



LIFE IN PROTO-AMAZONIA: MIDDLE MIOCENE MAMMALS FROM THE FITZCARRALD ARCH (PERUVIAN AMAZONIA)

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Abstract: The Middle Miocene has been identified as a time of great diversification in modern lineages now distributed in tropical South America, and when basic archetypal traits defining Amazonia appear, including climatic humid conditions, basic floral physiognomy and phylogenetic composition of modern rainforests. Nonetheless, Middle Miocene localities in South America are poorly known, especially at low latitudes where only one species-rich locality, La Venta in Colombia, has been extensively studied. The present contribution describes the mammal fauna of Fitzcarrald, a new Middle Miocene local fauna from western Amazonia in Peru. Fitzcarrald is correlated with the Laventan South American Land Mammal Age based on the presence of taxa defining the ‘*Miocochilius* assemblage zone’ in La Venta. The mammalian fauna of Fitzcarrald comprises 24 taxa among cingulates, folivores, astrapotheres, notoungulates, litopterns, rodents, odontocetes and a possible marsupial. At this time, tropical South America was characterized by the presence of the

Pebas megawetland, a huge lacustrine complex that provided unique ecological and environmental conditions most likely isolating northern South America from southern South America. These isolating conditions might have come to an end with its disappearance in the Late Miocene and the establishment of the subsequent Acre system, the predecessor fluvial system of modern Amazonia. Results of faunistic similarity between Fitzcarrald and other Miocene faunas throughout South America support these scenarios. The Fitzcarrald mammal fauna exhibits first appearance datums and last appearance datums of various taxa, showing that tropical South America has played a crucial role in the evolutionary history and biogeography of major clades, and revealing a more complex biological history than previously proposed, based on the record from the southern cone of the continent.

Key words: Middle Miocene, Fitzcarrald Arch, Pebas system, Amazonia, Laventan SALMA.

As a biodiversity hotspot, evidence suggests that western Amazonia experienced a long evolutionary history of extreme complexity in terms of tectonic activity and environmental conditions (Hoorn *et al.* 2010). Although molecular analyses date the origin of several clades of neotropical plants and animals to the Miocene, there are

few fossil remains to support these results, mainly due to the scarcity of accessible outcrops within the dense forest (Cozzuol 2006; Negri *et al.* 2010). However, vertebrate fossil remains from Peruvian Amazonia have been known since the beginning of the twentieth century, although they were mostly collected on river bank surfaces with

poor stratigraphic control (e.g. Raimondi 1898; Anthony and Richards 1924; Patterson 1942; Spillman 1949; Matthiessen 1961). In the years 2005–2007, our team explored the Ríos Inuya, Mapuya, Urubamba and Sepa (Fig. 1), focusing on geological data (tectonics, sedimentology, stratigraphy and palaeomagnetism) and palaeontological evidence (vertebrates, palaeobotany and palynology). The area covered coincides with the north-western flank of the Fitzcarrald Arch, which is an important geomorphic element located east to the central Peruvian Andes (Espurt *et al.* 2007, 2010). Due to river incision, Miocene beds crop out along the river banks. Preliminary studies of numerous vertebrate remains collected stratigraphically *in situ* in various loci led us to assume a late Middle Miocene biostratigraphical age for the fauna as a whole

(Salas-Gismondi *et al.* 2006, 2007; Antoine *et al.* 2007; Goillot *et al.* 2011; Bianucci *et al.* 2013; Pujos *et al.* 2013). This work aims to: (1) provide an up-to-date survey of this mammalian assemblage; (2) highlight the importance of tropical localities for the understanding of the evolutionary history of South American faunas; and (3) outline the biochronological, ecological and palaeogeographical significance of the Fitzcarrald fauna.

GEOLOGICAL SETTING

The Fitzcarrald Arch represents a major geomorphic feature of the Amazon foreland basin. It has been uplifting for 5 Ma due to subduction of the Nazca Ridge, and

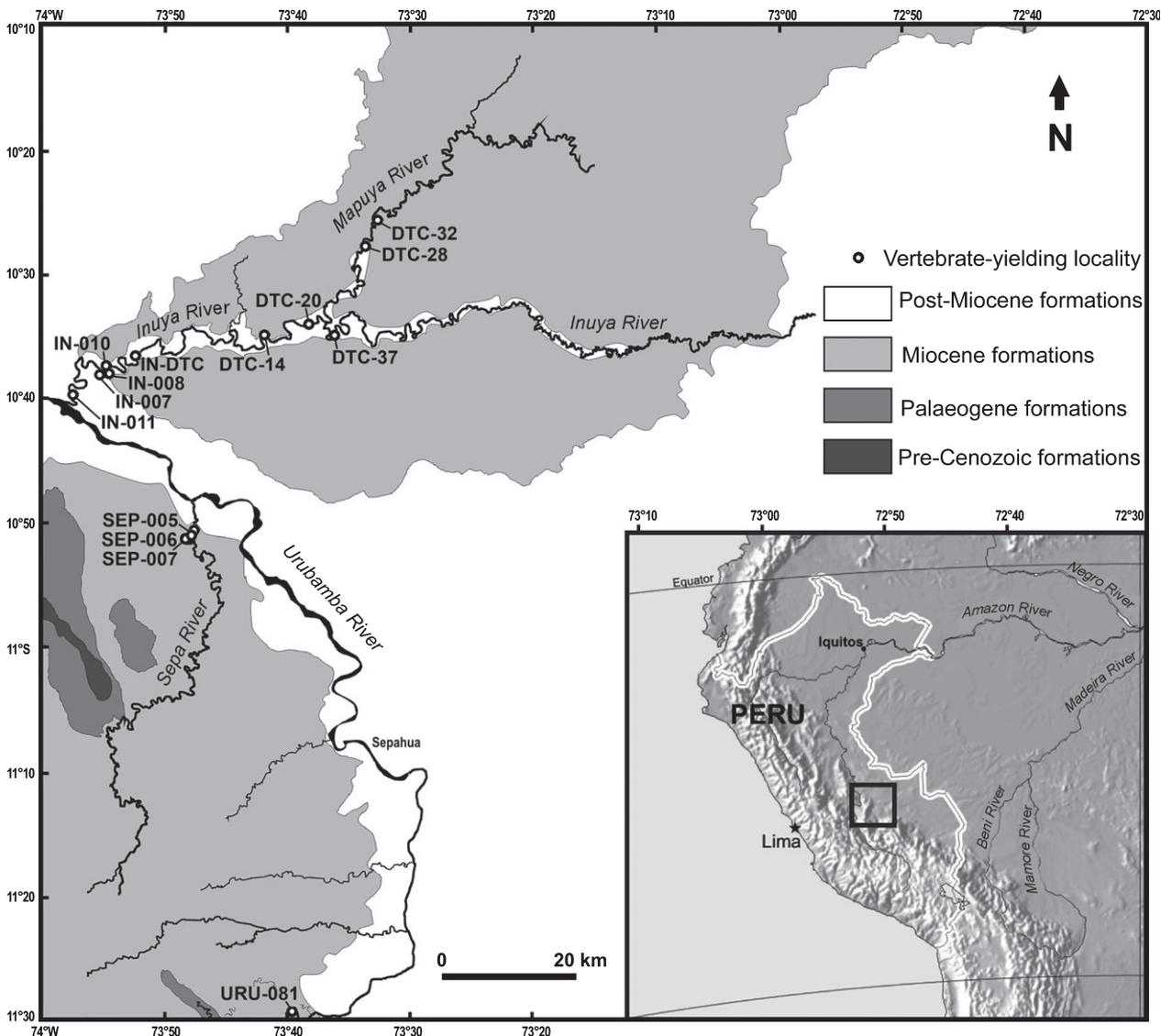


FIG. 1. Location of the main vertebrate localities discovered during the 2005–2007 field expeditions along the Inuya, Mapuya, Urubamba and Sepa rivers (Ucayali, Peru).

reveals widespread outcrops of Neogene sediments (Espurt *et al.* 2006, 2007, 2010; Regard *et al.* 2009). Recent studies of Neogene outcrops on the southern side of the arch have revealed a Miocene tide-influenced marine environment (Hovikoski *et al.* 2005, 2010), similar to the Pebas environment described farther to the north in the Iquitos area (e.g. Räsänen *et al.* 1995; Roddaz *et al.* 2005, 2010; Boonstra *et al.* 2015). The Pebas depositional system was that of a freshwater lacustrine tidal basin with occasional marine incursions, termed ‘marine-like megalake’ by Wesselingh *et al.* (2002) or ‘megawetland’ by Horn *et al.* (2010). This long-lasting lacustrine system was maintained from the late Early to the early Late Miocene (c. 17–10 Ma; Wesselingh *et al.* 2002, 2010). Our recent studies of the northern flank of the Arch have confirmed the presence of tidally influenced Miocene deposits in this area, similar to the Pebas environment, and suggest that the ‘Pebas megawetland’ extended into the northern Fitzcarrald Arch area (Espurt *et al.* 2006, 2007, 2010; Boonstra *et al.* 2015).

The Inuya–Mapuya localities are located in the less deformed part of the Fitzcarrald Arch (Fig. 1). They correspond to outcrops of Neogene Amazon foreland strata with tidal facies, attesting to the presence of Middle Miocene giant estuaries fed by Andean rivers (Fig. 2). The geometry of the conferred deposits in the Fitzcarrald Arch is well constrained by both surface geological mapping and correlations of seismic reflectors (Espurt *et al.* 2007, 2010) showing the contemporaneity of the fossiliferous strata. Vertebrate specimens associated with these strata accumulate mainly in conglomerates of sand and mud clasts incorporated in a sandy matrix, which are interpreted as storm deposits channelized in nearshore environments that likely cap transgressive erosional surfaces (Fig. 2; Baby *et al.* 2005; Espurt *et al.* 2006, 2010; Salas-Gismondi *et al.* 2006). These conglomerates are topped by tidal deposits (sandy clays) yielding a few scattered vertebrates and fossil wood. Pliocene(?) conglomerates and sandstones, containing fossil wood but no vertebrates, unconformably overlay these tidal Miocene layers. Pleistocene units correspond to terrace deposits, placed 50 m above the Río Mapuya (Regard *et al.* 2009). Farther to the south, fossil remains from the Río Sepa are found either in similar conglomeratic channels or in sandy tidal deposits (e.g. SEP-006 locality, with sub-connected *Mourasuchus* remains; Pujos *et al.* 2013).

Vertebrate localities from the Alto Urubamba are situated in the thrust-deformed zone (sub-Andean zone) of the Fitzcarrald Arch, near the Camisea anticline (Fig. 1). Although they are tentatively correlated with the Middle Miocene Inuya–Mapuya localities (Pebas equivalent), these fossil-yielding sub-Andean outcrops contain more continental facies, due to the presence of incipient reliefs from the Eastern Cordillera of the Andes. Such species-

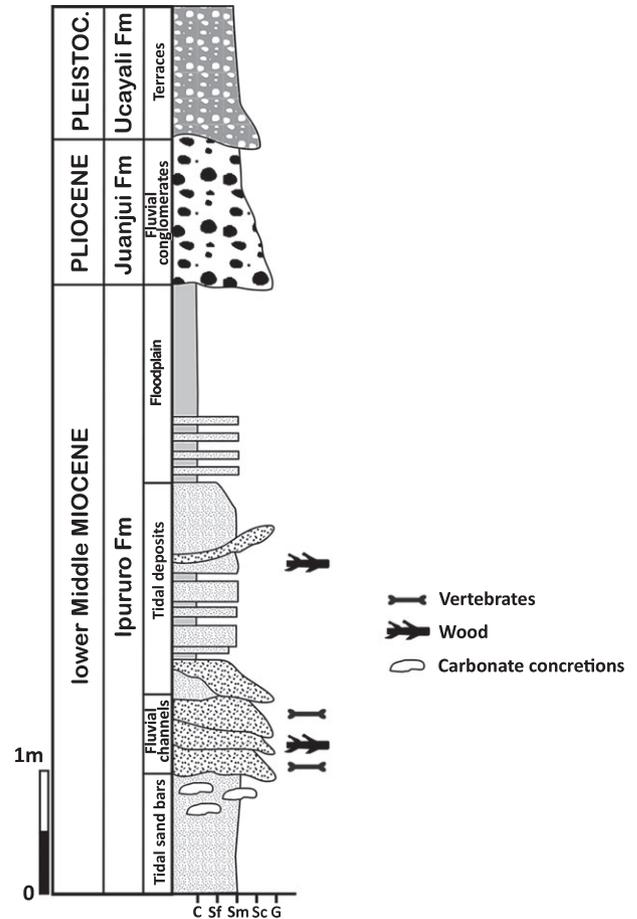


FIG. 2. Synthetic geological section for the Fitzcarrald Arch area (Rivers Inuya, Mapuya, Urubamba and Sepa; Ucayali, Peru). *Abbreviations:* C, clay; S, sand (fine, medium, coarse); G, gravel. Modified after Espurt *et al.* (2006).

poor fossiliferous outcrops mainly consist of sandy and conglomeratic fluvial channels.

MATERIAL AND METHODS

All the large-sized fossils described hereunder were found *in situ*, either while prospecting (most localities) or quarrying (DTC-20, DTC-32, DTC-37 and IN-008 localities). Small remains (rodent and intertheriine notoungulate teeth; fish spines and teeth) were collected by screen washing at DTC-32 and IN-008 localities (1 mm mesh). Unfortunately, our efforts at recovering pollen and spores from these sections were not fruitful. Only carbonized wood was collected, with no diagnostic features. Taxa already described from the Fitzcarrald area (astroptheres (Goillot *et al.* 2011) and the periotic of a platanistid cetacean (Bianucci *et al.* 2013)) will not be described again herein, but the corresponding results will be taken into account for the discussion. The megatheriid sloth

Megathericulus described by Pujos *et al.* (2013) is included in the description because new observations are mentioned.

Terminology for rodent dentition follows that proposed by Patterson and Wood (1982) and Marivaux *et al.* (2004). Luo and Marsh (1996) and Ichishima and Kimura (2000) provided the anatomical terminology for cetacean ear bones. General classification of mammals follows McKenna and Bell (1997).

Upper case letters are used for upper dentition (I, C, P, M and D) and lower case letters for lower dentition (i, c, p, m and d). All measurements are given in millimetres, except when mentioned. The specimens are stored in the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú (MUSM).

Institutional abbreviations. LACM, Los Angeles County Museum; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MLP, Museo de Ciencias Naturales, La Plata; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima, Perú; UCMP, University of California Museum of Paleontology, Berkeley; UFAC, Universidade Federal do Acre, Rio Branco.

Other abbreviations. APD, anteroposterior diameter; ant, anterior; DVH, dorsoventral height; FAD, first appearance datum; GABI, Great American Biotic Interchange; GMPTS, Global Magnetic Polarity Time Scale; H, height; L, length; LAD, last appearance datum; LLL, labiolingual length; max, maximum; MDL, mesiodistal length; post, posterior; SALMA, South American Land Mammal Age; T, thickness; TD, transverse diameter.

VERTEBRATE ASSEMBLAGE

Thirty-five Miocene vertebrate localities were identified during our 2005–2007 fieldtrips along the Ríos Inuya, Mapuya, Urubamba and Sepa, mostly in channel-shaped conglomerates. Given the stratigraphic context (autocyclic sedimentation in the Pebas tidal environment) and the taxonomic composition of the unearthed samples, all these localities are assumed to document a single and consistent vertebrate assemblage, here named ‘Fitzcarrald local fauna’ (see Discussion of Age for further details). Fourteen localities have yielded fossil mammals of which five represent major bonebeds. These localities have borne diverse assemblages with at least 30 associated vertebrate species including crocodiles, chelonians, snakes, fishes and mammals (IN-008, DTC-20, DTC-32 and DTC-37, and SEP-007; Fig. 1). Among the vertebrate remains unearthed in the Fitzcarrald area, anurans, ophidians and lacertilians are not identified.

Fish fossils consist mainly of isolated teeth, spines, ornamented scales and a few cranial and mandibular

fragments. Pending a thorough review of the ichthyofauna, preliminary identification led to the recognition of a provisional fish assemblage (Boonstra *et al.* 2015). Chondrichthyans are represented by one or two stingrays (unidentified myliobatiforms, referable to either Dasyatidae and/or Potamotrygonidae: teeth and tail stings), a myliobatid cownose ray (*Rhinoptera* sp., distinct from the extant western Atlantic *R. bonasus*: teeth), a pristid sawfish (*Pristis* sp.: oral and rostral teeth) and a large lamniform shark (vertebra, surface collected). Osteichthyans from the Fitzcarrald local fauna consist of a lepidosirenid sarcopterygian (lungfish *Lepidosiren* sp.: mandibular and maxillar fragments), a taxon of enigmatic affinities (acregoliathid *Acregoliath* Richter, 1989: large and ornate scales; Richter 1989; Lundberg *et al.* 2010), as well as characiform, siluriform and perciform actinopterygians. Characiforms are the most common fishes in the Fitzcarrald assemblage. They are represented by a few dog-like caniniform teeth similar to the extant and fossil dogtooth tetra *Hydrolycus* Müller and Troschel, 1844 (Lundberg 1997), and by a large number of isolated cuspidate teeth referable to large herbivore serrasalmids (pacus; Lundberg *et al.* 2010). The large pimelodid catfish *Phractocephalus* Bloch and Schneider, 1801, was recognized through cranial fragments (DTC-32 and URU-55 localities) and a large and ornate pectoral spine (URU-074 locality), similar to those of the extant species *P. hemiliopterus* and to the fossil species *P. nassi* Lundberg and Aguilera, 2003, from the Late Miocene of Acre, Brazil (Lundberg 1997; Lundberg and Aguilera 2003). Small spines collected by screen washing are strongly reminiscent of those of sciaenid perciform(s) as detailed by Monsch (1998).

