 locality most likely documents the late Middle Miocene Laventan SALMA, a time window with no platyrrhine record in Amazonian lowlands thus far (Tejada-Lara et al., 2015; Antoine et al., 2016, 2017).

2. Materials and methods

Fossil recovery and extraction The TAR-31 fossil-bearing locality is a 10–15 cm thick lens of microconglomerate. We excavated and collected ~550 kg of sediments of this lens. When fully dry, the gross sediments were treated by wet screening (two meshes of sieves; 2 mm and 1 mm) directly in the water of the Río Mayo. The coarse residues of screening (≥ 2 mm) were carefully scrutinized by naked eyes in situ (on the riverbank), in order to collect the medium-sized fossil elements. The fine residues (1 mm ≤ fossils < 2 mm) were generally screen/washed twice, dried, and observed under stereomicroscopes in our laboratory camp. The fossil material consists primarily of bone fragments and tens of isolated teeth, among which the few specimens of primates reported here.

Fossil repository The fossil specimens are permanently housed in the collections of the Vertebrate Paleontology Department of the Museo de Historia Natural – Universidad Nacional Mayor San Marcos in Lima, Peru.

Dental loci, nomenclature and measurements The terminology for primate dentition follows Marivaux (2006) and the literature cited therein. Teeth were measured (maximum mesiodistal length and maximum buccolingual width) with a microscope fitted with a calibrated reticle (Measuroscope Nikon 10).

High-resolution µCT scan We used X-ray microtomography (µCT scan) for obtaining three-dimentional digital models (3D rendering) of the fossils (Figs. 3–5). Each specimen was scanned with a resolution of 6 µm using a µCT-scanning station EasyTom 150 / Rx Solutions (Montpellier RIO Imaging, ISE-M, Montpellier, France). The crown and roots of each tooth have been virtually delimited by manual segmentation under AVIZO 7.1 software (Visualization Sciences Group). The teeth were prepared within a 'Label Field' module of

AVIZO, using the segmentation threshold selection tool. The renders of the 3D digital models of the teeth of *N.* cf. *fieldsi* described in this paper are available on "MorphoMuseum" (Marivaux et al., 2020), an online open access platform that aims at enhancing accessibility to 3D models (http://morphomuseum.com).

Optical photography The pictures of *Neosaimiri fieldsi* teeth from La Venta (Fig. 5) are photographs of casts (originals published by Takai, 1994), whitened using magnesium smoke. These views are the result of the fusion of multifocus images obtained with an optical stereomicroscope (Leica M 205C) connected to a camera (Leica DFC 420C).

Abbreviations IGM-KU = IGEOMINAS-Kyoto University; MUSM = Museo de Historia Natural – Universidad Nacional Mayor San Marcos; SALMA, South American Land Mammal Ages; † = extinct taxa.

3. Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Primates Linnaeus, 1758

Suborder Anthropoidea Mivart, 1864

Infraorder Platyrrhini Geoffroy Saint-Hilaire, 1812

Family Cebidae Bonaparte, 1831

Subfamily Cebinae Bonaparte, 1831

Included genera *Cebus* Erxleben, 1777; *Sapajus* Kerr, 1792; *Saimiri* Voigt, 1831; *Neosaimiri*†[2] Stirton, 1951; *Chilecebus*†[3] Flynn et al., 1995; *Acrecebus*† Kay and Cozzuol, 2006; *Panamacebus*† Bloch et al., 2016.

Neosaimiri Stirton, 1951

Neosaimiri cf. *fieldsi*

Studied material MUSM-3888, right M_3 (Fig. 3A–H); MUSM-3890, left dP_2 (Fig. 3I–M); MUSM-3891, lingual part of a fragmentary right M^1 or M^2 (Fig. 4B–E); MUSM-3892, distobuccal part of a fragmentary right upper molar (metacone region; Fig. 4F, G); MUSM-3893, buccal part of a fragmentary right P^3 or P^4 (Fig. 4H–L); MUSM-3894, lingual part of a fragmentary left P^3 or P^4 (Fig. 4M–Q); MUSM-3895, right dC^1 (Fig. 4R–V).

Locality Tarapoto/Juan Guerra locus n°31 (TAR-31), Río Mayo, Shapaja road, San Martín Department, Western Amazonia, Peru (Fig. 1).

Formation and age Ipururo Formation, lower member (Sánchez Hernández et al., 1997; Hermoza et al., 2005), late Middle Miocene (i.e., Laventan SALMA), based on biochronological data.

3.1. *Description*

Only three of the seven dental specimens found and attributed to this taxon are complete and well preserved. They consist of a M_3 (Fig. 3A), a dP_2 (Fig. 3I), and a dC^1 (Fig. 4R).

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[2] *Laventiana* Rosenberger et al., 1991, is a genus considered as a junior synonym of *Neosaimiri* (see Takai, 1994; Meldrum and Kay, 1997; Kay, 2015).

[3] *Chilecebus* was originally referred to as Platyrrhini incertae sedis (Flynn et al., 1995). A recent revision of the fossil material led Kay et al. (2019) to include this taxon in the Cebinae.

Other fossil teeth are broken and the fragments document either halves or quarters of premolars (Fig. 4H, M) and molars (Fig. 4A).