SYSTEMATIC PALAEOLOGY

MAMMALIA Linnaeus, 1758
 MARSUPIALIA Illiger, 1811
 SPARASSODONTA Ameghino, 1894
 BORHYAENOIDEA Ameghino, 1894
 Gen. et sp. indet.

Figure 3

Referred material. MUSM 1649, upper left caniniform tooth, locality DTC-32.

Description and remarks. This caniniform tooth, excavated *in situ* at locality DTC-32, is much eroded. The tip of the crown is broken (anteroposterior length = 11.22 mm; mediolateral width = 8.9 mm; Fig. 3), but the presence of a sharp tip can be assumed. No enamel is preserved. A putative neck is visible, approximately

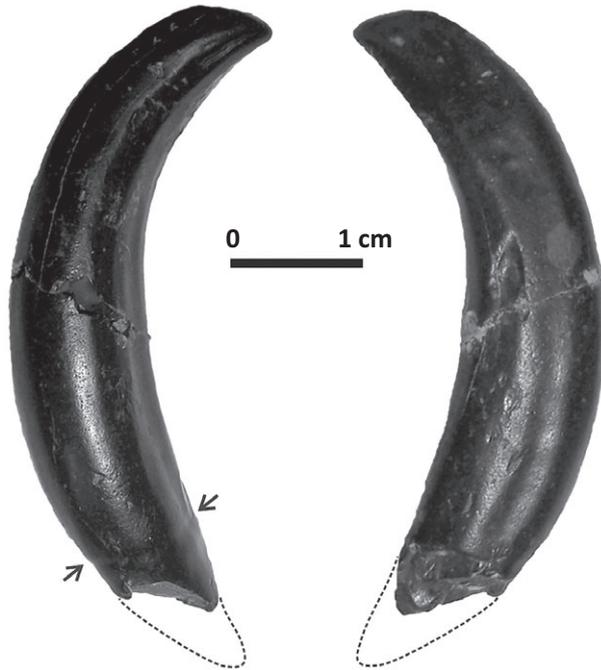


FIG. 3. *Borhyaenoidea* gen. et sp. indet. Upper left caniniform tooth, MUSM 1649.

1 cm from the hypothesized tip. The root is regularly curved and flattened labiolingually at its tip. A shallow longitudinal groove runs along the mesial third in what is interpreted to be the lingual side of the crown. The curvature of the tooth and the sharpness of the crown point to an upper left canine, indicating a large flesh eater. Given its morphology, size and the stratigraphical context of the discovery (i.e. Middle Miocene; no placental carnivore is mentioned in coeval South American assemblages), we tentatively refer it to a canine of an unidentified non-thylacosmilid borhyaenoid marsupial. Its shape and dimensions compare well with upper canines of the Santacrucian *Prothylacynus*, and the dimensions fall between those of Santacrucian *Borhyaena* and *Arctodictis* on the one hand (bigger; Sinclair 1906; Marshall 1976; Argot 2004), and Laventan *Lycopsis* and *Hondadelphis* (smaller; Marshall 1977; Goin 1997) on the other. Additionally, it is much smaller than corresponding remains of the giant Laventan *Dukecynus* (Marshall 1978; Goin 1997), bigger than a new species of sparassodont from Quebrada Honda (UF 27881; Engelman and Croft 2014) and about the same size as the ‘Tasmanian wolf’ *Thylacinus cynocephalus* (Engelman and Croft 2014), extinct in historical times. If confirmed, it would be both the only fossil referred to a marsupial and the only mammalian predator specimen recorded within the available sample of the Fitzcarrald local fauna.

EUTHERIA Gill, 1872
XENARTHRA Cope, 1889
CINGULATA Illiger, 1811
GLYPTODONTOIDEA Gray, 1869
GLYPTODONTIDAE Gray, 1869

Genus *PARAPROPALAEHOPHOPHORUS* Croft *et al.*, 2007
Parapropalaeohoplophorus septentrionalis Croft *et al.*, 2007
Figure 4A

Referred material. MUSM 980, portion of dorsal carapace with 10 osteoderms, and MUSM 982, dorsal osteoderm; both originate from locality DTC-32.

Description. The osteoderms are hexagonal and anteroposteriorly elongated ($L_{\max} = 32.3$ mm; $W_{\max} = 23.8$ mm), with a large, hexagonal to round principal figure (Fig. 4A). The principal figure is located on the posterior edge of each osteoderm, and the general morphology varies from flat to concave, although some exhibit a slight convexity in their posterior halves (MUSM 980). The principal figure occupies around the 60% of the osteoderm length. Peripheral figures are reduced in size and quantity: three anterior and three posterior, the latter ones much reduced or absent. There are neither lateral nor medial figures. The sculpturing is faint and the surface punctuated. No piliferous pits are observable. Thickness varies from 7.4 to 14.3 mm.

Remarks. Specimens MUSM 982 and MUSM 980 have most characteristics in common with *Parapropalaeohoplophorus septentrionalis*, including the presence of flat to concave principal figures, although some osteoderms of MUSM 980 have a slight posterior convexity on it. According to the phylogenetic analysis performed by Croft *et al.* (2007), the monotypic genus *Parapropalaeohoplophorus* is, together with *Neoglyptatelus* Carlini *et al.*, 1997, the first offshoot within Glyptodontidae. The presence of *Parapropalaeohoplophorus* in the Middle Miocene of Peru increases the temporal and geographical range of this Santacrucian genus, so far restricted to the Early Miocene Chucal fauna of Chile (Croft *et al.* 2007).

Gen. et sp. indet. A
Figure 4B

Referred material. MUSM 934, indetermined osteoderm, locality DTC-32.

Description. The osteoderm MUSM 934 (Fig. 4B) is large, elongated and subtriangular in dorsal view ($L_{\max} = 40.4$ mm; $W_{\max} = 31.7$ mm; $T = 11.9$ mm), with a very porous surface. The principal figure is polygonal, bears a central knob and occupies almost the entire surface of the osteoderm. Peripheral figures are reduced and poorly distinguished. Sculpturing is faint.

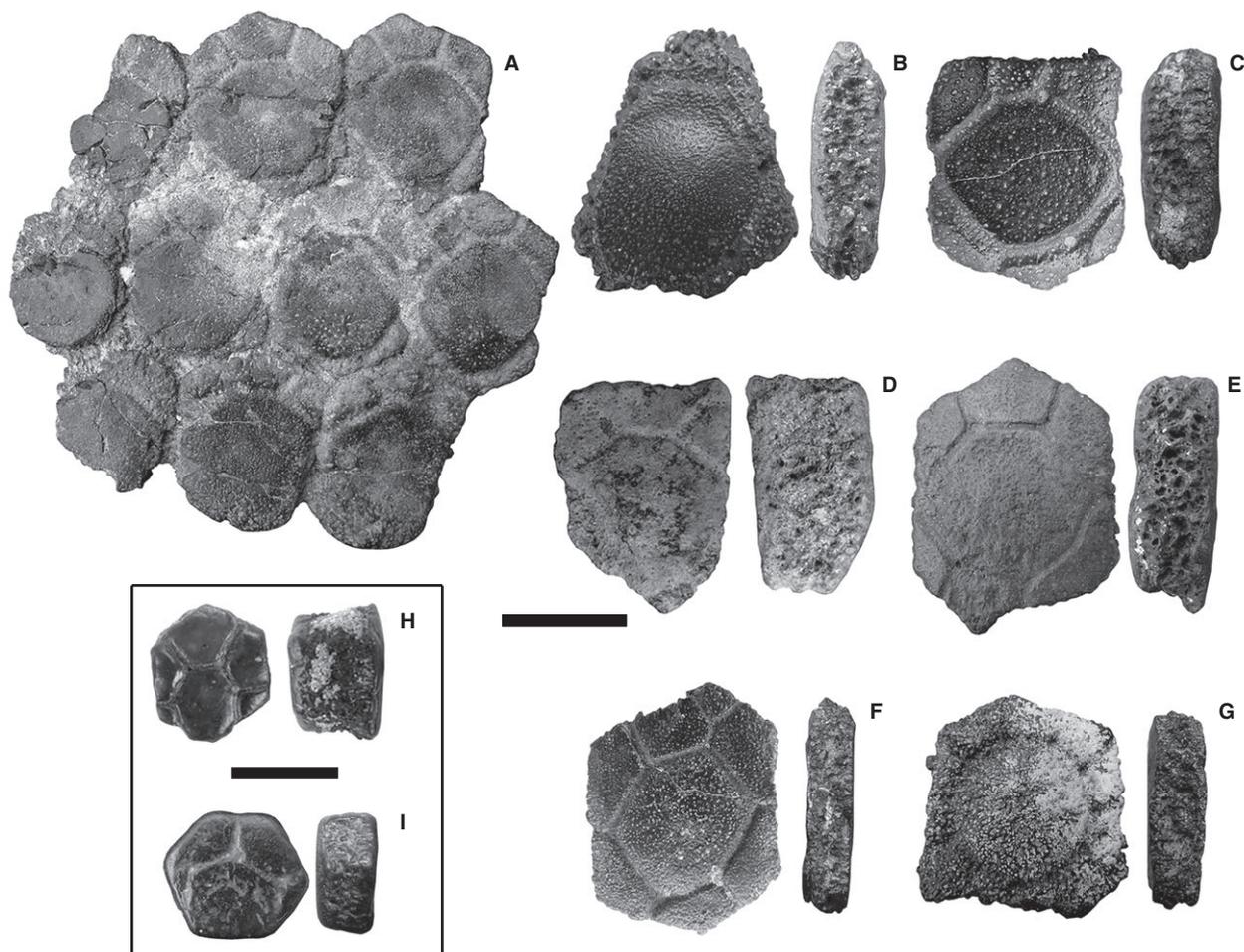


FIG. 4. Glyptodontid osteoderms from the Fitzcarrald local fauna. A, *Parapropalaeohoplophorus septentrionalis*, MUSM 980, dorsal portion of the carapace with 10 osteoderms. B–C, indeterminate isolated osteoderms; B, gen. et sp. indet. A, MUSM 934; C, gen. et sp. indet. B, MUSM 1603. D–G, *Boreostemma* sp., dorsal osteoderms; D, MUSM 1608; E, MUSM 932; F, MUSM 933; G, MUSM 1602. H–I, *Neoglyptatelus originalis*, dorsal osteoderms; H, MUSM 1573; I, MUSM 1601. Scale bars represent 2 cm, except H–I, which is 1 cm.

The principal sulcus is wide and shallow. Two large piliferous pits are visible at the intersection between the principal and radial sulci. The edge of the osteoderm is serrated.

Remarks. The principal figure of MUSM 934 is polygonal, which is possibly the ancestral condition in Glyptodontidae (Croft *et al.* 2007). It is distinct from *Parapropalaeohoplophorus*, *Boreostemma* and from recognized glyptatelines in having a principal figure with a central elevation or knob, as in *Propalaeohoplophorus* and *Cochlops*. Piliferous pits are large. The porous surface is reminiscent of *Boreostemma* (Carlini *et al.* 2008), so are the U-shaped sulci, although much wider in MUSM 934. We consider MUSM 934 to document an unidentified form potentially close to Propalaeohoplophoriinae because of the knob of the central figure, synapomorphic of the subfamily. Propalaeohoplophoriinae glyptodontids were originally recognized in the Early and Middle Miocene of Argentinian

Patagonia (e.g. Ameghino 1889, 1891; Scott 1904; Rusconi 1946). Subsequently, the genus *Asterostemma* was tentatively recognized in the Middle and Late Miocene of Colombia and Venezuela, respectively (Simpson 1947; De Porta 1962; Villarroel 1983; Carlini *et al.* 1997). Later, Carlini *et al.* (2008) erected the genus *Boreostemma* for the specimens previously referred to as ‘tropical *Asterostemma*’.

Gen. et sp. indet. B
Figure 4C

Referred material. MUSM 1603, lateral osteoderm, locality DTC-20.

Description. MUSM 1603 (Fig. 4C) is a medium-sized osteoderm, thick, pentagonal, with a porous surface ($L_{\max} =$

32.8 mm; W_{\max} = 25.9 mm; T = 11.8 mm). The principal figure is a large eye-shaped form, slightly concave, transversally extended and placed towards the posterior edge of the osteoderm. Posterior peripheral figures are reduced in size and number (three), and there are neither lateral nor medial figures. The principal and radial sulci are wide and shallow. Two large piliferous pits are located at the intersection between principal and radial sulci. The edge of the osteoderm is serrated.

Remarks. Despite the fact that MUSM 1603 cannot be assigned to any known genus, it does exhibit some features that could represent a primitive condition among glyptodontines. For instance, the principal figure is flat to concave, which is considered a plesiomorphic character state as it is observed in basal cingulates (Croft *et al.* 2007). The ‘eye-shaped’ principal figure seems to be a transition state between a straight-sided and a rounded form. The orientation of this figure is also peculiar; among cingulates, the principal figure is usually elongated anteroposteriorly, while in MUSM 1603, the main diameter is transverse. Glyptatelines possess reduced medial and lateral peripheral figures, whereas these figures are absent in pampatheres, *Parapropalaehoplophorus*, and MUSM 1603 (Fig. 4C). Large piliferous pits are present in both basal (i.e. Pampatheriidae and Glyptatelineae) and most derived cingulates (e.g. Hoplophorinae and Doedicurinae).

GLYPTATELINEAE Castellanos, 1932

Genus NEOGLYPTATELUS Carlini *et al.*, 1997

Neoglyptatelus originalis Carlini *et al.*, 1997

Figure 4H–I

Referred material. MUSM 1573, dorsal osteoderm, locality SEP-005; MUSM 1601, dorsal osteoderm, locality IN-DTC.

Description. The osteoderms MUSM 1573 (L_{\max} = 12.1 mm; W_{\max} = 10.6 mm; T = 8.7 mm; Fig. 4H) and MUSM 1601 (L_{\max} = 11.3 mm; W_{\max} = 12.1 mm; T = 5.7 mm; Fig. 4I) are small, thick and hexagonal, with a smooth and shiny surface. MUSM 1601 is eroded, and its original texture is difficult to distinguish. The principal figure is subelliptical (MUSM 1573) or polygonal (MUSM 1601) in shape and located on the posterior edge of the osteoderm, so posterior figures are absent. Peripheral figures are bulged (MUSM 1573) and variable in number (4–5). The three piliferous pits are large and located at the intersection of the principal sulcus and the radial sulci, which are narrow but deep. The margins of the osteoderms are smooth.

Remarks. The systematics and evolution of glyptateline glyptodontids are poorly known and understood because most of the species are based on small numbers of iso-

lated osteoderms. Three genera constitute this subfamily: *Glyptatelus* Ameghino, 1897; *Clypeotherium* Scillato-Yané, 1977; and *Neoglyptatelus* Carlini *et al.*, 1997. Osteoderms of *Neoglyptatelus* from the Fitzcarrald local fauna are slightly smaller and proportionally thicker than the osteoderms of *N. originalis* from the late Middle Miocene of La Venta, Colombia (JTL and RSG pers. obs. 2010). Additionally, piliferous pits are smaller. The surface is smooth, as in *N. originalis* from La Venta, but shinier. *Neoglyptatelus* from Fitzcarrald and La Venta have both well-defined sulci, and the principal and peripheral figures are slightly convex. *Neoglyptatelus* from Fitzcarrald differs from *N. sincelejanus* (Villarroel and Clavijo 2005) in having much thicker osteoderms, bigger piliferous pits, convex figures and deeper sulci. This last aspect also differentiates it from *Neoglyptatelus* sp. from Uruguay (MNHN 1483; Vizcaíno *et al.* 2003). Considering the important morphological variability between osteoderms depending on their position along the carapace, and pending the discovery of more material, MUSM 1573 and MUSM 1601 are referred to *N. originalis* (because of the well-defined sulci + convex principal and peripheral figures + bigger and thicker osteoderms than *N. sincelejanus*). Based on the schematic drawings provided by Spillman (1949), the ‘dasypodid osteoderms’ from Utoquina River in Peru are consistent with the above-mentioned characteristics of this genus. *Neoglyptatelus* is, together with *Parapropalaehoplophorus*, consensually considered to be the most basal taxon within Glyptodontidae (e.g. Croft *et al.* 2007). Indeed, the osteoderm sculpture in *Neoglyptatelus* is more similar to Dasypodidae (e.g. *Pachyarmatherium*, *Propaopus*) than to any Glyptatelineae. *Neoglyptatelus* has even been suggested as a junior synonym of *Pachyarmatherium* (e.g. Vizcaíno *et al.* 2003), an enigmatic cingulate from the Late Pliocene and Early Pleistocene of Florida and South America. Tejada *et al.* (2011) referred MUSM 1573 to *Pachyarmatherium*; however, morphological differences considered diagnostic such as: (1) the size of piliferous pits (considerably bigger in *Pachyarmatherium*); and (2) the morphology of the principal and radial sulci (wider and deeper in *Pachyarmatherium*), together with the temporal difference between these two genera, strengthen its assignation to *Neoglyptatelus*. Although long considered the last member of the Glyptatelineae clade (Carlini *et al.* 1997), there is evidence to cautiously treat this taxon (as well as *Pachyarmatherium*) as a glyptodont (Porpino *et al.* 2009). The geographical distribution of *Neoglyptatelus* is wide, ranging from Venezuela to Uruguay in South America, whereas its chronological distribution is so far restricted to the late Middle Miocene (*N. originalis* from Colombia and Peru, and *N. sincelejanus* from Colombia) and Late Miocene (*Neoglyptatelus* sp. from Uruguay).

GLYPTODONTINAE Gray, 1869

Genus BOREOSTEMMA Carlini *et al.*, 2008*Boreostemma* sp.

Figure 4D–G

Referred material. MUSM 1608, osteoderm, locality IN-007; MUSM 932, dorsal osteoderm close to the caudal notch, locality DTC-32; MUSM 933, dorsal osteoderm, close to the caudal notch locality DTC-32; MUSM 1602, dorsal osteoderm, locality DTC-28.

Description. The osteoderm MUSM 1608 (Fig. 4D) is large, thick and pentagonal in shape with a slightly porous surface ($L_{\max} = 38.0$ mm; $W_{\max} = 27.5$ mm; $T = 19.2$ mm). The thickness of the osteoderm reduces posteriorly. The principal figure is polygonal and flat, occupies most of the osteoderm and is located in its posterior half. Three anterior peripheral figures are visible. The posterior figures are extremely reduced in size, whereas lateral figures, medial figures and piliferous pits are absent. Sculpturing is shallow and faint. MUSM 932 ($L_{\max} = 45.2$ mm; $W_{\max} = 31.5$ mm; $T_{\max} = 13.1$ mm; Fig. 4E) and MUSM 933 ($L_{\max} = 41.4$ mm; $W_{\max} = 30.1$ mm; $T_{\max} = 8.3$ mm; Fig. 4F) are large hexagonal dorsal osteoderms. The principal figure is also hexagonal in both specimens, slightly displaced posteriorly and surrounded by six peripheral figures. MUSM 933 shows a secondary peripheral figure. Principal and radial sulci are wide and deep. MUSM 932 shows two small piliferous pits, while no piliferous pits are discernible in MUSM 933. The surface is punctuated, and the edges are serrated. The osteoderm MUSM 1602 is hexagonal ($L_{\max} = 30.6$ mm; $W_{\max} = 27.5$ mm; $T = 10.9$ mm; Fig. 4G) and shows the typical ‘rosette’ pattern of glyptodontines and the strong porous surface of *Boreostemma*. The principal figure is large, round and located at the centre of the osteoderm. Peripheral figures are numerous (11) and reduced in size, especially the posterior ones. Sculpturing is faint. Principal and radial sulci are wide and shallow. Eleven small piliferous pits are present at the intersection of the principal sulcus and the radial sulci. The edges of the osteoderm are serrated.

Remarks. The size and thickness of MUSM 1608 are comparable to those observed in Palaeogene glyptatelines such as *Clypeotherium magnum* Scillato-Yané 1977, from the Deseadan of Patagonia. Such notable thickness has never been observed in available specimens of *Boreostemma*; however, osteoderm thickness is highly variable and should not be used as a diagnostic character. The great size of the dorsal osteoderms MUSM 932 and MUSM 933, the polygonal shape and position of the principal figure (posteriorly displaced and occupying most of the osteoderm) are reminiscent traits of Deseadan glyptatelines (e.g. *Glyptatelus* and *Clypeotherium*). However, the Fitzcarrald specimens are not assignable to either of the two aforementioned Deseadan glyptodonts. Carlini *et al.* (2008) erected *Boreostemma* based on the remains from the Pliocene of the Codore Formation in Venezuela, referring into this genus the species

previously identified as ‘tropical’ *Asterostemma* (e.g. Carlini *et al.* 1997). Thus, the clade Propalaeohoplophorinae was again restricted to the southern cone of the continent. Later, Zurita *et al.* (2013) described a magnificent specimen of *Boreostemma acostae* from the Middle Miocene of La Venta (Colombia) and placed the taxon in phylogenetic context. *Boreostemma* is recognized as an early form of the clade Glyptodontinae and is considered to be the sister taxon of the other Glyptodontinae (Zurita *et al.* 2013). Interestingly (though not completely unexpectedly), this phylogeny shows two natural groups within Glyptodontinae, one composed of the northern South American forms and the other one of the southern South American forms. Before the discovery of glyptodontine material in tropical South America, the earliest record of this group was *Glyptodontidium tuberifer* Cabrera, 1944, from the Late Miocene – Early Pliocene of Argentina (Cabrera 1944; Oliva *et al.* 2010). Following these new discoveries, a northern South American origin for glyptodontines and their subsequent dispersion towards the south of the continent arose as a new scenario for the evolutionary history of this clade (Carlini *et al.* 2008; Zurita *et al.* 2013). The recognition of this genus in the late Middle Miocene Fitzcarrald local fauna of Peruvian Amazonia substantiates this scenario.

PILOSA Flower, 1883

FOLIVORA Delsuc *et al.*, 2001

MYLODONTOIDEA Gill, 1872

MYLODONTIDAE Gill, 1872

Gen. et sp. indet.

Figure 5A–C

Referred material. MUSM 938, upper right molariform, locality IN-010; MUSM 1588, upper left molariform, locality IN-B-002/003; MUSM 947, right M5, locality DTC-20.

Description. MUSM 938 is subtriangular in cross section, and mesial and distal sides are rectilinear, with the distal side slightly longer than the mesial one (MDL = 14.6 mm, LLL = 14.82 mm; Fig. 5A). The lingual side is concave because of a wide and shallow sulcus that runs along the length of the crown. The centre of the tooth is composed of vasodentine (which constitutes the thickest layer) and surrounded by thin layers of orthodentine and cement. As occurs in MUSM 938, the cross section of MUSM 1588 is triangular with the mesial and distal sides of equivalent transversal length (MDL = 14.5 mm; LLL = 17.5 mm; Fig. 5B). The tooth MUSM 947 is bilobated with the mesial lobe larger than the distal one and with the characteristic ‘8’-shape of the M5 of Mylodontidae (MDL = 17.2 mm; LLL = 13.9 mm; Fig. 5C). The two lobes are separated by two deep labial and lingual sulci that run along the entire length of the crown. Lingually, a thick layer of orthodentine constitutes the major component of the tooth. The nucleus of vasodentine is also thick

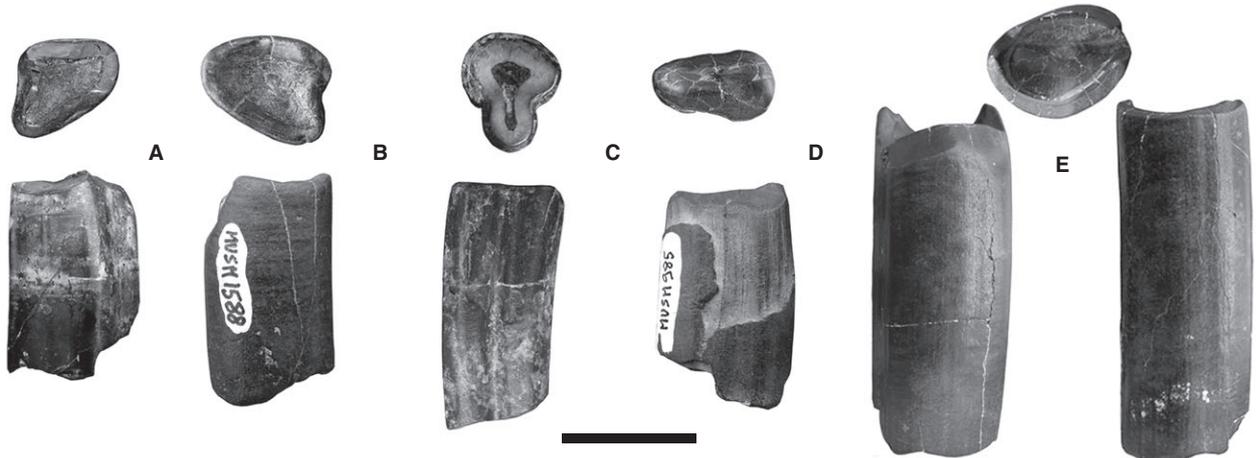


FIG. 5. Folivores from the Fitzcarrald local fauna. A–C, Mylodontidae indet.; A, upper right molariform, MUSM 938; B, upper left molariform, MUSM 1588; C, right M5, MUSM 947. D, *Urumacotherium* sp., molariform, MUSM 985. E, Megalonychidae indet., MUSM 904, third lower right molariform. Scale bar represents 2 cm.

and adopts the shape of the lobes (i.e. mesiodistally compressed in the anterior lobe and labiolingually in the posterior).

Remarks. The subtriangular shape as well as the uniform wear with no or minimal loph formation of MUSM 938 fits better with what is observed in scelidotheriines than to mylodontines. In cross section, this tooth is similar to the M5 of *Neonematherium*, but considerably larger and without a distal sulcus. It also resembles the M3 of *Proscelidodon patrius*, but MUSM 938 is more robust and smaller. We cautiously refer MUSM 938 to Mylodontidae on account of dental features not exclusive of scelidotheriines and common in more derived mylodontines such as *Eumylodon chapadmalensis*, *Myodon* and *Glossotherium*. Characters used to distinguish these two subfamilies (i.e. Mylodontinae and Scelidotheriinae) are based mainly on skeletal features and more particularly the articulation astragalus–cuboid (McDonald 1997). Similarly, the occlusal surface shape of MUSM 1588 is equivalent to the M2 of *Proscelidodon patrius* and M4 of *Eumylodon chapadmalense*. Bilobate teeth such as MUSM 947 are observed in mylodontids and orophodontids. In occlusal view, MUSM 947 is similar to the M5 of *Pseudopreotherium confusum* from La Venta but also to that of *Octodontotherium grande* from the Deseadan SALMA of La Flecha, Patagonia. However, unlike *P. confusum* but similar to orophodontids and other mylodontids such as *Nematherium*, the wear of MUSM 947 is uniform (i.e. the three layers have the same rate of wear implying the presence of vasodentine and orthodentine of similar hardness). Consequently, there are neither concave areas nor well marked facets on the occlusal surface. We do not consider MUSM 947 to be a possible orophodontid based on the presence of a large nucleus of vasodentine, which is extremely reduced in this clade.

URUMACOTHERIINAE Negri and Ferigolo, 2004

Genus URUMACOTHERIUM Bocquentin-Villanueva, 1984

Urumacotherium sp.

Figure 5D

Referred material. MUSM 985, molariform, locality DTC-32.

Description. This taxon is represented by a medium-sized monolophodont tooth (MDL = 12.3 mm; LLL = 20.0 mm; Fig. 5D), mesiodistally compressed with an elliptical to subrectangular cross section. There are two wear surfaces both diverging mesially and distally from the apex of the loph. The orthodentine is the predominant layer of the tooth while the cementum layer is extremely reduced; the vasodentine is not observable.

Remarks. Urumacotheriinae is a poorly known group erected for specimens from the Late Miocene Urumaco Formation, Venezuela (*Urumacotherium garciai*), and the Late Miocene – Pliocene Solimões Formation, Brazil (*U. garciai* and *U. campbelli*). MUSM 985 represents the earliest record of Urumacotheriinae. The exclusive presence of this subfamily in tropical localities of South America is evidence of its endemism to this region.

MEGATHERIOIDEA Gray, 1821

MEGALONYCHIDAE Gervais, 1855

Gen. et sp. indet.

Figure 5E

Referred material. MUSM 904, third lower right molariform, locality DTC-32.

Description. MUSM 904 is a large tooth subelliptical in cross section (MDL = 17.8 mm; LLL = 20.2 mm; Fig. 5E). Its longitu-

dinal axis is nearly straight, and a longitudinal groove is present on the labial side. It possesses two transverse crests or lophs (i.e. bilophodont) of uneven wear and morphology. The two lophs are convergent labially and lingually in occlusal view and are separated by a V-shaped transverse valley. The higher loph (distal) bears a flat and sloping wear facet. This wear facet is crescent-shaped (in both occlusal and distal view) and presents the two cusps A and B of Bargo *et al.* (2009) on its extremities. The mesial loph is markedly lower and bears a convex and sloping wear facet. The lateromedial mid-point of this crest corresponds to the cuspid C of Bargo *et al.* (2009). The main component of the tooth is vasodentine. A thick and uniform layer of cement surrounds the thin layer of orthodentine. The cement is generally thick in megatheriines, but just in mesial and distal faces.

Remarks. MUSM 904 is a large tooth corresponding in size to the alveoli of the Amazonian megatheriine *Megathericulus* (MUSM 1564) described later in this section. This molariform presents the general occlusal pattern of megalonychid sloths (e.g. Naples 1982; Bargo *et al.* 2009). In this respect, it possesses similarities with some Santacrucian genera of uncertain affinities such as *Analcimorphus* and *Schismotherium*, the megalonychid *Eucholoeops* and the planopsine *Prepothierium* (see Scott 1904). MUSM 904 has a subelliptical to rectangular cross section of transverse extension that is also present in some megalonychids, nothrotheres and planopsines, in contrast to the completely rectangular molariforms with square corners observed in known megatheriines. Interestingly, MUSM 904 also has a V-shaped valley and is similar in size to basal megatherer molariforms. Hirschfield (1985) identified megatheriine molariforms among the sloth material from La Venta. The teeth were described as mesiodistally compressed, with the corners ‘somewhat squared’, and ‘worn in typical megalonychoid fashion’ (Hirschfield 1985). Based on the strong mesiodistal compression and the presence of cusps, Pujos *et al.* (2013) assigned this Laventan specimen to *Planops* sp. Megalonychids of equivalent age are extremely rare in tropical localities and generally considerably smaller in size. On the other hand, teeth of basal megatheres, such as *Megathericulus*, are unknown.

MEGATHERIIDAE Gray, 1821

MEGATHERIINAE Gray, 1821

Genus MEGATHERICULUS Ameghino, 1904

Megathericulus sp.

Figure 6A, D–E

Referred material. MUSM 1564, right edentulous hemimandible from locality SEP-007.

Description. MUSM 1564 was described by Pujos *et al.* 2013. Here, we provide a general description with special emphasis in the anatomical features of potential phylogenetic significance.

MUSM 1564 is a robust dentary with four continuous alveoli without diastema, and a prominent ventral bulge, especially at the level of m3 and m4. Alveoli for m2 and m3 are mesiodistally compressed and rectangular-shaped. Alveolus for m1 is trapezoidal, whereas the corresponding alveolus for m4 is nearly square. Internally, the alveoli show a strong keel on the lingual and labial sides, though less distinctive on the latter. The premental portion of the dentary, although partially preserved, shows that this region was high due to the gentle slope of its ventral margin as in *Megathericulus patagonicus* (Fig. 6A–B). In occlusal view, the symphysis is wide and its posterior edge is anterior to m1. The posterolateral opening of the mandibular canal is located on the anterior edge of the base of the ascending ramus, at the level of the posterior half of m4 and under the alveolar plane (Fig. 6A). The ascending ramus is perpendicular to the horizontal ramus, and its anterior margin is placed behind m4; therefore, the m4 is entirely visible in lateral view.

Measurements. Length of the dental series (m1–m4) = 83.7 mm; m1 MDL = 18.4 mm, LLL = 21.7 mm; m2 MDL = 18.2 mm, LLL = 23.4 mm; m3 MDL = 19.2 mm, LLL = 23.6 mm; and m4 MDL = 20.2 mm, LLL = 20.2 mm.