MUSM-3888 (Fig. 3A–H) is identified as a M_3, with a crown oval in occlusal outline, longer than wide (Fig. 3A; Table 1), and bearing a single and massive root that results from the complete fusion of a slender mesial root with a large and robust distal root (Fig. 3E–H). Only shallow and vertical grooves, visible on the lingual and buccal aspects of this apparent single-root, testify to the fusion of the mesial and distal roots. The trigonid is slightly wider and taller than the talonid (Fig. 3A, C, D). The occlusal surface is characterized by four main cuspids (protoconid, metaconid, hypoconid, and entoconid). These cuspids are well defined, somewhat bulbous, and roughly equal in size, except the slightly smaller entoconid (Fig. 3A). The position of the cuspids describes a square, the two lingual and the two buccal cuspids being aligned mesiodistally, and the two mesial and the two distal cuspids being aligned buccolingually. The trigonid basin is oval, mesiodistally compressed (buccolingual long axis), but particularly broad, approximating half the surface area of the talonid basin (Fig. 3A). The distal margin of the trigonid basin is closed and formed by the sloping mesiolingual and mesiobuccal flanks of the bulbous protoconid and metaconid, respectively, the latter cuspids being linked together by a strong but short, straight (transverse) and moderately-elevated protocristid (Fig. 3A, B, H). The mesial margin of the trigonid basin is formed by an elevated, long and arcuate cristid, which is continuous and uniform, including the premetacristid and the preprotocristid (paracristid). The preprotocristid, strongly attached to the protoconid, extends mesiobuccally (appearing as a long and slightly oblique anterior arm of the protoconid), then it turns abruptly lingually, forming a right angle, and runs lingually to the premetacristid (Fig. 3A–D). The latter cristid is similarly strongly attached to the metaconid, extends mesially (appearing as a long anterior arm of the metaconid), then it turns sharply buccally and runs to the preprotocristid, thereby closing the trigonid basin lingually (Fig. 3A–D). There is no distinct junction between the preprotocristid and the premetacristid (Fig. 3A, B, F). The talonid basin is well delineated, deep, and its bottom is clearly lower than that of the trigonid basin. Its mesial margin appears as a steep-sided wall, formed by the distal flanks of the protoconid and metaconid, and by the straight protocristid linking these two cuspids (Fig. 3A, B, H). Its lingual and buccal margins are elevated and consist of trenchant cristids, which form well-defined walls closing the basin lingually and buccally. The lingual cristid is made by a strong and long pre-entocristid and by a postmetacristid sloping gently backwardly from the apex of the metaconid (Fig. 3A, C, D, G). These two lingual cristids are merged but their junction is undistinguishable. The buccal wall of the talonid basin is made by a trenchant and almost mesiodistally oriented cristid obliqua (marginally positioned). The latter runs from the hypoconid to reach the trigonid wall at a point distal to the protoconid tip (Fig. 3A, C–E). With such a cristid obliqua configuration, the hypoflexid is virtually inexistent. Distally, the hypocristid is strong, arcuate and links the hypoconid to the entoconid. With wear, the hypoconid and hypocristid form together a claw-like structure, the tip of which (i.e., lingual extremity of the hypocristid) is connected to the entoconid. Due to their bulbous condition, the buccal aspect of the entoconid and the lingual aspect of the hypoconid protrude within the talonid basin, thereby limiting the distal surface of the basin, as if the latter was pinched buccolingually.

MUSM-3890 is a left dP_2 (Fig. 3I–M), identified as such thanks to a comparison with homologous dental loci available for *N. fieldsi* (described and illustrated in Takai, 1994). This tooth appears single-rooted but a shallow groove visible on the lingual aspect of this buccolingually compressed root (suboval in cross section, with a mesiodistal long axis; Table 1), suggests the presence of both a mesial and a distal roots, strongly merged. The occlusal crown outline of this tooth is triangular, being dominated by a tall and pyramidal protoconid. In lingual (Fig. 3K) and buccal (Fig. 3M) views, the protoconid apex looks like the sharp tip of a dagger, due to the presence of sloping and trenchant paracristid and protocristid. In occlusal view (Fig. 3I), these two cristids form a nearly flat angle. From the protoconid, the paracristid runs mesially to reach the mesial margin of the tooth. There is no well-defined paraconid in its mesial extremity. In occlusal view, the protocristid is short and slightly arcuate, running distally to reach a minute but conspicuous metaconid, well-separated from the protoconid. This small metaconid is well inferior to the protoconid tip and situated only slightly more lingually to it. There is no talonid development, and the distal sloping flank of the metaconid thus forms the distal margin of the crown. The tooth bears a crowning cingulid at cervix, which is particularly well marked lingually (Fig. 3K), whereas it is more discreet buccally (Fig. 3J, L, M). In mesial (Fig. 3J) and distal (Fig. 3L) views, the buccal cingulid extends inferiorly beyond the inferior margin of the lingual side of the tooth, thereby describing an exodaenodont pattern.

Among upper teeth, only MUSM-3895 is complete (Fig. 4R–V). This simple single-rooted and single-cusped tooth is identified as a right dC^1. The crown is dominated by a strong and pyramidal cusp, being buccolingually compressed (its base is longer that it is wide; Table 1). Its buccal aspect is steep-sided and marginally positioned, nearly aligned with the vertical buccal margin of the root (Fig. 4S, U). In contrast, its lingual aspect is sloping gently. At the base of the crown, there is no well-marked development of buccal and lingual cingula, but the tooth seems to be eroded, which could have strongly attenuated or erased these traits. There are only small islets of a cingulum observable at the base of the mesiolingual margin of the crown. Lingually, there is a small enamel swelling situated directly lingual to the main cusp apex. It is not well defined but could point to the presence of a tiny mesiostyle. The latter is linked to the main cusp by a smooth crest, somewhat hardly noticeable, running on the lingual slope of the cusp. The mesial and distal slopes of the main cusp are made by well-marked pre- and postcristae. The precrista is rounded and not well defined, and ends on the mesial crown margin, without noticeable style development. The postcrista, better defined and sharp, ends its course in the distal margin of the crown, where a tiny enamel swelling could correspond to a minute distostyle.