Remarks. *Megathericulus patagonicus* is the earliest megatheriine, based on fragmentary remains from the Middle Miocene of Argentina (Ameghino 1904; De Iuliis *et al.* 2008). Recently, other Middle Miocene species originally assigned to *Eomegatherium* were referred to the genus *Megathericulus* (*M. andinum*, *M. primaveum* and *M. cabrerai*; Pujos *et al.* 2013). *Megathericulus* specimen from Fitzcarrald corresponds in size to an animal slightly bigger than *M. patagonicus* (MACN A 11151) but smaller than *M. andinum* (MLP 2-204). MUSM 1564 possesses several features considered ancestral among megatheriines, such as molariforms mesiodistally compressed and a symphysis that ends anterior to the m1. These characters are observed in all *Megathericulus* species as well as in *Anisodontherium halmyronomum* (Brandoni and De Iuliis 2007). Additionally, the morphology of the mandibular spout and the position of the posterolateral opening of the mandibular canal deserve special mention because they are crucial for the understanding of the basal stages in sloth evolution (De Iuliis 1994). In dorsal view, the premental dorsal rim is oblique, suggesting that the spout was expanded (Fig 6D–E), contrary to the parallel-sided borders of most other megatheriine species (Pujos *et al.* 2013). Putting together the pile of fragments of MLP 2-204 belonging to *Megathericulus* (= *Eomegatherium*) *andinum*, some of the authors (RSG, JTL) partially reconstructed its mandibular spout (Fig. 6F). It is relatively long, particularly thick and transversely expanded at the mid-length, as might be the case in MUSM 1564. Anteri-

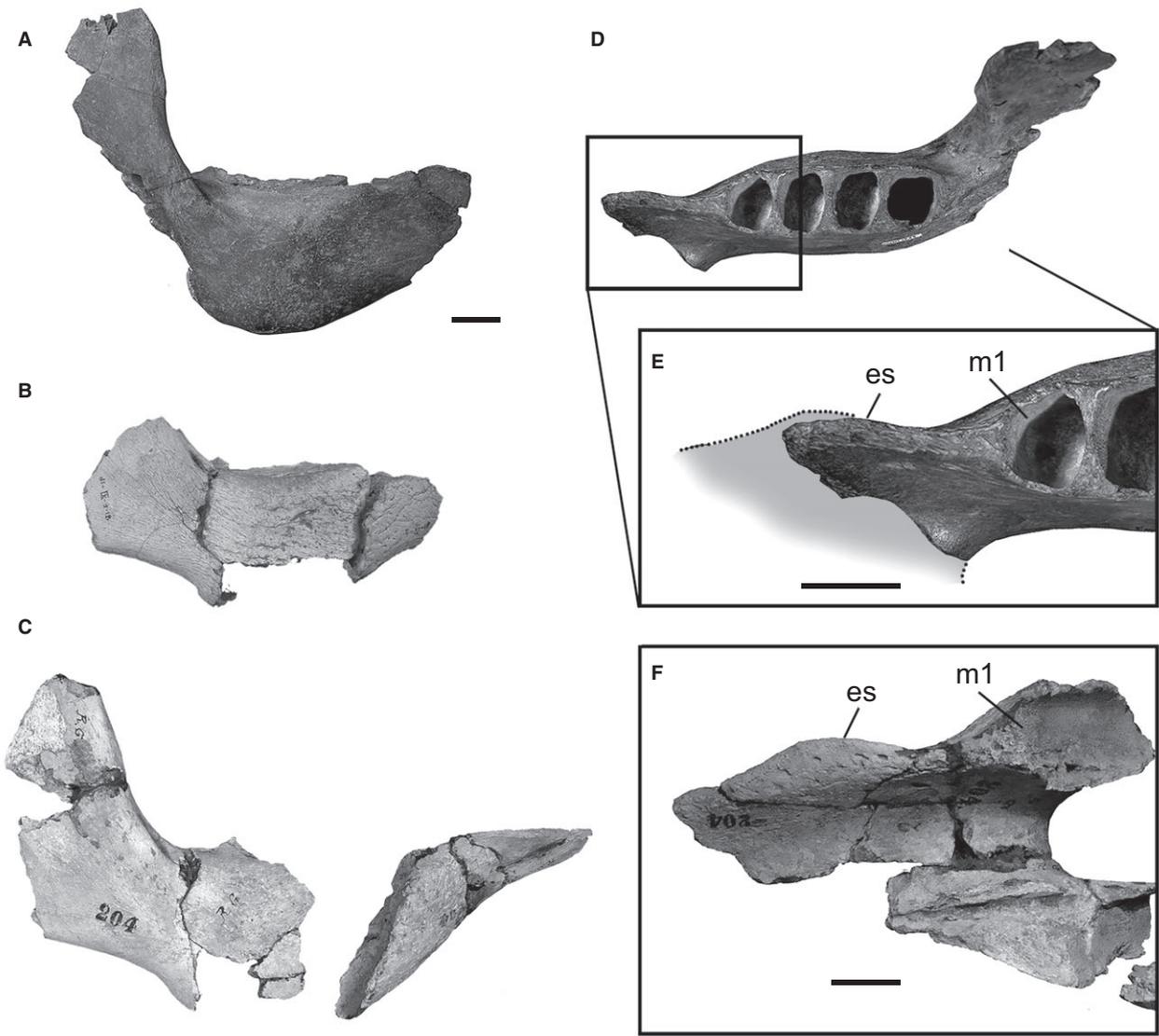


FIG. 6. *Megathericulus* sp. from Fitzcarrald and *Megathericulus* spp. from Argentina. A, D–E, *Megathericulus* sp. from Fitzcarrald; A, right edentulous hemimandible, MUSM 1564 in lateral view; D–E, occlusal view. B, dentary of *Megathericulus patagonicus*, MLP 91-IX-7-18, from the Río Mayo Fm in Argentina. C, F, *Megathericulus andinum*, MLP 2-204, from the Río Mayo Fm in Argentina; C, lateral view; F, occlusal view. Abbreviations: es, expanded spout; m1, alveolus for m1. All scale bars represent 2 cm.

only the lateral margins are convergent, which is common among *Pilosa* (Gaudin 2004). However, within *Megatheria*, an expanded spout is known only in *M. andinum* and in the *Megathericulus* specimen from Fitzcarrald. This anatomical area is unknown in *M. patagonicus*. In MUSM 1564, the posterolateral opening of the mandibular canal lies on the anterior edge of the base of the ascending ramus, a condition that only occurs within megatheriines in *M. patagonicus* and *M. andinum* (Fig. 6C) but is also present in some *Hapalops* species (De Iuliis 1994). In *Megatherium* species, this opening is located dorsally, and medial to the base of the ascending ramus, and in the problematic taxon *Promegatherium*, on the lateral surface

of the ascending ramus (Brandoni and Scillato-Yané 2007). With the exception of *M. patagonicus*, the posterolateral opening in all megatheriines is located opposite to m4 (De Iuliis *et al.* 2008). In this respect, *Megathericulus* from Fitzcarrald presents an intermediate condition considering that this opening is located at the level of the posterior half of m4 and not entirely posterior to it as in *M. patagonicus* and *M. andinum*, which corresponds to the ancestral condition (see De Iuliis 1994). *Megathericulus* from Fitzcarrald has the m4 entirely visible in lateral view, as in *M. patagonicus*, *M. andinum* and other early members of the subfamily such as *Anisodontherium hal-mironomum* and the ‘Conglomerado Osífero species’

(Brandoni and Scillato-Yané 2007; De Iuliis *et al.* 2008). The dentary from Peruvian Amazonia also gives new information about the morphology of the ventral bulge in *Megathericulus*. This area of the mandible is prominent in *M. patagonicus*, as has been noted by De Iuliis *et al.* (2008), but the fragmentary condition of the Patagonian material did not allow the much detail to be discerned. MUSM 1564 reveals that the ventral bulge was displaced posteriorly, at the level of m3–m4, rather than at the centre of the dental series as in all other megatheriines and nothrotheriids (see De Iuliis 1994). This peculiar morphology might be of phylogenetic relevance as it is observed in the Santacrucian planopsine *Prepothorium* (Scott 1904, pl. 60, fig. 1). Additionally, as in *M. patagonicus*, the ventral margin of the horizontal ramus does not slope markedly in the prementary region, but differs in this respect from *M. andinum* and derived megatheres. The degree of hypsodonty has been tested in megatheres by the Hypsodonty Index (HI; sensu Bargo *et al.* 2006a). *Megathericulus* from Fitzcarrald presents a HI of 0.92, which is high for the group, although unsuitable for comparison with derived megatheres due to its relatively shorter dental series. The Amazonian *Megathericulus* shows that primitive megatheres were relatively widely distributed in South America during the Middle Miocene (Pujos *et al.* 2013), pushing back the origin of the clade. It has furthermore allowed the phylogenetic and biochronological reassessment of basal megatheriines restraining the clade *Megathericulus* (*M. patagonicus*, *M. primaevus*, *M. andinum* and *M. cabrerai*) to the Middle Miocene (Colloncuran–Laventan–Mayoan) of South America, and the genus *Eomegatherium* to the Late Miocene (Huayque-rian) of Argentina.

General comments on *Xenarthra*

Considering the short period of sampling, the xenarthran diversity reported in Fitzcarrald is large, with at least seven taxa identified (although neither armadillo nor pamapathere remains were recovered). The record of Glyptodontidae, the only cingulate clade documented, is particularly interesting for its taxonomic diversity, biogeographical implications and especially because of the basal evolutionary stage of the forms identified. Indeed, *Parapropalaeohoplophorus (incertae sedis)* and the glyptateline *Neoglyptatelus* are considered the earliest offshoots within Glyptodontidae (Croft *et al.* 2007), and *Boreostemma* currently represents the most basal and oldest glyptodontine known (Zurita *et al.* 2013).

The Fitzcarrald fauna includes at least four taxa of Phyllophaga. This material consists of isolated teeth hardly identifiable at genus or species level. The most

complete material is the hemimandible of *Megathericulus*, the most basal megatheriine currently known. This material is significant as it preserves new characters of phylogenetic relevance allowing reassessment of the phylogenetic relationships and biochronology of basal megatheriines (see Pujos *et al.* 2013). Moreover, it shows that basal megatheriines were widely distributed throughout South America at least since the Middle Miocene. A large tooth (MUSM 904, Fig. 5E) assigned to Megalonychidae represents a size previously unknown for this clade during this period in South America.

NOTOUNGULATA Roth, 1903

Remarks. Among notoungulate remains from the Fitzcarrald Arch, large specimens referable to dinotoxodontine toxodonts dominate, with 13 large hypselodont isolated teeth unearthed at various localities (IN-008; IN-010; DTC-14; DTC-32; DTC-37), an edentulous maxilla excavated in DTC-32 (MUSM 1493) and several postcrania (patella MUSM 1479 (H = 54.75 mm; APD = 53.73 mm; TD = 77.35 mm), IN-010, and astragali MUSM 1480 and 1486 (Fig. 7J), IN-010). Even though this complete collection is likely to document a single taxon, only a few teeth were diagnostic enough to be identifiable to genus and/or species level.

TOXODONTIA Owen, 1853

TOXODONTIDAE Gervais, 1847

DINOTOXODONTINAE Madden, 1997

Genus PERICOTOXODON Madden, 1997

Pericotoxodon cf. *platignathus* Madden, 1997

Figure 7C–I

Referred material. MUSM 1506, left I2, locality DTC-37; MUSM 1501, lower left premolar, locality DTC-37; MUSM 1503, right I2, locality IN-010; MUSM 1500, left M1?, locality DTC-32; MUSM 922, left m1/2, locality DTC-32; MUSM 1478, right dp2, locality IN-008; MUSM 1487, right m1/2, locality DTC-14; MUSM 1489, mandibular symphysis with left and right i1, locality IN-DTC.

Description. MUSM 1503 (MDL = 20.5 mm; LLL = 17.2 mm; crown H = 60.7 mm; Fig. 7H) and MUSM 1506 (MDL = 22.1 mm; LLL = 16.0 mm; crown H = 53.8 mm) are hypselodont second upper incisors of triangular cross section. The tips are worn obliquely. A thick enamel layer covers the labial and mesial surfaces, and there is no enamel on the lingual or distal sides. A mesiolingual projection (indicative of a male according to Madden *et al.* 1997) is observed in MUSM 1503. MUSM 1501 is a lower left premolar (MDL = 15.52 mm; LLL = 8.52 mm; preserved crown H = 43.62 mm; Fig. 7D). The tooth

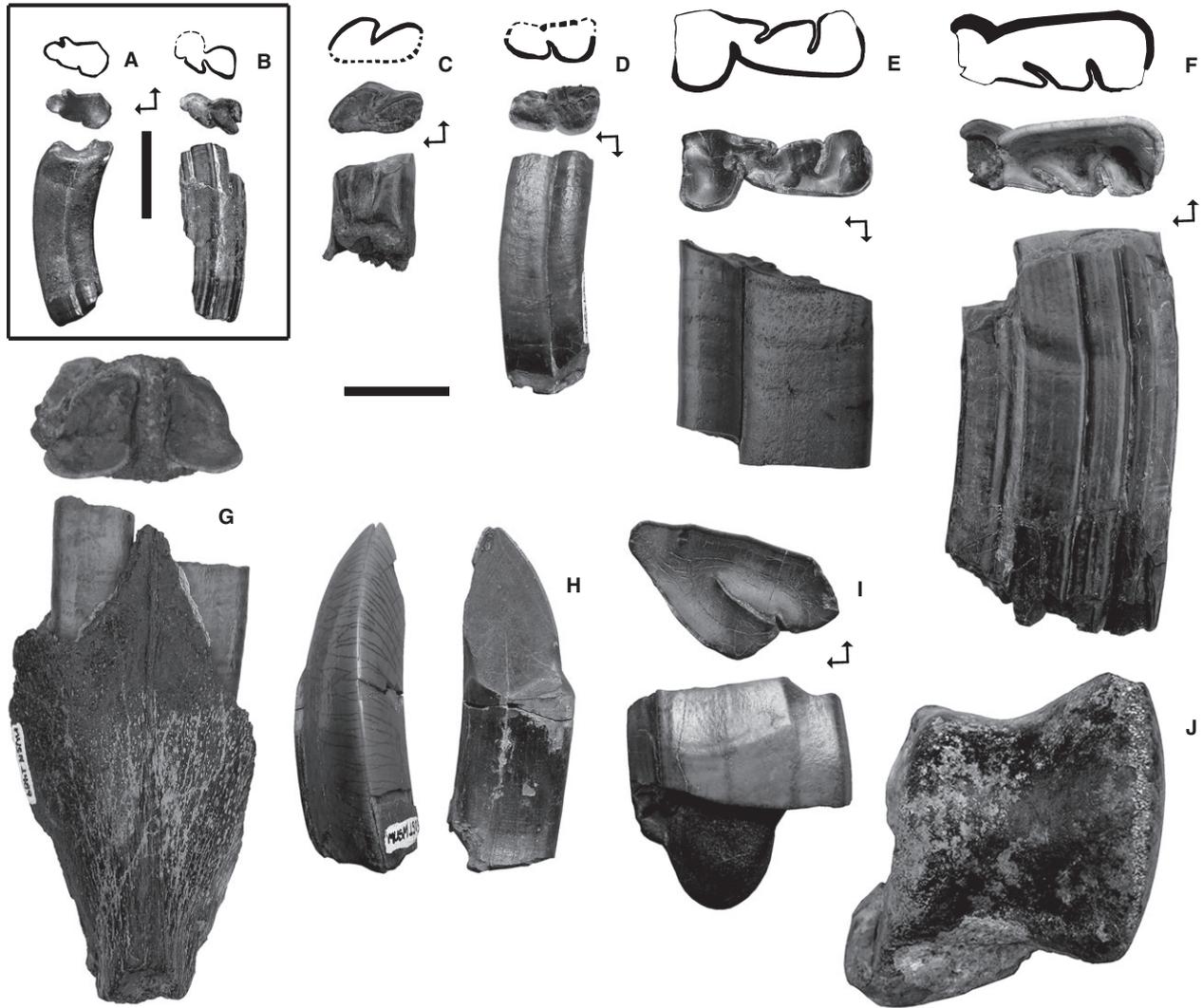


FIG. 7. Notoungulates from the Fitzcarrald local fauna. A–B, *Miocochilius anomopodus*; A, left P3/4, MUSM 986; B, right lower cheek tooth, MUSM 1494. C–I, *Pericotaxodon cf. platignathus*; C, right dp2, MUSM 1478; D, lower left premolar, MUSM 1501; E, left m1/2, MUSM 922; F, right m1/2, MUSM 1487; G, mandibular symphysis in anterior and ventral view preserving both left and right i1, MUSM 1489; H, right I2 in labial and lingual view, MUSM 1503; I, left M1?, MUSM 1500. J, left astragalus of Notoungulata indet., MUSM 1486. Scale bars represent 1 cm for A–B and 2 cm for C–J. Arrows indicate mesial and labial directions.

shows conspicuous buccal and lingual folds separating the mesial and distal crescents. The mesial crescent is slightly longer than the mesial one, but the latter is slightly wider. Mesial and distal sides are flat. MUSM 1501 seems to differ from figured lower molars of *P. platignathus* from La Venta (Madden *et al.* 1997) in having a deeper lingual fold and a convex lingual side of the talonid in dorsal view, although these traits might change with wear. MUSM 1500 (MDL = 38.4 mm; LLL = 24.9 mm; preserved H = 32.2 mm; Fig. 7I) is a prismatic jugal tooth (possibly a M1), with a trapezoid cross section. Its pattern is simple, with a single and conspicuous lingual groove and no mesial groove on the protocone. The distolingual enamel inflection is not discernible. The lingual column supported by the protoloph is eroded. The ectoloph has three equally distant styles. Enamel covers the crown except on lingual, mesiolabially and distal sides. MUSM 1478 (MDL = 15.4 mm; LLL = 7.9 mm; crown

H = 19.4 mm; Fig. 7C) is a lower deciduous tooth considered to be dp2 (low-crowned, short and distinct roots, thin enamel and trigonid widening with wear). In occlusal view, the tooth tapers distally. The labial groove is deep and oblique backwards. MUSM 922 is a prismatic lower molar with a large hemicircular paraconid (MDL = 36.9 mm; ant. LLL = 16.4 mm; post. LLL = 14.6 mm; crown H = 38.0 mm; Fig. 7E). In occlusal view, the mesial side is wide and flat, forming a right angle with the lingual side. The ento-hypoconid fold is approximately straight and marked and penetrates more than the transverse middle line of the tooth. The meta-entoconid fold is slightly shorter and directed forward. The anterior fold is rather a shallow inflection located slightly anterior to the level of the labial fold. Enamel covers the whole crown with the exception of the lingual areas corresponding to the paraconid and the hypoconulid. MUSM 1487 is similar in size and proportions to

MUSM 922 (MDL = 39.9 mm; ant. LLL = 14.5 mm; post. LLL = 13.8 mm; crown H = 75.3 mm; Fig. 7F). The meta-entoconid fold is much more marked than in MUSM 922 and oriented forward. The ento-hypoconid fold, on the other hand, is straighter (i.e. labiolingually oriented). The ectolophid in both MUSM 922 and 1487 is slightly convex.