Other dental remains are documented by fragments of upper teeth. MUSM-3893 corresponds to the buccal part of a right P^3 or P^4 (Fig. 4H–L), whereas MUSM-3894 is the lingual part of a left P^3 or P^4 (Fig. 4M–Q). Despite the fragmentary nature of these specimens, their association documents the morphology of a P^3 or P^4. The latter, when complete, was likely triangular to suboval in occlusal crown outline, with a buccal margin longer than the lingual one (Table 1). The buccal part is dominated by a tall paracone displaying trenchant pre- and postparacristae, mesiodistally aligned, and sloping gently mesially and distally, respectively (Fig. 4J, L). The postparacrista is barely longer than the preparacrista, and connects to a minute but well-defined metacone distally (Fig. 4H–J). The mesial extremity of the preparacrista is faintly damaged, and does not allow the presence or absence of a parastyle to be assessed (Fig. 4H, J, K). The buccal aspect of the paracone is nearly steep sided (Fig. 4I), and bears at it base a discreet and mesiodistally limited buccal cingulum (Fig. 4H, L), which gradually fades distally before to reach the metacone (Fig. 4H, L), whereas it disappears rapidly mesially (Fig. 4K, L). The lingual aspect of the paracone is gently sloping. The distal cingulum and the preprotocrista are well marked (at least their preserved part), and buccally connected at the base of the metacone and the mesial extremity of the preparacrista, respectively. The preserved lingual part (MUSM-3894) is circular, displays a cuspate protocone (but well-inferior to the paracone) and a strong lingual cingulum (Fig. 4M). The protocone is mesially canted, and the cingulum ends directly mesiolingual to the protocone. There is no mesial cingulum. The protocone displays a well-defined but low postprotocrista, which is curved and distolingually oriented, ending on the lingual cingulum, at the place where a hypocone would normally occur.

Only two small dental fragments document parts of a right upper molar (Fig. 4A): MUSM-3891, a mesiolingual part (Fig. 4B–E), and MUSM-3892, a distobuccal part (Fig. 4F, G). The lingual fragment includes a well-defined and acute protocone, and a strong mesiolingual cingulum, likely bearing a small pericone. The distobuccal fragment documents a metacone region. This buccal cusp displays well-developed and mesiodistally aligned pre- and postmetacristae, the latter being short and connected to a minute metastyle. There is no development of hypometacrista on the lingual aspect of the metacone. The distal aspect of the metacone bear a small spur (enamel accessory ridge), which could correspond to a distal extension of a mesostyle. Given the size of the fragment preserved, we cannot evaluate if a buccal cingulum is present.

3.2. *Comparisons*

The dental material of primates assembled in TAR-31 is quite limited, but the isolated and partial teeth display morphological attributes and proportions (Table 1) that match those characterizing teeth of the cebine cebid *Neosaimiri*, so far known only by *N. fieldsi* (Table 2) from La Venta, Colombia (late Middle Miocene; Stirton, 1951; Takai, 1994). This is particularly shown in the configuration of the trigonid of the lower molar available (M_3, MUSM-3888; Figs. 3A–H and 5A), which is mesiodistally compressed but particularly broad, approximating half the surface area of the talonid basin, and also markedly taller than the latter. As on M_3 of *N. fieldsi* (e.g., IGM-KU 89090; Fig. 5B), the trigonid of the MUSM-3888 M_3 (Fig. 5A) is lingually closed by the presence of a strong, elevated and mesially elongated premetacrista. The latter generates, in association with the also long, elevated and mesiobuccally-oriented preprotocristid, an unusual broad trigonid basin, characteristic of cebids (notably cebines), especially well marked on lower molars of *Neosaimiri* (see Takai, 1994: Figs. 4–6). As on the M_3 of *N. fieldsi* (e.g., IGM-KU 89090; Fig. 5B) and M_3 of cebids in general (cebines and aotines), MUSM-3888 has no buccal cingulid, but a cristid obliqua that is long, trenchant, mesially oriented and marginally sided, a configuration which makes the hypoflexid inexistent. MUSM-3888 differs from documented M_3 of *N. fieldsi*, notably in having its main cuspids appearing slightly more bulbous (but this can be moderated due to wear on MUSM-3888; Figs. 3A–D and 5A), the entoconid occupying a more distal position and being lingually opposed to the hypoconid rather than being mesially displaced with respect to the hypoconid, as it does in *N. fieldsi* (e.g., IGM-KU 89090; Fig. 5B). In addition, the protoconid and metaconid on MUSM-3888 appear buccolingually closer than on M_3 of *N. fieldsi* (Fig. 5B), and the protocristid seems shorter in the former as a result. Regarding the dP_2, in addition to a small difference in size (Tables 1 and 2), some distinctive morphological details can also be noted between MUSM-3890 (Figs. 3I–M and 5C, E) and the known dP_2 of *N. fieldsi* (see Takai, 1994). The structural complexity of this dental locus is limited, but one of the main noticeable differences relies in the structure of the distal part of the tooth, in particular the development of a tiny hypoconid and a stronger cristid obliqua on known dP_2 of *N. fieldsi* (e.g., IGM-KU 89125; Fig. 5D), dental traits which are only faintly marked on MUSM-3890 (Fig. 5C). The lingual cingulid on MUSM-3890 may also appear somewhat better developed, notably distolingually (Fig. 5E) than on dP_2 of *N. fieldsi* (Fig. 5F), but this dental trait may also vary within the species. Distinctions on the upper premolars are also tenuous. The composite P^3 or P^4 (MUSM-3893 and 3894; Fig. 5G, H) is slenderer than its counterparts in *N. fieldsi* (e.g., IGM-

KU 90009; Fig. 5I), in having buccal and lingual aspects of the paracone and protocone, respectively, much steep sided and less sloping (i.e., less inflated), and in showing a triangular occlusal outline (V-shaped mesial and distal margins) rather than oval (parallel mesial and distal margins). On upper premolars referred to as *N. fieldsi* (see Takai, 1994), the crests and cingula (lingual and distal) are also better marked than on MUSM-3893 and 3894. The hypocone, although tiny in upper premolars of *N. fieldsi* (notably on P^4; e.g., IGM-KU 90009; Fig. 5I), is still less pronounced in MUSM-3894 (Fig. 5H), appearing as a very discreet small enamel swelling situated at the union of the distal extremity of the postprotocrista with the lingual cingulum. Finally, the upper deciduous canine from TAR-31 (MUSM-3895, a right dC^1; Figs. 4R–V and 5J), although slightly smaller (Tables 1 and 2), is morphologically roughly similar to its homologous in *N. fieldsi* (e.g., IGM-KU 89136; Fig. 5K), except for its oval occlusal outline (Fig. 5J) that differs from the rounded outline of this tooth in *N. fieldsi* (i.e., more inflated). On MUSM-3895 (Figs. 3R–T and 5J), the lingual cingulum is also less developed than on known dC^1 of *N. fieldsi* (Fig. 5K). The primate dental specimens collected in TAR-31 are strongly reminiscent morphologically to the teeth of *N. fieldsi* from La Venta, Colombia (Stirton, 1951; Takai, 1994). However, given that several aspects of the dental variability from TAR-31 are unknown, we prefer to provide an assignment with open nomenclature (i.e., *Neosaimiri* cf. *fieldsi*), instead of formally referring these remains to *N. fieldsi*, pending the discovery of additional specimens.

4. Discussion and conclusions

Neosaimiri fieldsi is one of the first primates that was discovered and described from La Venta, Colombia (Stirton, 1951; Fig. 1A). In the original description, Stirton (1951) noted the close relationships between *Neosaimiri* and the living squirrel monkey, *Saimiri*, a member of the Cebinae. In being recognized as a distant relative of the modern cebines, *Neosaimiri* thus emphasized the presence of crown platyrrhines as early as the age documenting the La Venta fauna of the Honda Group (i.e., late Middle Miocene, Laventan SALMA; Madden et al., 1997). In the same publication, Stirton (1951) also completed the description of *Cebupithecia* Stirton and Savage, 1950, another primate from La Venta widely recognized as a representative of the Pitheciinae, a main subfamily of crown platyrrhines (Pitheciidae; e.g., Fleagle et al., 1997; Kay, 2015). Since then, continuing field efforts in the La Venta region (along the Upper Magdalena Valley) have yielded a wide array of stem representatives of modern (crown) Platyrrhini families and subfamilies, including members of atelids, other pitheciids (pitheciines and callicebines), and cebids (notably several callitrichines; see Rosenberger and Hartwig, 2013 and Kay, 2015 for recent summaries and references therein). Over the last decades, the numerous fossil-bearing localities of the Honda Group of La Venta have thus documented a remarkable past diversity of modern Platyrrhini at low latitudes in the Neotropics. Such an exceptional record, however, is unique, and represents only a snapshot of the evolutionary history of New World monkeys. Although the primate fossil record has continued to improve (slowly but considerably) in South America (e.g., Fleagle and Bown, 1983; Fleagle et al., 1987; Fleagle, 1990; Flynn et al., 1995; Kay et al., 1998, 2008, 2019; Takai et al., 2000; Tejedor et al., 2005, 2006; Kay and Cozzuol, 2006; Kay, 2010; Kramarz et al., 2012; Marivaux et al., 2012, 2016a, b; Perry et al., 2014; Bond et al., 2015; Novo and Fleagle, 2015; Antoine et al., 2016; Bloch et al., 2016; Novo et al., 2018; Seiffert et al., 2020), virtually none of the species and genera recorded at La Venta had so far been found elsewhere. Only one lower molar recovered in much more recent levels (Huayquerian SALMA) in Acre, Brazil, was tentatively assigned to the alouattine *Stirtonia* known in La Venta (Kay and Frailey, 1993). This reflects the substantial incompleteness of the primate fossil record in South and Central America, rather than a provincialism effect, and shows how severely undersampled paleontologically the tropics are, especially Amazonia s.l., which harbors today's most diversified platyrrhine communities (e.g., Garber et al., 2009). The discovery of *Neosaimiri* in Peruvian Amazonia (TAR-31), in deposits coeval to those of La Venta (based on biochronological evidence), represents therefore a second record of that genus ca. 1100 km south of La Venta, thereby demonstrating a wider distribution of this taxon at that time (late Middle Miocene). The same is true for the caviomorph rodent cohort, since many of the La Venta genera (Walton, 1990, 1997) are also found in TAR-31 (*Ricardomys*, *Microsteiromys*, *Microscleromys*, and "*Scleromys*"; see Section 1.2; work in preparation). Tectonic and geomorphological studies indicate that the eastern Cordillera of Northern Andes, which separates today the Amazon from the Orinoco basin (and their respective tributaries Río Huallaga in Peru and Magdalena River in Colombia), had not yet uplifted sufficiently to produce a barrier to land vertebrate dispersals (e.g., Lundberg et al., 1986; Hoorn et al., 1995; Kay, 2015; Anderson et al., 2016; Jaramillo et al., 2017). The strong faunal similarities between the Fitzcarrald local fauna, TAR-31 and La Venta thus corroborate such a geological observation. The wide distribution of *Neosaimiri* and associated taxa also suggests that the Pebas Mega-Wetland System (PMWS; e.g., Hoorn et al., 2010), located at low latitudes of western South America during the late Middle Miocene (Fig. 6), was not a limiting factor for mammalian dispersals, notably due to the so-called Western Corridor, close to the Andes (Croft, 2007; Tejada-Lara et al., 2015; Marivaux et al., 2016b; Antoine et al., 2017). In contrast, as already advocated, the PMWS was also likely a source of speciation and diversification, via a complex patchwork of submerged/emerged lands varying through time (e.g., Boonstra et al., 2015; Marivaux et al., 2016b; Antoine et al., 2017; Meseguer et al., in press). The absence of monkeys in coeval deposits of Quebrada Honda (ca. 22°S; Fig. 6) appears to be primarily related to paleoenvironmental constraints, as the concerned area was then at a much lower elevation than today (<1000 m vs. 3200 m a.s.l.; Cadena et al., 2015) and as such likely to host primates.

In the Tarapoto/Juan Guerra locus n°31 (TAR-31) of Peruvian Amazonia, we have so far recorded only one primate (*Neosaimiri* cf. *fieldsi*), while about ten penecontemporaneous taxa are recorded in coeval deposits of Colombia (La Venta), further documenting the three main families of modern platyrrhines. We should expect a comparable diversity of primates in TAR-31, especially since the caviomorph rodent diversity of TAR-31 is similar or even higher than that of La Venta (work in preparation). Such contrast in the primate record between both fossil-bearing areas may be primarily due to the outcrop access: the TAR-31 locality is a single and finite two-meter wide fossil-bearing lens that was sampled for a short period of time (less than one month in 2016 and 2018), whereas La Venta includes numerous spots sampled during decades over a wider region. These new fossils of primates from TAR-31 are, however, of fundamental importance to further our understanding of the Middle Miocene historical paleogeography of platyrrhines in tropical South America. Paleontological field efforts and researches must then be sustained in this region of Amazonia.