Remarks. The Dinotoxodontinae are restricted to South American tropical lowlands ranging from north-eastern Argentina and Uruguay to Venezuela. Following Madden (1997), this clade includes *Dinotoxodon* Mercerat, 1895; *Plesiotoxodon* Paula Couto, 1982; *Gyrinodon* Hopwood, 1928; and *Pericotoxodon* Madden, 1997, but there are some disagreements about the validity of the clade (Saint-André 1993; Nasif *et al.* 2000). On the other hand, based on the fragmentary condition of the currently lost type material of *Neotrigodon utoquineae* Spillman, 1949, we consider it to be a *nomen nudum*. The dentition of dinotoxodontines is particularly invariable, with only a few distinctive features, which makes the identification of isolated teeth at species level very difficult (Nasif *et al.* 2000).

The specimens from Fitzcarrald show a combination of features consistent with *P. platignathus* (e.g. anterior fold on m1/2 smooth and anterior to the level of the labial fold, meta-entoconid fold of m1/2 marked, ento-hypoconid fold of m1–m2 marked and approximately straight, labial groove of molars deep and wide, and ectolophid slightly convex), although lower molars are not known in *Dinotoxodon* or *Plesiotoxodon* (Madden 1997; Nasif *et al.* 2000). MUSM 922 differs from *P. platignathus* in having a straight mesial border of the paraconid on m1 (concave in *P. platignathus*). On the other hand, the dimensions of the available teeth exceed those of the numerous specimens assigned to *P. platignathus* from La Venta by c. 15%. Pending a taxonomic revision of the Dinotoxodontinae – for which generic and/or specific oversplitting can be suspected – and/or the discovery of material contradicting our assignment, we have chosen to refer this material to *Pericotoxodon* cf. *platignathus*. Such a material confirms the mention of ‘probable Dinotoxodontinae’ in the Mapuya–Inuya area as reported by Madden (1997, 352).

TYPOTHERIA Zittel, 1893

INTERATHERIIDAE Ameghino, 1887

INTERATHERIINAE Ameghino, 1887

Genus MIOCOCHILIUS Stirton, 1953

Miocochilius anomopodus Stirton, 1953

Figure 7A–B

Referred material. MUSM 986, left P3/4, locality DTC-32; MUSM 1494, right lower cheek tooth, locality DTC-32.

Description. MUSM 986 is a small euhypsodont jugal tooth (MDL = 7 mm; ant. LLL = 3.9 mm; post. LLL = 4.5 mm; crown H = 18.7 mm; Fig. 7A), suboval in transverse section. The crown is patchily covered by cement. The mesial part of the tooth is more worn than the rest of the crown, which is characteristic of upper premolars. The paracone is distinct and mesiolabially projected. The parastyle fold and the parastyle are well developed. A shallow lingual groove located in the distal half of the tooth runs along the crown. A similar groove occurs on the labial side. In occlusal view, the distal border is convex. MUSM 1494 is bilobular in occlusal view (MDL = 7.2 mm; ant. LLL = 3.4 mm; post. LLL = 4.3 mm; crown H = 19.8 mm; Fig. 7B). External cement is only partially preserved on the lingual side of the crown. The labial side of the trigonid is eroded, but the reconstructed outline is shown in Figure 7B. Very deep lingual and labial grooves separate trigonid from talonid. There is a shallow lingual groove that runs along the crown between the ?paraconid and ?metaconid. The distal side of the crown is flat and transversely oriented, and trigonid and talonid have virtually the same MDL.

Remarks. The shape, euhypsodonty and overall dimensions of both teeth point to an interatheriid tytothere. The location of the labial and lingual grooves of MUSM 986 allows its referral to *Miocochilius* (Laventan SALMA, Middle Miocene of Colombia and Bolivia; Stirton 1953; Croft 2007) rather than to *Cochilius* (Colhuehuapian SALMA, Early Miocene of Argentina) or *Interatherium* (Santacrucian SALMA, late Early Miocene of Argentina and Chile; Reguero *et al.* 2003, fig. 7). MUSM 986 differs from *Protypotherium* by having a more open angle of the lingual enamel fold and a less broad posterior half. The shallow lingual groove and the convex distal border fit the topology of P3–P4s of *M. anomopodus* from La Venta, Colombia, rather than that of the smaller species *M. federicoi* from Quebrada Honda, Bolivia (Croft 2007, text-fig. 4). The occlusal surface of MUSM 986 is also more mesiodistally elongated than is observed in *M. federicoi*, *Protypotherium* or *Interatherium*, all of which have a somewhat more squared occlusal surface. This condition might change with wear (as evidenced when comparing the P3 proportions in the paratype of *M. anomopodus* in Stirton 1953, pl. 13C and the FMNH 54761 in Croft 2007, fig. 5), but the degree to which the length/width ratio changes with wear has not been determined in those species. The size and anatomical features of MUSM 1494 are reminiscent to m1s of *M. anomopodus*. However, because the labial side of the anterior lobe (trigonid) is eroded, it is not possible to propose a precise identification (i.e. if the trigonid is bigger than the talonid, then it would be a premolar rather than a molar). The lower dentition of *M. federicoi* is unknown to date, but it is assumed to be somewhat smaller than in *M. anomopodus*, given the size of its upper dentition (Croft 2007). In *Protypotherium*, the lin-

gual sulcus of molars and premolars is shallower than in *Miocochilius* and transversally oriented, whereas in the latter is deeper and mesially oriented (especially in premolars).

LITOPTERNA Ameghino, 1889
MACRAUCHENIIDAE Gervais, 1855
Gen. et sp. indet.
Figure 8C

Referred material. MUSM 1505, edentulous mandibular symphysis, locality DTC-32.

Description and remarks. The symphysis is edentulous and broken (preserved MDL = 58 mm; Fig. 8C), but the preserved alveoli indicate there was neither incisor/canine nor canine/premolar diastema. The incisors were procumbent. Jugal teeth are two-rooted. The distal border of the symphysis is rounded in ventral and dorsal views. The spatium intermandibulare was wide, that is exceeding 20 mm. Three wide and equidistant lateral foramina mentalia are located at mid-height of the corpus mandibulae (H = 18 mm), which is constant in height. The mesial foramen is the largest and deepest one. The symphyseal suture is well fused, indicative of

an adult. Given its bad state of preservation, MUSM 1505 cannot be identified at genus level, although it resembles more in size and proportions the Santacrucian cramaucheniine *Theosodon lallemani* than other macraucheniids, such as the Deseadan *Coniopternium andinum* (smaller; Cifelli and Soria 1983) or the post-Laventan *Promacrauchenia* sp. (bigger; Anaya and MacFadden 1995). It is quite distinct in size and foramina distribution from what is observed in the Santacrucian proterotheriids *Anisolophus australis* and *A. floweri*, senior synonyms of *Proterotherium intermedium* and *Licaphrium pyneanum*, respectively, following Soria (2001). The comparisons with these latter species were based on the specimens figured by Scott (1910, pl. 6, 8).

CRAMAUCHENIIDAE Ameghino, 1902

Genus THEOSODON Ameghino, 1887
cf. *Theosodon* sp.
Figures 8B, E-F

Referred material. MUSM 1509, right dp3, locality IN-008; MUSM 1654, fragmentary axis, locality IN-008; MUSM 1508, right calcaneus, locality IN-011.

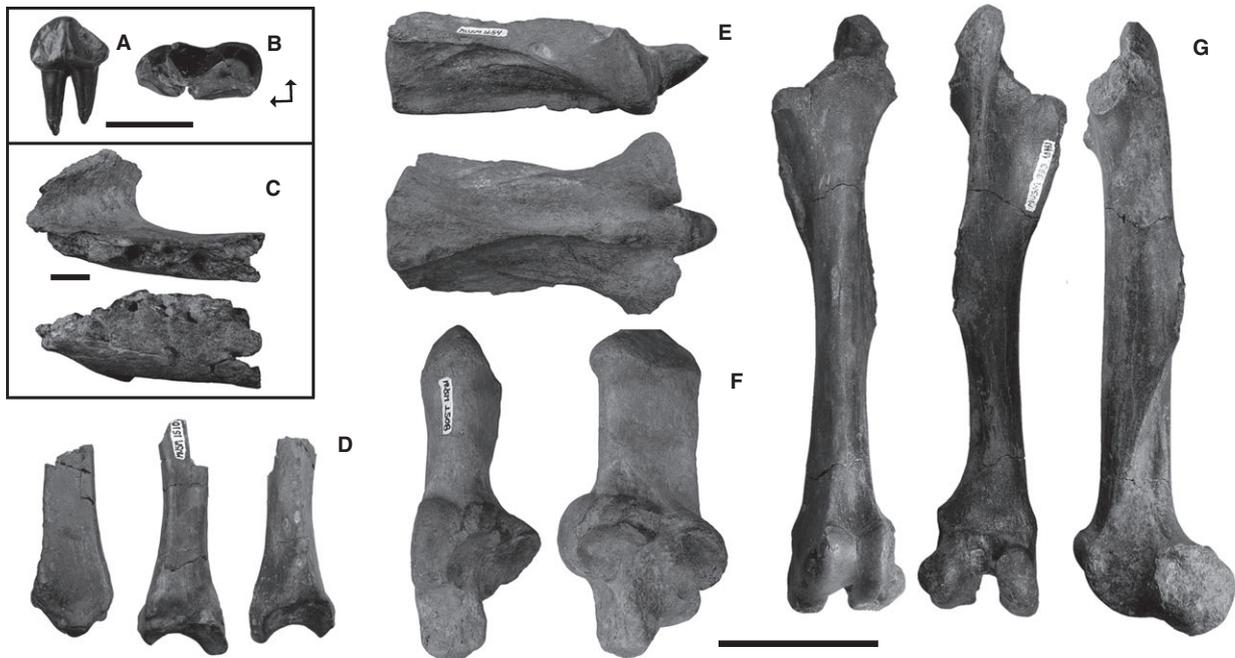


FIG. 8. Lithopterna remains from the Fitzcarrald fauna. A, Proterotheriidae indet., MUSM 1504, right p1. B, cf. *Theosodon* sp., MUSM 1509, right dp3. C, Macraucheniidae indet., edentulous mandibular symphysis, MUSM 1505. D, cf. *Tetramerorhinus* sp., MUSM 1510, distal fragment of a right tibia in anterior, medial and lateral views. E-F, cf. *Theosodon* sp.; E, fragmentary axis, MUSM 1654; F, right calcaneus, MUSM 1508. G, Proterotheriidae indet., MUSM 993, left femur in anterior, posterior, and lateral views. Scale bars represent 1 cm for A-C and 5 cm for D-G.

Description. MUSM 1509 is a two-rooted brachydont lower tooth, elongated mesiodistally (MDL = 13.8 mm; LLL = 5.9 mm; crown H = 4.3 mm; Fig. 8B). The occlusal pattern is birescentic, with a prominent protoconid and a shallow and smooth labial groove in occlusal view. Enamel is very thin, which allows interpreting the tooth as a deciduous molar. There is no cingulid.

MUSM 1654 is a fragmentary axis (APD = 100.6 mm; TD = 59.7 mm; preserved DVH = >36 mm; Fig. 8E). The preserved part is restricted to the corpus vertebrae and atlas facets. It is highly elongated anterodistally and compressed dorsoventrally. The odontoid process is long and conical, with a flat dorsal surface. In ventral view, a sagittal axial keel bifurcates backwards.

MUSM 1508 is a robust right calcaneus (L = 90.3 mm; APD = 41.3 mm; TD = 34.2 mm; Fig. 8F). The tuber calcanei are long, with a sharp apex. The fibular facet is narrow transversely and strongly convex dorsoventrally. The sustentaculum has an oval astragalar facet. The cuboid facet is oblique and saddle-shaped, with a low lateral process. There is no distal facet for the astragalus.

Remarks. The size and pattern of the deciduous tooth MUSM 1509 are compatible with those of several macraucheniid litopterns, including *Theosodon* (Scott 1910). Lower premolars of *Promacrauchenia* sp. from the Pliocene of InChasi, Bolivia (Anaya and MacFadden 1995), are bigger and have deeper lingual grooves than *Theosodon* and MUSM 1509. A long neck with elongated cervical vertebrae is characteristic of macraucheniiids among South American native ungulates. This axis is very similar in general morphology and size to the specimens identified as *Theosodon lallemanti* by Scott (1910). The calcaneus of *Theosodon* differs from *Coniopternium* by its robustness and from both *Coniopternium* and *Pternioconus* by its larger size. Its dimensions, robustness and the shape of fibular, astragalar and cuboid facets also resemble various species of *Theosodon* from the Santa Cruz beds (Scott 1910) and *Theosodon* sp. from the Chucal Fauna of Chile (Croft *et al.* 2004, fig. 17). We are unaware of described calcanei of *Promacrauchenia*, but they are expected to be bigger than *Theosodon* and MUSM 1508. Pending a large scale revision of cramaucheniine litopterns, we tentatively refer the specimens to *Theosodon* sp.

PROTEROTHERIIDAE Ameghino, 1887

Gen. et sp. indet.

Figure 8A, G

Referred material. MUSM 1504, right p1, locality DTC-32; MUSM 993, left femur, locality URU-081.

Description and remarks. MUSM 1504 is a brachydont and gracile biradicate tooth, bearing no cingulid

(MDL = 8.6 mm; LLL = 3.0 mm; crown H = 5.7 mm; Fig. 8A). In occlusal view, the pattern is simple, with a thick and central protoconid, from which run mesiodistally directed the pre- and postprotocristid. The ectolophid is convex but depressed vertically in its distal third. The posterior valley is open lingually. MUSM 1504 is morphologically identical to the p1 of *Villarroelia totoyoi* from La Victoria Fm in Colombia, but much smaller (10.2–14.3 mm; Cifelli and Guerrero 1997). A similar size (c. 10–12 mm) might be assumed for the p1 of *Prolicaphrium sanalfonensis* from La Venta (Cifelli and Guerrero 1997), the latter being smaller than *P. specillatum* from Colhuehuapian beds of Argentinian Patagonia (Ameghino 1902). The femur MUSM 993 is long, slender and mediolaterally compressed (L = 190.8 mm; distal TD = 37.9 mm; distal APD = 52.15 mm; Fig. 8G). The femoral head is not preserved. The greater trochanter is tall, which is characteristic of proterotheriids among litopterns (Croft *et al.* 2004, p. 37). Although damaged, the third trochanter is much developed dorsoventrally, with an elongated apex. The suprapatellar fossa is not as deep as in the macraucheniid? *Coniopternium* sp. from Salla beds described by Shockey (1999). Distal condyles are asymmetrical, the lateral one being more prominent and massive than the medial lip. Both are caudally projected, thus forming a deep intercondylar fossa, as observed in most litopterns and in camelids. Pending new findings, these isolated specimens are referred to an unidentified member of the Proterotheriidae, showing equal affinities with several species of *Tetramerorhinus* (Santacrucian; Scott 1910, pl. 10, figs 10, 15) and *Villarroelia* (Laventan; Cifelli and Guerrero 1997).