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Figure captions

Figure 1. Geographic location of the Tarapoto area, in Peruvian Amazonia (San Martín Department [SM]; A) and of the Tarapoto/Juan Guerra vertebrate fossil-bearing locus n°31 (TAR-31; B). The TAR-31 locality is exposed on the left bank of the Río Mayo during the climax of the dry season (photograph by L.M.).

Figure 2. Stratigraphic section and biochronological chart of the Tarapoto/Juan Guerra vertebrate fossil-bearing locus n°31 (TAR-31). A) Late Eocene–late Middle Miocene stratigraphic section along the Shapaja–Juan Guerra roadside (see Fig. 1), and detailed 60 m-thick section of the primate-yielding TAR-31 locality. See Boivin et al. (2018) and Assémat et al. (2019) for the age of TAR-21 and TAR-01 localities. B) Biochronological chart for TAR-31 locality, based on mammalian taxa of interest, as recorded at La Venta, Colombia (black) and at Quebrada Honda, Bolivia (red). Radioisotopic, biostratigraphic and geomagnetic ages from Kay et al. (1997), Hilgen et al. (2012), Antoine et al. (2013), and Brandoni et al. (2018). Preferred age hypothesis (light gray, ~13.1–12.6 Ma) based on the concurrent range.

Figure 3. Lower teeth of *Neosaimiri* cf. *fieldsi* from the late Middle Miocene (Laventan SALMA) of Tarapoto/Juan Guerra locus n°31 (TAR-31), Peruvian Amazonia. A–H) MUSM-3888, right M_3 in occlusal (A), mesial (B, F), lingual (C, G), buccal (D, E) and distal (H) views. I–M) MUSM-3890, left dP_2 in occlusal (I), mesial (J), lingual (K), distal (L) and buccal (M) views. B–D) the tooth is slightly inclined with respect to the occlusal plane to appreciate the relief of the structures in a mesio-occlusal, linguo-occlusal and bucco-occlusal perspective. Images are

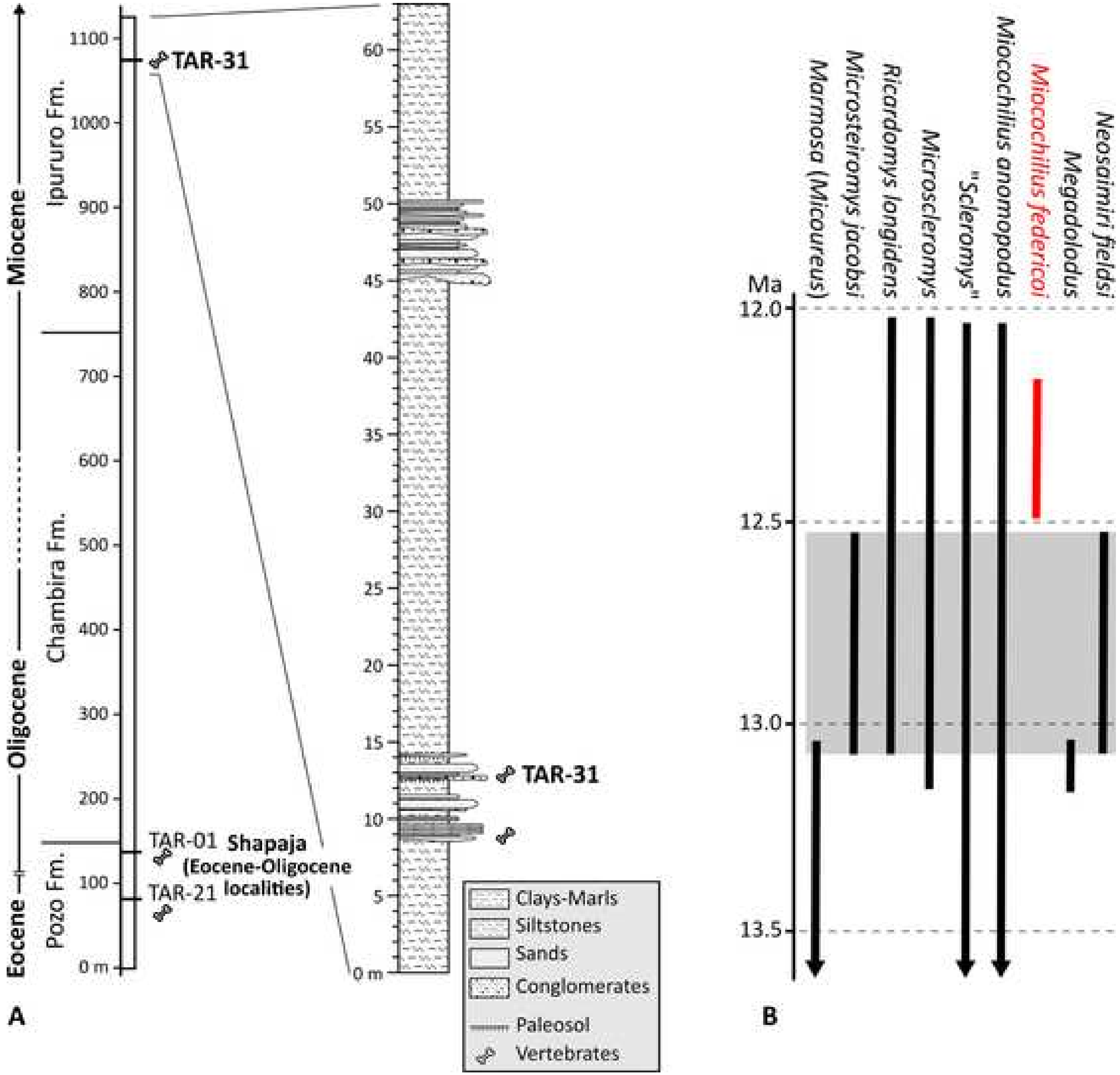
renders of 3D digital models of the fossil specimens, obtained by X-ray µCT surface reconstruction. Scale bar = 1 mm.

Figure 4. Upper teeth of *Neosaimiri* cf. *fieldsi* from the late Middle Miocene (Laventan SALMA) of Tarapoto/Juan Guerra locus n°31 (TAR-31), Peruvian Amazonia. A) dashed line drawing of a right M^2 of *Neosaimiri fieldsi* (from La Venta, specimen IGM-KU 89018; Takai, 1994), on which we have superimposed MUSM-3891 and MUSM-3892. B–E) MUSM-3891, lingual part (protocone region) of a fragmentary right M^1 or M^2 in occlusal (B), lingual (C), mesial (D) and distal (E) views. F–G) MUSM-3892, distobuccal part of a fragmentary right upper molar (metacone region) in occlusal (F) and distal (G) views. H–L) MUSM-3893, buccal part of a fragmentary right P^3 or P^4 in occlusal (H), distal (I), lingual (J), mesial (K) and buccal (L) views. M–Q) MUSM-3894, lingual part of a fragmentary left P^3 or P^4 in occlusal (M), distal (N), lingual (O), mesial (P) and buccal (Q) views. R–V) MUSM-3895, right dC^1, in occlusal (R), distal (S), lingual (T), mesial (U) and buccal (V) views. Images are renders of 3D digital models of the fossil specimens, obtained by X-ray µCT surface reconstruction. Scale bars = 1 mm.

Figure 5. Dental comparisons of *Neosaimiri* cf. *fieldsi* from TAR-31 (A, C, E, G, H, J) with *N. fieldsi* from La Venta, Colombia (B, D, F, I, K). A) MUSM-3888, right M_3 in occlusal view. B) IGM-KU 89090, left M_3 in occlusal view (reversed). C, E) MUSM-3890, left dP_2 in occlusal (C) and lingual (E) views. D, F) IGM-KU 89125, right dP_2 in occlusal (D) and lingual (F) views (reversed). G) MUSM-3893, buccal part of a fragmentary right P^3 or P^4 in occlusal view. H) MUSM-3894, lingual part of a fragmentary left P^3 or P^4 in occlusal view (reversed). I) IGM-KU 90009, right P^4 in occlusal view. J) MUSM-3895, right dC^1 in occlusal view. K) IGM-KU 89136, right dC^1 in occlusal view. Scale bar: 1 mm.

Figure 6. Paleogeographic map of Northern South America by late Middle Miocene times (ca. 13 Ma). Red dots denote vertebrate-yielding localities of interest. Low-elevation terra firma forests in light green. Shape and size of emerged landmasses within the Pebas Mega-Wetland System are tentative. Map (by P.-O.A.) modified from Hoorn et al. (2010), Antoine et al. (2013), Boonstra et al. (2015), and Anderson et al. (2016). Paleoecological data from Croft (2007), Cadena et al. (2015), Tejada-Lara et al. (2015), and Antoine et al. (2016, 2017).


A
PACIFIC OCEAN
Bogota
La Venta
COLOMBIA
ECUADOR
PERU
Amazon R.
Tarapoto
SM
BRAZIL
Lima
BOLIVIA
500 km
B
Tarapoto
N
2 km
TAR-31
Juan Guerra
Shapaja
Huallaga
Mayo
TAR-31