PROTEROTHERIINAE Ameghino, 1887

cf. *Tetramerorhinus* sp.

Figure 8D

Referred material. MUSM 1510, distal fragment of a right tibia, locality SEP-007.

Description. Based on the preserved part, this tibia was sheep-sized and very slender (preserved L = 64.6 mm; distal TD = 25.2 mm; distal APD = 23.88 mm; Fig. 8D). The diaphysis is triangular in cross section, with sharp edges. A small triangular astragalar facet is visible on the distal margin of the anterior intercondylar process. The fibular facet is small and triangular. There is no medial malleolus. The posterior intercondylar crest is thick, high and rounded. In ventral view, the astragalar cochlea is deep and asymmetrical, more developed medially.

Remarks. The overall shape points undoubtedly to a litoptern. Among its distinctive features, the anterior

astragalus facet is sigmoidal in macraucheniiids and most proterotheriids, such as *Diadiaphorus* and *Thoatherium*. To our knowledge, a similar triangular shape is observed only in *Tetramerorhinus* spp. from the Santa Cruz beds (Scott 1910, pl. 11, fig. 7). The tibia of *Megadolodus molariformis* from La Venta (Colombia) is bigger and much more robust.

RODENTIA Bowdich, 1821
HYSTRICOGNATHI Tullberg, 1899
CAVIOMORPHA Wood, 1955
CAVIOIDEA Fischer de Waldheim, 1817
DINOMYIDAE Peters, 1873
POTAMARCHINAE Kraglievich, 1926
Potamarchinae indet.
Figure 9A–B

Referred material. MUSM 945, right dp4, locality DTC-32; MUSM 1583, left p4, locality SEP-005.

Description. MUSM 945 is much elongated mesiodistally (MDL = 11.3 mm; LLL = 4.7 mm; H = 9.9 mm; Fig. 9A) and displays a complicated lophid pattern pointing to a dp4. The anterior lophid is U-shaped in occlusal view, with a lingual flexid and a strong labial connection (bifid metalophulid I of Marivaux *et al.* 2004). The lophid immediately posterior to it (metalophid or protolophid?) is Y-shaped, that is bifurcated lingually. The two posterior lophids (hypolophid and posterolophid?) display the ‘usual’ pattern for dp4s and p4s (disconnected one from another, oblique, thick and curved backwards). The enamel is regularly distributed around the crown, and no cementum is discernible. MUSM 945 is low-crowned and has two roots. MUSM 1583 is a left p4, with a trapezoid and compressed mesiodistally occlusal outline (MDL = 5.1 mm; LLL = 4.1 mm; H = 7.8 mm; Fig. 9B). The lingual side is straight in occlusal view. Lophids are connected both lingually and labially, with the exception of the posterolophid, which has only a lingual connection with the hypolophid. Metalophulid I is connected labially to the protoconid, and the hypolophid is connected to the ectolophid. The metalophid (or metalophulid II *sensu* Marivaux *et al.* 2004) is interrupted by a short enamel bridge in its labial third.

Remarks. Even though lophid homology for dp4s is questionable and tentative, as already established at the caviomorph scale by Patterson and Wood (1982), the dp4 MUSM 945 is very similar to the ‘molariforme inferior esquerdo’ AMNH 55824 from the ?late Middle Miocene Upper Juruá fauna of Acre, Brazil, referred to as ‘Dinomyidae indet.’ (Sant’Anna Filho 1994, pl. 7, fig. 1). Concerning MUSM 1583, although it resembles ‘*Scleromys*’ cf. *S. schurmanni* from La Venta in both morphology and size, it differs from all the other speci-

mens here referred to that genus in having a much thicker enamel layer.

Genus SCLEROMYS Ameghino, 1887
‘*Scleromys*’ cf. ‘*S. schurmanni*’ Stehlin, 1940
Figure 9C–F

Referred material. MUSM 939, left M1/2; MUSM 940, left P4; MUSM 941, right m1/2; all three originate from locality DTC-32. MUSM 1566, left m3, locality DTC-37.

Description. The available cheek teeth are protohypsodont, subquadrate and tetralophodont, with loph/lophids oblique (c. 45 degrees with respect to the mesiodistal line) and curved. MUSM 940 (MDL = 3.8 mm; LLL = 3.4 mm; H = 8.1 mm; Fig. 9D) is unilaterally hypsodont, which allows it to be interpreted as an upper tooth. Probably due to the early stage of wear of the tooth, all the lophs are disconnected one from another, with the exception of the mesoloph, connected both lingually and labially to the posteroloph. The hypoflexus reaches the labial side of the tooth (no mure), and the mesoflexid reaches the lingual side. The posterior flexus has closed, forming a narrow and elongated metafossette. Because the anteroloph is transversally shorter than the protoloph, it is more likely to be a P4 than a molar. MUSM 939 (MDL = 4.2 mm; LLL = 3.6 mm; H = 8.4 mm; Fig. 9C) and MUSM 941 (MDL = 4.6 mm; LLL = 3.6 mm; H = 9.5 mm; Fig. 9E) are more elongated mesiodistally than MUSM 940 and bear a contact facet for a distal tooth. In both teeth, the first lobe is prismatic and the second lobe is laminar. We identify MUSM 939 as an upper left molar (M1/2) in which all the lophs but the posteroloph are connected at both ends. The latter is connected labially to the hypoloph. All the lophs are curved backwards. The anterofossette is narrow and located at the mesiolabial angle of the tooth. The mesoflexus closes, forming a very narrow and elongated mesofossette. The hypoflexus is posteriorly convex. MUSM 941 is a right m1/2. As in MUSM 939, all the lophids except the posterolophid are connected at both ends. The latter is only connected lingually to the hypolophid (the hypofossettid extends labiolingually). The metalophulid II is sigmoid. A small, narrow and oblique anterofossettid is located at the mesiolingual angle of the tooth. The mesoflexid closes, forming a very narrow and elongated mesofossettid. The hypoflexid is sigmoid. MUSM 1566 is a left m3, elongated mesiodistally and at an early stage of wear (MDL = 4.4 mm; LLL = 3.1 mm; H = 8.4 mm; Fig. 9F). The anterolophid (metalophulid I) and the metalophid (metalophulid II) are connected at both ends. The hypolophid and the posterolophid (damaged in its distolingual part) are connected lingually.

Remarks. The available teeth have a typical dinomyid occlusal pattern (hypsodont, tetralophodont and with oblique loph/lophids). The specimens are very similar in terms of dimensions and morphological features to those referred to as ‘*Scleromys*’ cf. ‘*S. schurmanni*’ from the Middle Miocene of La Venta, Colombia, and, to a lesser

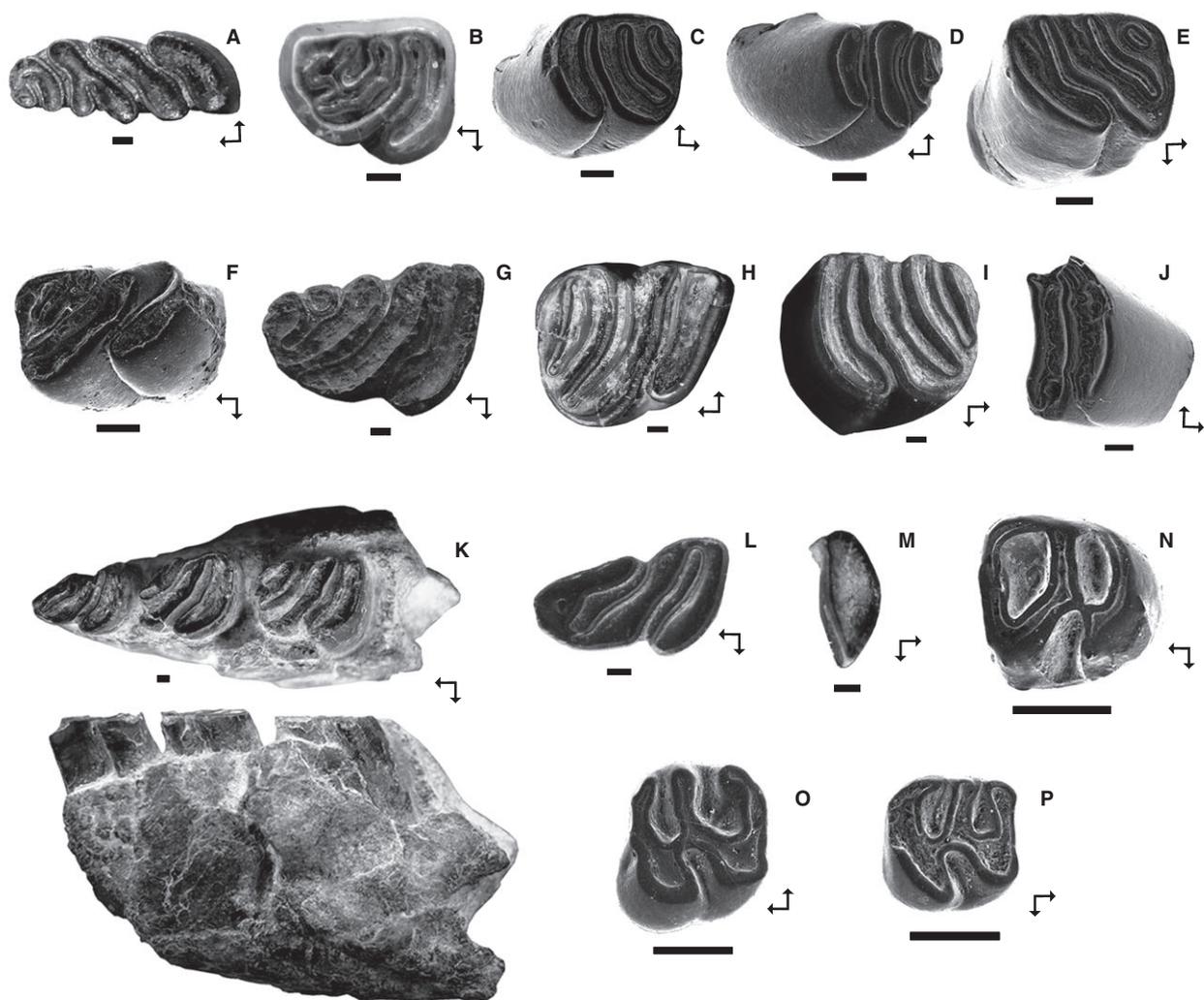


FIG. 9. Rodents from the Fitzcarrald fauna. A–B, Potamarchinae indet; A, right dp4, MUSM 945; B, left p4, MUSM 1583. C–F, ‘*Scleromys*’ cf. ‘*S. schurmanni*’; C, left M1/2, MUSM 939; D, left P4, MUSM 940; E, right m1/2, MUSM 941; F, left m3, MUSM 1566. G–I, *Drytomomys* cf. *aequatorialis*; G, left p4, MUSM 946; H, right M1/2, MUSM 1680; I, right m2, MUSM 942. J, *Potamarchus murinus*, MUSM 1576, right upper molar fragment. K–L, *Neopiblema* sp.; K, left mandibular fragment with p4–m2 in occlusal and labial views, MUSM 1607; L, left p4, MUSM 944. M, *Prodolichotis pridiana*, MUSM 1584, mesial prism of a right upper molar. N, *Acarechimys* sp., MUSM 1569, left m3. O–P, Octodontoidea indet.; O, left M2, MUSM 1570; P, right m1/2, MUSM 1567. All scale bars represent 1 mm. Arrows indicate mesial and labial directions.

extent, to the larger ‘*Scleromys*’ cf. ‘*S. colombianus*’ from the same locality (Walton 1997, p. 397, fig. 24.3). The molars MUSM 939 and 941 do not display the Y-shaped metaloph(id)/anteroloph(id) pattern as observed in ‘early’ representatives of the former taxon in La Venta (Walton 1997, p. 398). In that aspect, they are more similar to the m2 DGM 582M from the Upper Juruá (?late Middle Miocene, Brazil) attributed to ‘cf. ‘*Scleromys colombianus*’ by Sant’Anna Filho (1994, pl. 7, fig. 7). Both upper and lower teeth from the Fitzcarrald fauna closely resemble the specimens of *Scleromys quadrangulatus* from the late

Early Miocene Pinturas Formation of Patagonia as described by Kramarz and Bellosi (2005) and Kramarz (2006, p. 58, fig. 3D), and from ‘Pinturan’ beds of the upper Madre de Dios basin, as mentioned by Marivaux *et al.* (2012). However, in *S. quadrangulatus*, the m1 already has the hypoflexid closed on the lingual side, the mesofossettid recently closed and the anterofossettid, although present, is smaller and less persistent than in ‘*Scleromys*’ from La Venta. Additionally, in *S. quadrangulatus*, the hypoflexid is less convex and sigmoid than the one observed in Fitzcarrald. ‘*Scleromys*’ teeth from

Fitzcarrald are more elongated mesiodistally and more hypsodont than *Scleromys* sp. from the Early Miocene Mariño Fm of northern Argentina (Cerdeño and Vucetich 2007), while *S. angustus* and *S. osbornianus* (Early Miocene, Santa Cruz, Patagonia) display a simpler pattern at early stages of wear (i.e. trilophodont; Kramarz 2006). MUSM 1566 is virtually identical in morphology (but slightly different proportions) to the isolated dinomyid molar ('*Scleromys*' sp. MUSM 1972) from Colloncuran beds of the upper Madre de Dios, Peru, described and figured by Antoine *et al.* (2013, fig. 3J). The '*Scleromys*' tooth from Madre de Dios is, however, more quadrangular and was interpreted by Antoine *et al.* (2013) as an m1 at 'stage of wear n°2'.

Genus DRYTOMOMYS Anthony, 1922
Drytomomys cf. aequatorialis Anthony, 1922
 Figure 9G-I

Referred material. MUSM 943, left M1/2; MUSM 946, left p4; MUSM 942, right m2; all from locality DTC-32. MUSM 1680, right M1/2, locality DTC-37.

Description. All available teeth are large, protohypsodont and tetralophodont. MUSM 943 (MDL = 7.1 mm; LLL = 6.3 mm; H = 19.3 mm) and MUSM 1680 (MDL = 9.6 mm; LLL = 8.1 mm; H = 18.4 mm; Fig. 9H) are much worn M1/2s, quadrate and with weakly oblique lophs in occlusal view. The anteroloph is straight and connected labially to the protoloph. The latter connects the metaloph only lingually. The metaloph joins the posteroloph labially. MUSM 943 displays a small anterofossette. MUSM 946 is a tetralophodont p4, elongated mesiodistally in occlusal view (MDL = 10.7 mm; LLL = 7.1 mm; H = 25.0 mm; Fig. 9G). The anterolophid (or metalophulid I) and the metalophulid II are connected anterolabially. There is a small circular lingual island (mesostilid?) between the metalophulid I and the metalophulid II at the given stage of wear. The hypolophid is the longest lophid, much oblique and curved backwards, united distolingually to the posterolophid. The right m2 MUSM 942 (MDL = 8.3 mm; LLL = 7.8 mm; H = 24.2 mm; Fig. 9I) is quadrate in occlusal view. The anterolophid is restricted to the mesiolingual angle of the tooth. The metalophulid II is larger and connects labially to the hypolophid. The latter joins the posterolophid only lingually. The hypoflexid almost reaches the lingual side of the tooth. The distal lamina of enamel is at least twice as thick as the mesial one.

Remarks. The tetralophodont design of the p4 (MUSM 946) is similar to that observed in p4s of *D. aequatorialis*, although p4s of *D. typicus* are not known (the holotype includes a dp4, not p4). The measurements of the m2 (MUSM 942) remain the same along the crown, whereas in *D. typicus*, the m2 gets narrower towards the base of the tooth. Most of the differences between *D. typicus* and

D. aequatorialis are based on mandibular traits which make isolated teeth very difficult to identify. However, the cheek tooth referred to as *D. cf. typicus* from north-eastern Argentina (MLP 15-250; Candela and Nasif 2006) is clearly different from MUSM 942 in having the anterior edge of the enamel layers crenulated, thinner and lower than the posterior edge, a deeper hypoflexid that extends towards the base of the tooth and a posterior flexid that has become a metafossettid. These traits are not observed in MUSM 942, although the latter trait might change with wear. Molars assigned to *D. aequatorialis* are generally more quadrangular than available molars referred to *D. typicus*, which are more mesiodistally elongated. In this respect, the Fitzcarrald teeth fit better with the teeth dimensions and proportions of *D. aequatorialis*. The remains from the Fitzcarrald fauna strongly resemble the specimens of '*Olenopsis* sp. (large)' from the late Middle Miocene of La Venta, Colombia (Walton 1997, p. 397, fig. 24.3 I-K). In particular, the pattern of p4 is strikingly comparable. The taxonomic revision of large Miocene dinomyids led Candela and Nasif (2006) to assign specimens recovered from La Venta and previously referred to as '*Olenopsis* sp. (large)' to *Drytomomys aequatorialis*. We follow their opinion here. To date, however, the two different species recognized in La Venta and differing mainly in size (Walton 1997) have not been formally named or described.