Miocene
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Eocene
Ipururo Fm.
Chambira Fm.
Pozo Fm.
1100
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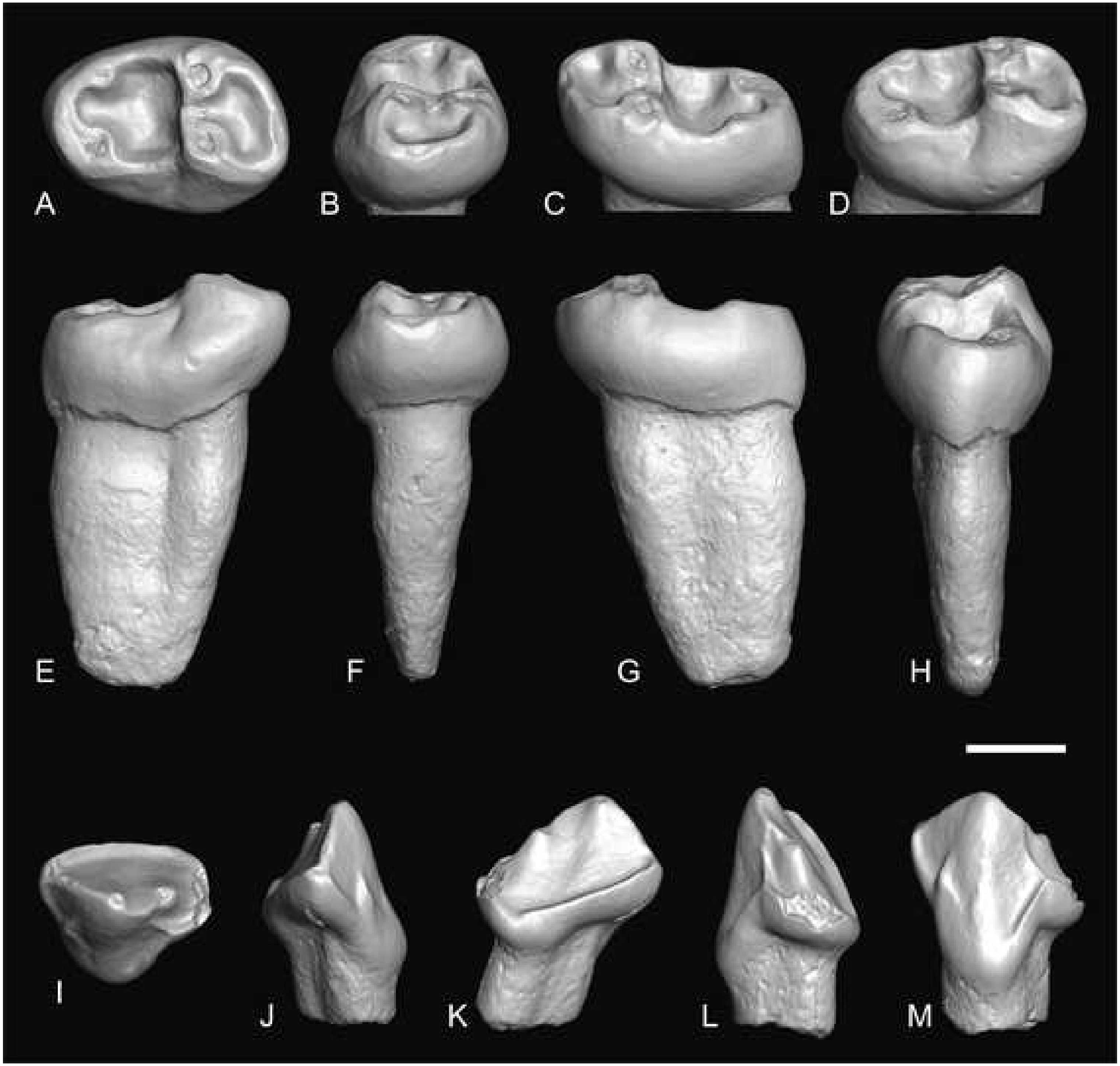
TAR-31
TAR-01
TAR-21
Shapaja
(Eocene-Oligocene
localities)
60
55
50
45
40
35
30
25
20
15
10
5
0 m
TAR-31
Clays-Marls
Siltstones
Sands
Conglomerates
Paleosol
Vertebrates
A
Ma
12.0
12.5
13.0
13.5
Marmosa (Micoureus)
Microsteiromys jacobsi
Ricardomys longidens
Microscleromys
"Scleromys"
Miocochilius anomopodus
Miocochilius federicoi
Megadolodus