Genus POTAMARCHUS Burmeister, 1885
Potamarchus murinus Burmeister, 1885
 Figure 9J

Referred material. MUSM 1576, right upper molar fragment, locality IN-008.

Description. The available tooth fragment is large and protohypsodont (LLL = 6.07 mm; H = 7.07 mm; Fig. 9J). Only the two mesial lophs are preserved. They are closely appressed but not oblique, which places it as an upper molar, possibly M3. Both lophs are united labially by a thin enamel bridge and separated lingually. The distal enamel blade of each loph is densely crenulated. The enamel is thinner in the crenulated layers than in the non-crenulated layers. Lophs are connected by cementum.

Remarks. Crenulation of the distal enamel blades points unambiguously to *Potamarchus murinus*, from the Late Miocene of Argentina, Brazil and Venezuela (Burmeister 1885; Frailey 1986; Linares 2004) and the late Middle or Late Miocene of the Upper Juruá, Brazil (Sant'Anna Filho 1994). Such a feature is not observed in *P. sigmodon* Ameghino, 1891, from the Late Miocene of Patagonia and Brazil (Sant'Anna Filho 1994). Size is consistent with the former (Frailey 1986). Although crenulation has also

been observed in one isolated m2 of *Drytomomys typicus* (MLP 15-250) from the Mesopotamian (Late Miocene) of Argentina, the crenulated layer in the latter is in the mesial side and is much thinner than in *P. murinus*. The occurrence of *P. murinus* in the late Middle Miocene Fitzcarrald fauna may represent the FAD of the species.

CAVIIDAE Fischer de Waldheim, 1817
DOLICHOTINAE Pocock, 1922

Genus PRODOLICHOTIS Kraglievich, 1932
Prodolichotis pridiana Fields, 1957
Figure 9M

Referred material. MUSM 1584, mesial prism of a right upper molar, locality DTC-32.

Description. MUSM 1584 is a fragment of a hypselodont and prismatic cheek tooth (4.44 mm wide labiolingually; Fig. 9M). The available prism is lobulated in occlusal view, with a rounded tip and a vestige of an enamel bridge (distolabial sulcus) on one side. Such features place this fragment as the mesial prism of a right upper cheek tooth of a caviid. The convexity of the mesial border, together with the subrectilinearity of the distal border, suggests this fragment may belong to an upper molar rather than to a P4. The enamel is much thicker lingually than labially, and it vanishes on the rounded part of the labial side of the prism. No dentine central crest is observable.

Remarks. The shape of MUSM 1584 is consistent with many upper molars of dolichotines. The prism differs from those of the Late Miocene *Orthomysetera* Ameghino, 1889, and the extant *Dolichotis* Desmarest, 1820, by being slightly more compressed mesiodistally. Although its dimensions are much smaller, its pattern is much reminiscent of the extant genus *Dolichotis* Desmarest, 1820. The thickness and the distribution of the enamel point to *Prodolichotis* (Walton 1997; Ubilla and Rinderknecht 2003). Within this genus, MUSM 1584 closely resembles the mesial prisms referred to as *Prodolichotis pridiana* Fields, 1957, from the late Middle Miocene of La Venta, Colombia (Walton 1997, 201, fig. 24.7), *P. lacunosa* Kraglievich, 1930, and *P. prisca*, from the Late Miocene of Argentina (Ubilla and Rinderknecht 2003). The absence of a dentine central crest on the occlusal surface is considered to be a plesiomorphic trait (Pérez and Vucetich 2011) observed in basal caviids (e.g. eocardiids), hydrochoerids, *Guiomys unica* and *Prodolichotis pridiana*. Based on this diagnostic trait, MUSM 1584 is herein placed in the latter species. *Prodolichotis* has a late Middle Miocene range in northern South America (Colombia, Bolivia and Peru; Walton 1997; Chick 2009) and a Late Miocene to early Pliocene range in

southern South America (Argentina and Uruguay; Ubilla and Rinderknecht 2003). There seems to be a southward distributional shift of representatives of this genus in South America through the Late Neogene.

CHINCHILLOIDEA Bennett, 1833
NEOEPIBLEMIDAE Kraglievich, 1926

Genus NEOEPIBLEMA Ameghino, 1889
Neopiblema sp.
Figure 9K–L

Referred material. MUSM 1607, left mandibular fragment with p4–m2; MUSM 944, left p4; both from locality DTC-32.

Description. The left mandibular fragment MUSM 1607 is broken in front of p4, and the symphysis is not preserved. The preserved part displays the p4–m2 series (L = 25.7 mm; Fig. 9K), a triangular cross section of the lower incisor within the corpus mandibulae and a mesial print of the alveolus of m3. The masseteric crest is oblique and restricted to the ventral half of the corpus mandibulae; its anterodorsal limit (for the insertion of the masseter lateralis muscle) is located below the boundary between m1 and m2. The incisor runs along the ventral margin of the corpus, deeper and more robust distally (preserved H = 20.7 mm). The jugal teeth are oriented upward and forward in labial view. All teeth are hypselodont and trilophodont, with a thick layer of coronar cement between all the lophids. The lophids are oblique and either curved frontward (metalophulid I), straight (metalophulid II) or curved backward (hypolophid). The p4 MUSM 944 (MDL = 8.1 mm; LLL = 5.0 mm; H = 16.1 mm; Fig. 9L), p4 MUSM 1607 (MDL = 7.5 mm; LLL = 5.9 mm; Fig. 9K) and m1 MUSM 1607 (MDL = 7.0 mm; LLL = 6.5 mm; Fig. 9K) have an S-shaped occlusal pattern, with the metalophulid II connected mesiolabially to the metalophulid I and distolingually to the hypolophid. The m2 MUSM 1607 (MDL = 8.3 mm; LLL = 6.6 mm; Fig. 9K) is tetralophodont but displays a globally similar pattern (metalophulid I and metalophulid II connected mesiolabially), with the exception of the hypolophid, free of any contact with the metalophulid II as the hypoflexid crosses the tooth labiolingually. The advanced wear stage prevents establishing the presence or absence of an antero-fossettid.

Remarks. The hypselodontology of the jugal teeth, their occlusal pattern (trilophodont and tetralophodont, with remote lophids) and the abundance of coronar cement filling the flexids point unequivocally to their belonging to neopiblemid hystricognath rodents. The dental morphology is highly reminiscent of that observed in *Neopiblema ambrosettianus* (Ameghino 1889) from the Late Miocene of Patagonia and Amazonian Brazil (for comprehensive synonymy, see Negri and Ferigolo 1999). Yet, in the latter, only p4 might be S-shaped, while all the lower molars have an isolated hypolophid (Mones and de

Toledo 1989). The metalophulid I of p4 is much narrower in MUSM 1607 and MUSM 944 than in the specimens from the Acre fauna of Amazonian Brazil (Mones and de Toledo 1989; pers. obs. of UFAC PV82, Niterói locality). Furthermore, the specimens are twice as small as the smallest specimens of *N. ambrosettianus* from the Acre fauna (Bocquentin-Villanueva *et al.* 1990; pers. obs. of UFAC collection). In the cow-sized neoeplemid *Phoberomys* Kraglievich, 1932, from the Late Miocene and Pliocene of South America, all the lophids are distinct in shape and orientation, at least in m1–m3 (Kraglievich 1926, 1932; Patterson 1942; Candela 2005). The much smaller neoeplemid *Perimys* Ameghino, 1887, from the Miocene of Patagonia and Chile has bilophodont teeth (e.g. Flynn *et al.* 2002; Candela 2005; Kramarz and Bellosi 2005). As a consequence, we refer the mandible MUSM 1607 and the p4 MUSM 944 to as *Neoeplema* sp. This might represent the earliest occurrence of the genus, so far restricted to the Late Miocene.

OCTODONTOIDEA Waterhouse, 1839

Incertae sedis

Octodontoidea indet.

Figure 9O–P

Referred material. MUSM 1570, left M2; MUSM 1567, right m1/2; both from locality IN-008.

Description. Specimens are small, brachydont, with a trilophodont pattern, alternating flexuses/flexids, and a quadrangular contour. In the M2 MUSM 1570 (MDL = 1.75 mm; LLL = 1.79 mm; Fig. 9O), the labial flexuses are open at the observed stage of wear (adult specimen). The metaflexus is much wider and deeper than the paraflexus. The hypoflexus is deep transversely, and its internal angle points anteriorly. The protocone and hypocone areas are enlarged and have somewhat squared lingual borders. MUSM 1567 is interpreted as a right m1/2 (MDL = 1.45 mm; LLL = 1.43 mm; Fig. 9P). All flexids are anteriorly oriented. The meso- and metaflexid are open lingually and show a constricted opening. The closure of the mesoflexid would have occurred first. The hypoflexid is as developed transversely as the lingual flexids but with a much wider opening.

Remarks. Among Miocene South American rodents, small-sized brachydont and tri/tetralophodont teeth with alternate flexuses/-ids are characteristic of octodontoids. They are referred either to heteropsomyine echimyids (Wood and Patterson 1959; Frailey 1986; McKenna and Bell 1997; Walton 1997; Vucetich *et al.* 1999), to ctenomyine octodontids, based notably on their flexid closure sequence (Verzi 1999; Croft *et al.* 2011), or to octodontoids with uncertain affinities (Kramarz 2004; Arnal *et al.* 2014). We follow the latter opinion. In the present specimens, the flexids are oriented mesially, as in *Acarechimys*

from the late Early, Middle and late Middle Miocene of South America (Pascual 1967; Walton 1997; Croft *et al.* 2011) and *Chasichimys* from the late Middle Miocene of Patagonia (Pascual 1967). The lingual flexid closure sequence in MUSM 1567 is identical to that observed in *Acarechimys* but the reverse of that in *Chasichimys* (Pascual 1967). MUSM 1567 differs from *Acarechimys* by having the talonid wider (transversely) than the trigonid and a comparatively small metaconid without a posterior arm. Although size and general shape of MUSM 1567 resemble *Acarechimys* sp. from the early Middle Miocene of Collon-Curá (Vucetich *et al.* 1993), in this latter specimen, the protoconid is more lingual than the hypococonid, the metaconid is larger, and the hypolophid is transverse, unlike MUSM 1567. It resembles *Theridomysops parvulus* (late Miocene of Argentina, Vucetich 1995) in its general morphology, including a flat mesial border and convex distal border, constricted opening of the meso- and metaflexids, and a hypoflexid that is oblique backwards. A small metaconid without a posterior arm is also observed in m1s of *Theridomysops parvulus*. The talonid wider than the trigonid remains, however, a peculiar trait of MUSM 1569. MUSM 1570, on the other hand, differs from *Acarechimys* by showing an anterior fold on the anteroloph. Additionally, the paraflexus and metaflexus in upper molars of *Acarechimys* are early closed labially with wear, which is not the case in MUSM 1570. MUSM 1570 is also different from *Willidewu esteparius* in having a bigger protocone area, wider and deeper flexuses and a more complex posteroloph that has a broad lingual area (hypocone area) and a mesially oriented labial region.

Genus ACARECHIMYS Patterson (*in* Kraglievich, 1965)

Acarechimys sp.

Figure 9N

Referred material. MUSM 1569, left m3, locality IN-008.

Description. MUSM 1569 is a small and brachydont m3 (MDL = 5.79 mm; LLL = 5.69 mm; Fig. 9N). It has a trilophodont pattern with alternating flexuses/flexids and subquadrangular contour. The lophid pattern is similar to that of MUSM 1567, but with closed meso- and metafossettids. The mesoflexid closed prior to the metaflexid. The anterolophid is flat, and the posterolophid is convex, with no trace of posterior tooth.

Remarks. In MUSM 1569, the lingual flexid closure is identical to that observed in *Acarechimys* but the reverse of that in *Chasichimys* (Pascual 1967). The trigonid is slightly larger than the talonid, as in *Acarechimys*. (In *Theridomysops parvulus* and *Willidewu esteparius*, trigonid and talonid are of about the same dimensions.) Orienta-

tion of lingual flexids is transverse, as in *Acarechimys*. MUSM 1569 does not possess the spur that originates from the protoconid of the m3 in *Willidewu esteparius*, nor does it have the small fossettoid on the posterolingual side of the anterolophid present in this taxon (Vucetich and Verzi 1991). The size and general morphology of this tooth is consistent with 'A. cf. *A. minutissimus*' from the late Middle Miocene of La Venta, Colombia (Walton 1997), and is therefore identified as *Acarechimys* sp. pending the discovery of more complete material.

CETARTIODACTYLA Montgelard, Catzeflis, and Douzery,
1997

CETACEA Brisson, 1762
ODONTOCETI Flower, 1867
DELPHINIDA Muizon, 1984

Gen. et sp. indet.

Figure 10

Referred material. MUSM 1612, left tympanic bulla, locality IN-008.

Description and remarks. MUSM 1612 (Fig. 10) has been identified as Delphinida because of the excavation, although weak, of the posterodorsal region of the involucrum. It is referable to the Delphinoidea + Inoidea clade because of the lack of an anterior apophysis (present in Lipotoidea). The persistence of the lateral furrow excludes it from Delphinidae, Phocoenidae and Monodontidae. It shares some weak affinities with *Inia* because of the presence of a deep lateral furrow, a robust base to the sigmoid process and a wide and shallow medial furrow. In spite of its peculiar morphology, it is difficult to make any generic or even suprageneric assignment.

DISCUSSION

Age

Geomorphological and sedimentological data allow the fossiliferous deposits from the Fitzcarrald Arch reported



FIG. 10. Delphinida gen. et sp. indet. A–C, left tympanic bulla, MUSM 1612; A, ventral; B, lateral; and C, dorsal views. Scale bar represents 1 cm.

here to be assigned a Middle Miocene age (Espurt *et al.* 2006, 2007). The synchronicity of vertebrate-yielding deposits from the Inuya and Mapuya rivers area is further supported by the geometry of channelized deposits that can be followed at both local and regional scales in the field and as individual reflectors through seismic cross sections (see Espurt *et al.* 2007, 2010).

The localities with the most diversified mammalian faunas reported here correspond either to moderate-/high-energy facies (e.g. IN-008, DTC-37) or to low-energy facies (lignite-rich clays at DTC-32). These localities yield very similar mammalian assemblages (Table 1) further indicating their contemporaneity. Moreover, they preserve delicate and relatively complete fragile bones (octodontoid teeth; mandibles and maxillae; complete turtle carapaces). As such, they are likely to attest to: (1) the unambiguous absence of significant transport or bypass; and (2) short-term deposition processes, consistent with the nearshore environments suggested by the fossiliferous channelized conglomerates (see Espurt *et al.* 2010; Pujos *et al.* 2013). Consequently, although these assemblages include a wide spectrum of mammalian species, supposedly spanning a long interval (late Early Miocene – early Late Miocene) in other South American areas, we favour the hypothesis of the Fitzcarrald area as a palaeobiodiversity hotspot, encompassing both early offshoots and late representatives of mammalian clades.

The Fitzcarrald fauna (summarized in Table 2) is furthermore assigned a Laventan age (late Middle Miocene) based on the presence of mammals belonging to the 'Miocochilius assemblage zone' defined in La Venta, Colombia (Madden *et al.* 1997), in most of the localities sampled. Indeed, *Miocochilius anomopodus*, *Prodolichotis pridiani*, *Drytomomys aequatorialis* and *Pericotaxodon platignathus* are present in Fitzcarrald and span the whole Laventan SALMA (13.5–11.8 Ma) in La Venta, while *Granastrapotherium snorki* and 'Scleromys' *schurmanni* are restricted to the 13.46- to 12.29-Ma interval in Colombia (Madden *et al.* 1997; Croft 2007). Eight of the 14 fossiliferous localities sampled have yielded genera restricted to the Laventan age (Table 1). Some of these localities have also yielded genera recorded in the 'Miocochilius assemblage zone' but not restricted to the Laventan age (*Neoglyptatelus*, *Boreostemma*, *Xenastropotherium*, *Theosodon* and *Acarechimys*), and/or taxa that have not been previously recorded from this time period. For instance, DTC 32 (the richest and most diverse locality sampled) bears Laventan taxa (*P. platignathus*, *M. anomopodus*, *G. cf. snorki*, *D. aequatorialis*, *P. pridiani*, 'Scleromys' cf. 'S'. *schurmanni*) but also Late Miocene (*Urumacotherium*, *Potamarchus* and *Neopiblema*) and Early Miocene (*Parapalaehoplophorus*) taxa. Moreover, the crocodyliform assemblage is also congruent with a late Middle Miocene age, especially based on the presence of *Langstonia huilen-*

TABLE 1. Taxonomic composition of the Fitzcarrald local fauna per locality.