Neosaimiri fieldsi
B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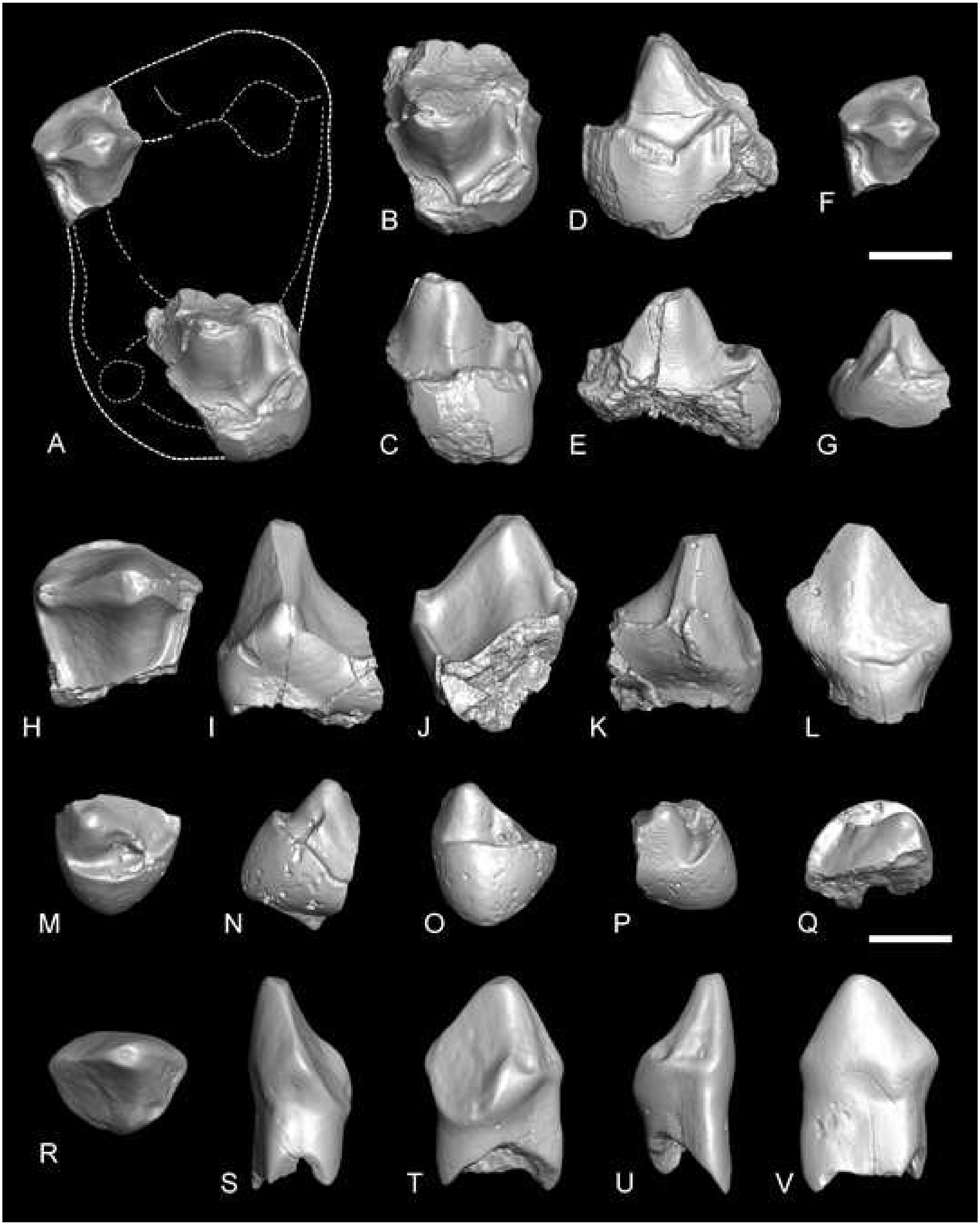
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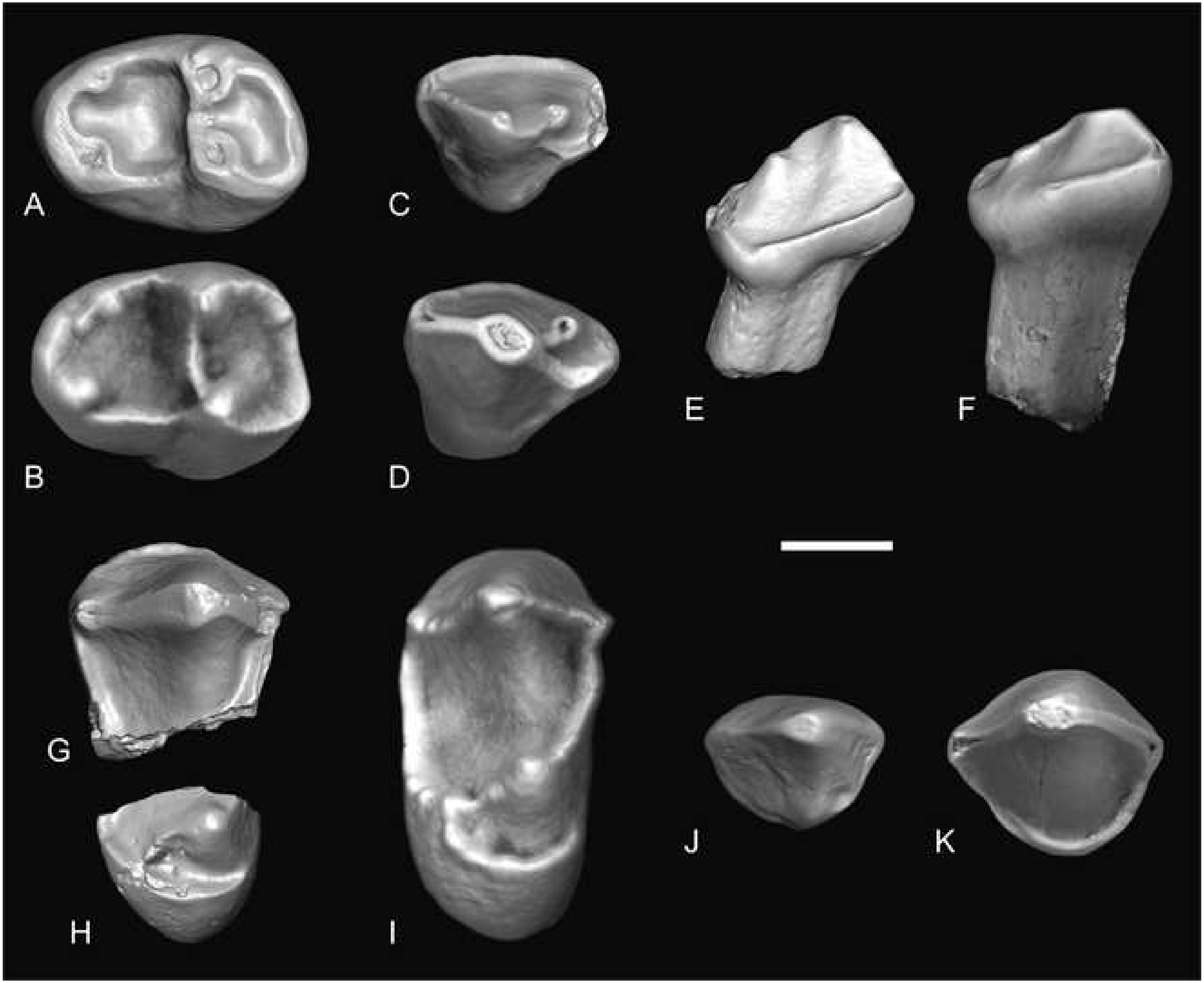
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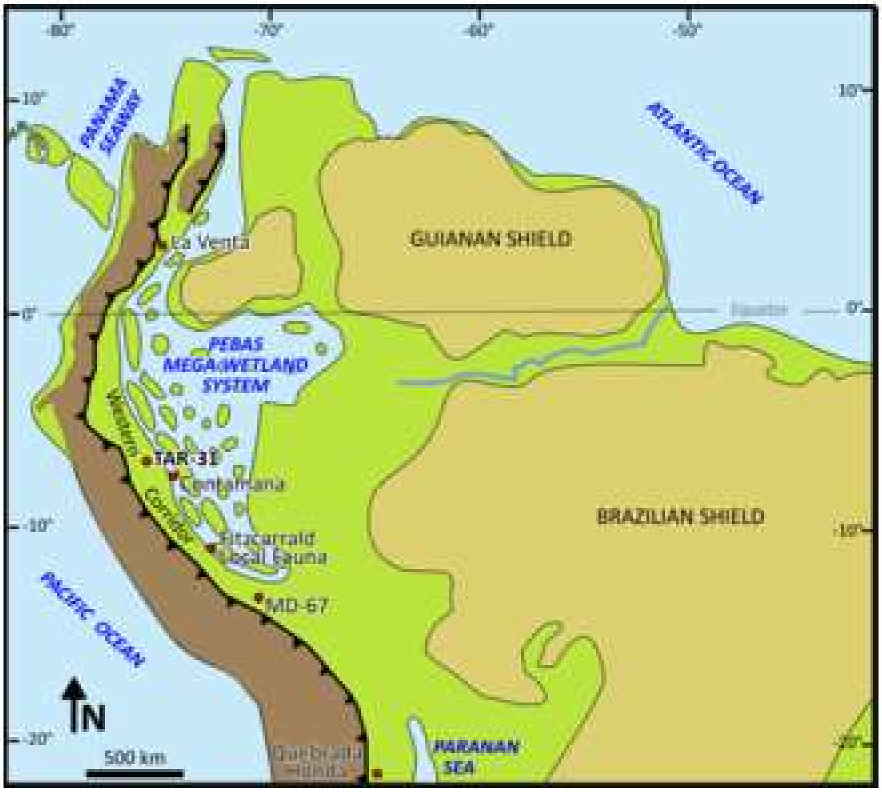
-80°
-70°
-60°
-50°
10°
0°
-10°
-20°
PANAMA SEAWAY
ATLANTIC OCEAN
La Venta
GUIANAN SHIELD
Equator
PEBAS MEGA-WETLAND SYSTEM
TAR-31
Contamana
BRAZILIAN SHIELD
Fitzcarrald Local Fauna
MD-67
PACIFIC OCEAN
N
500 km
Quebrada Honda
PARANAN SEA