	IN-007	IN-B-002/003	DTC-14	IN-011	URU-081	DTC-28	SEP-005	IN-010	IN-DTC	SEP-007	DTC-20	DTC-37	IN-008*	DTC-32*
Borhyaenoidea														1649
<i>Parapalaehoplophorus</i>														980, 982
<i>septentrionalis</i>														
<i>Neoglyptatelus originalis</i>							1573	1601						932, 933
<i>Borestemna</i> sp.	1608					1602				1603				934
Glyptodontidae indet.														985
<i>Urumacotherium</i> sp.									1564					
<i>Megatheriiculus</i> sp.								938						
Mylodontidae indet.	1588									947				904
Megalonychidae indet.											1468	1467		
<i>Xenastropotherium</i> sp.														1477
<i>Granastropotherium</i>						994								
cf. <i>storki</i>														
<i>Pericotaxodon</i> cf.			1487					1503	1489			1501, 1506	1478	1500, 922
<i>Platignathus</i>														
<i>Miocochilus</i>														986, 1494
<i>anomopodus</i>														
cf. <i>Theosodon</i> sp.				1508									1509, 1654	
cf. <i>Tetramerorhinus</i> sp.										1510				1504
Proterotheriidae indet.					993									1505
Macraucheniiidae indet.												1566		939, 940, 941
' <i>Scleromys</i> ' cf. <i>S.</i>							1583							
<i>schurmanni</i>														
<i>Drytomomys</i> cf.												1680		943, 946, 942
<i>aequatorialis</i>													1576	
<i>Potamarchus murinus</i>														945
Potamarchinae indet.														1584
<i>Prodolichotis pridianae</i>														1607, 944
<i>Neoeptlema</i> sp.														
Octodontoidea indet.														1570, 1567
<i>Acarechimys</i> sp.														1569
Delphinida indet.														1612
Platanistinae indet.														1611

*Localities where several teeth of the Laventan sebecid *Langstonia hutilensis* (Salas-Gismondi et al. 2007) have been found *in situ*. NB all specimens were collected *in situ*; numbers refer to MUSM catalogue numbers.

TABLE 2. Taxonomic mammal list for Fitzcarrald local fauna.

Marsupialia	Litopterna
Sparassodonta	Macraucheniiidae
(1) Borhyaenoidea	(13) cf. <i>Theosodon</i> sp.
Xenarthra	Protheroheriidae
Cingulata	(14) cf. <i>Tetramerorhinus</i> sp.
Glyptodontidae	Rodentia
(2) <i>Parapropalaehoplophorus septentrionalis</i>	Dinomyidae
(3) <i>Neoglyptatelus originalis</i>	(15) ' <i>Scleromys</i> ' cf. ' <i>S</i> ' <i>schurmanni</i>
(4) <i>Boreostemma</i> sp.	(16) <i>Drytomomys</i> cf. <i>aequatorialis</i>
Pilosa	(17) <i>Potamarchus murinus</i>
(5) <i>Urumacotherium</i> sp.	(18) Potamarchinae indet.
(6) <i>Megathericulus</i> sp.	Caviidae
(7) Mylodontidae gen. et sp. indet.	(19) <i>Prodolichotis pridiana</i>
(8) Megalonychidae gen. et sp. indet.	Neopiblemidae
Astrapotheria	(20) <i>Neopiblema</i> sp.
(9) <i>Xenastrapotherium</i> sp.	Octodontoidea
(10) <i>Granastrapotherium</i> cf. <i>snorki</i>	(21) Octodontoidea indet.
Notoungulata	(22) <i>Acarechimys</i> sp.
Toxodontidae	Cetacea
(11) <i>Pericotoxodon</i> cf. <i>platignathus</i>	(23) Platanistinae gen. et sp. indet.
Interatheriidae	(24) Delphinida gen. et sp. indet.
(12) <i>Miocochilius anomopodus</i>	

sis, the youngest known sebecid, so far restricted to the Laventan stage. (For instance, there is no evidence of sebecids in Late Miocene faunas such as Urumaco or Acre.) In Fitzcarrald, several teeth of *L. huilensis* have been found at localities DTC-32 and IN-008. In fact, excluding localities IN-B-002/003 and URU-81 whose fossils are not sufficiently well preserved to allow for a precise identification, the sole locality without any formal Laventan taxon is SEP-007, yielding *Megathericulus* and *Tetramerorhinus*. However, megatheriine specimens have been described in La Venta (although no specific assignation was made), and *Megathericulus* spp. have been recorded in Middle Miocene faunas of Argentina (see Pujos *et al.* 2013). In summary, the assignment of a Middle Miocene age (Laventan SALMA) to the Fitzcarrald local fauna is supported by stratigraphical and sedimentological analyses, as well as biochronology, as most localities have borne taxa belonging to or defining Laventan SALMA.

In the section at DTC-32, palaeomagnetic polarity switches from normal to reverse, which hypothetically provides a numerical age around 13.20, 12.83 or 12.58 Ma, owing to Laventan biochronology and GMPTS (Madden *et al.* 1997). This supports previous estimates based on the vertebrate fauna as a whole (Antoine *et al.* 2007; Salas-Gismondi *et al.* 2007).

The cramaucheniine litoptern *Theosodon* ranges geographically from Patagonia to Colombia, and temporally from the Colhuehuapian up to the Chasicuan SALMAs (Early to early Late Miocene; Croft *et al.* 2004). *Tetramerorhinus* is documented in late Early Miocene localities of

Argentina and Chile (Croft *et al.* 2004). The Fitzcarrald local fauna records at least two FADs, *Potamarchus murinus* and *Neopiblema* sp., both previously reported from the Late Miocene of Argentina, Brazil and Venezuela (*P. murinus*) and from the Late Miocene of Argentina and Brazil (*Neopiblema*). Concerning xenarthrans, *Megathericulus* has been reported in the Middle Miocene of Argentina in localities stratigraphically referred to the SALMA Friasian *sensu lato* (e.g. Scillato-Yané 1998), but with radiometric dates specifically pointing to SALMA Mayoan (De Iuliis *et al.* 2008). Based on phylogenetic studies (e.g. Croft *et al.* 2007; Zurita *et al.* 2013), the Fitzcarrald glyptodonts appear to be basal forms within their lineages. For instance, *Boreostemma* documents an early step of northern glyptodont diversification. The presence of taxa with basal traits (e.g. with glyptateline-like osteoderm ornamentation) and affinities suggests either the continued presence of basal clades at tropical areas throughout the Tertiary or the survival of early glyptodont offshoots. Fitzcarrald also records a Santacrucian stem glyptodont, *Parapropalaehoplophorus*, a taxon previously considered endemic to the Chucal area, in Chile (Croft *et al.* 2007). The apparent multitemporal character of the Fitzcarrald fauna can be explained in the context of some tropical faunistic features, such as high-diversity, stable and long-lasting environmental conditions and survival of lineages of former wider distribution (e.g. Wesselingh and Salo 2006). From Middle to Late Miocene, climatic and environmental differences between low and high latitudes increased notably, a fact that might have

affected the distribution of organisms of limited habitat tolerance. Due to the expansion of drier, open habitats at middle to high latitudes, clades previously distributed in forested environments throughout the continent might have become restricted to lower latitudes. In any case, tropical localities can provide key data to understand the phylogenetic history and subsequent geographical distribution of major mammalian clades.

Ecology

The megawetland Pebas complex, identified in the Neogene Fitzcarrald deposits (Hovikoski *et al.* 2005; Espurt *et al.* 2006), constitutes a long-lasting ecosystem that provided favourable conditions for the adaptative radiation of endemic taxa in tropical South America (Hoorn *et al.* 2010). As part of the Pebas system, the Fitzcarrald and La Venta localities might have shared somewhat similar environmental, if not depositional, conditions proposed for the latter, at least for their terrestrial components (Espurt *et al.* 2007, 2010), whereas the Late Miocene localities of Acre (Cozzuol 2006; Negri *et al.* 2010) and Urumaco (Sánchez-Villagra and Aguilera 2006) might represent a later stage in the development of major fluvial basins in tropical South America. It has been suggested that tropical conditions have occasionally extended to the South into the northern Parana region (Lundberg *et al.* 1998).

Ecological interpretations for the Fitzcarrald fossil mammals, as in other tropical localities in South America, are mostly based on extrapolations of studies from the southern cone of the continent (which are better represented in the fossil record). These, in turn, are mostly based on morphological comparisons with modern taxa and their distribution in extant ecosystems. Thus, toxodonts are traditionally considered to be grassland inhabitants and possessors of grazing habits on the basis of their hypselodont dentition and the ability that it confers to feed on hard abrasive grasses (e.g. Kay and Madden 1997). In Fitzcarrald, the two notoungulates recorded differ strongly in size, *Pericotoxodon* being a mega-mammal (>500 kg) and *Miocochilius* a small-sized mammal (<10 kg; Kay and Madden 1997). According to Kay and Madden (1997), a possible ecological analogue for *Miocochilius* is the extant lagomorph *Sylvilagus*, a grazer that inhabits transitional forests and grasslands in the Neotropics. In general, tyotherid notoungulates are referred to as rodent/rabbit-like forms (e.g. Ameghino 1889; Croft 1999), capable of fast locomotion but poor digging capabilities compared with rodents (Cassini *et al.* 2012). Astrapotheres, on the other hand, are graviportal mega-herbivores that have long been considered associated with amphibious habits (e.g. Riggs 1935; Webb 1978). As such, they could have lived in riparian areas and fed upon leafy

and soft vegetation because of their brachyodont dentition. More recent studies based on *Astrapotherium magnum* data have questioned its supposedly amphibious affinities, pointing rather to a cursorial type of locomotion similar to that of modern large ungulates (e.g. Avilla and Vizcaíno 2005; Cassini *et al.* 2012). According to the hypothesis proposed by Kay and Madden (1997), the three large herbivores present in the Fitzcarrald local fauna (*Pericotoxodon*, *Xenastrapotherium* and *Granastrapotherium*) were likely to create and maintain 'edge habitats' within the surrounding forested area.

Concerning litopterns, the presence of opposite archetypal morphological traits has given rise to contradictory ecological interpretations. On the one hand, the presence of mesaxonic limbs and general appendicular skeletal morphology convergent with modern horses allowed Scott (1937) to interpret them as grazers; however, their brachyodont selenodont dentition (similar to that found in modern artiodactyls) rather points to a browser/mixed-feeder ecological behaviour (e.g. Webb 1978; Soria 2001). Regarding *Tetramerorhinus* and *Theosodon*, the lack of bunodont dentition (observed for instance in Laventan litopterns) allows an omnivorous feeding behaviour to be ruled out. In fact, very little has been written about specific ecologies and resource partitioning among litopterns, but the marked difference in body masses (obtained by Cassini *et al.* 2012) between *Theosodon* (120–160 kg) and *Tetramerorhinus* (30–45 kg) would have allowed niche partitioning. Litopterns, like astrapotheres, would have been inhabitants of closed habitats, according to studies based on craniodental data of modern taxa (Cassini *et al.* 2012).

Feeding habits of xenarthrans are even more difficult to assess due to their peculiar dental anatomy (e.g. lack of enamel, reduced dentition, homodonty). Masticatory apparatuses of glyptodonts do not show a broad range of morphological diversity, and, although some ecological partitioning has been identified in Patagonian representatives of the group (Vizcaíno *et al.* 2012), the ecology of tropical fossil cingulates has not been thoroughly studied. Glyptodonts are traditionally considered to be grazers on the basis of their hypselodont teeth and stout masticatory apparatuses (e.g. Carlini and Zurita 2010; Vizcaíno *et al.* 2012). In any case, the persisting conservative nature of their dental morphology throughout their evolutionary history suggests multicological competence. Having unspecialized teeth is not necessarily an indicator of a generalistic diet, but is definitively an indicator of a generalistic feeding ability. The three genera identified at Fitzcarrald are small (*Neoglyptatelus*) to medium-sized glyptodonts (*Boreostemma* and *Parapropalaehoplophorus*). *Neoglyptatelus* is approximately one-third to one-half the size of the Santacrucian glyptatelines *Glyptatelus* and *Clypeotherium* (Vizcaíno *et al.* 2003), whereas *Boreostemma*

and *Parapropalaeohoplorus* would have sizes ranging from that of *Propalaeohoplorus australis* to *Eucinepeltus crassus* (Carlini *et al.* 2008).

The two genera of fossil sloths identified in Fitzcarrald, namely *Megathericulus* and *Urumacotheirus*, are poorly represented in the fossil record, and no ecological study has been carried out on them to our knowledge. Most ecological interpretations are based on the level of hypsodonty, a characteristic that seems to increase over time and is associated with open environments (Bargo *et al.* 2006a). However, xenarthran hypsodonty, or even hypselodonty, is supposed to have originally appeared as a response to the lack of both deciduous teeth and enamel (Vizcaíno 2009) and is a trait present early in the phylogenetic history of the group, seen for instance in the Palaeogene xenarthrans *Utaetus* (Simpson 1948) or *Pseudoglyptodon* (McKenna *et al.* 2006). Dietary interpretations for Pleistocene ground sloths are mostly based on the shape and width of the muzzle (e.g. Bargo *et al.* 2006b), and the variation in body sizes, skull and dental morphologies are also indicative of wide niche diversification (e.g. Bargo *et al.* 2006b). However, pre-Pleistocene sloths, especially from tropical areas, are still far too scarce and fragmentary to allow for detailed interpretation.

The rodent assemblage represents an important cluster in terms of abundance and diversity. At least seven taxa have been recognized, mostly dominated by dinomyids, the only extant representative of which (*Dinomys branickii* Peters, 1873) is a tropical forest dweller (Walton 1997). Interestingly, rodents in Fitzcarrald are composed of small forms, similar to those observed at La Venta. The biggest rodents are *Drytomomys aequatorialis*, with an estimated weight between 8 and 15 kg (Kay and Madden 1997) similar to the extant *Cuniculus paca* (5–13 kg, Emmons and Feer 1990), and *Dinomys branickii* (10–15 kg, Nowak 1991). The other two rodents, the dinomyid '*Scleromys*' *schurmanni* and the cavioid *Prodolicholitis pridiani*, have weights estimated between 1 and 10 kg. The smallest rodent is the octodontoid *Acarechimys*, similar in size to *A. cf. minutissimus* from La Venta, whose body weight is estimated to range between 100 g and 1 kg (Kay and Madden 1997). Based on taxonomic affinity with extant forms (rather than on morphological assessment), Kay and Madden (1997) proposed a terrestrial/fossorial substrate preference and a diet based on fruits and leaves for *Drytomomys aequatorialis* and '*Scleromys*' *schurmanni*, terrestrial/fossorial and grazing habits for *Prodolicholitis pridiani*, and a scansorial substrate preference and a diet based on small seeds and grasses for *Acarechimys*. Habitat preferences of *Acarechimys*, however, are difficult to assess because Miocene octodontoids are not directly related to modern groups (Arnal *et al.* 2014). Their brachydont dentition would suggest closed environments and/or browsing habits, contrary to previous interpretations,

which were based on supposed affinities between *Acarechimys* and octodontoids (Verzi 2002). Additionally, its broad geographical and temporal range would rather indicate broad habitat tolerances (Croft *et al.* 2011). Neoeplemids are represented in Fitzcarrald by *Neoeplema*. *Neoeplema* is a medium-sized rodent (Vucetich *et al.* 2010) that has been associated with aquatic habitats (similar to those of living capybaras) due to the fluvial-dominated depositional environments where it has been found (e.g. Ituzaingó Fm in Argentina, Solimoes Fm in Brazil, and Urumaco and San Gregorio Fms in Venezuela; Vucetich *et al.* 2010).

It is worth noting that specific ecological preferences of fossil tropical mammals have not been assessed, and, as mentioned previously, traditional ecological interpretations based, for example, on dental crown height have proven to be rather inaccurate even in better understood systems (e.g. high-latitude localities or Pleistocene faunas). For instance, enamel microwear analyses on high-crowned notoungulates from the Early Miocene of Argentina indicate that they were primarily browsers (Townsend and Croft 2008). Stable isotope analyses on Pleistocene toxodonts, on the other hand, show a latitudinal shift in their diet preferences that ranged from C3 forest browsers in Amazonia to specialized C4 grazers in northern Argentina (MacFadden 2005). The presence of hypsodont teeth therefore results in the evolutionary capability to be a feeding generalist and does not imply necessarily an exclusive grazing habit (MacFadden 2005).

Among mammals, predator diversity was exceptionally low in South America during pre-GABI times (Croft 2006). Our sample substantiates this statement, with a single putative dog-sized predator specimen (a caniniform tooth, referred to a borhyaenid sparassodont; Fig. 3), the only example among hundreds of mammalian remains. The size of this sparassodont canine coincides with that of an adult *Prothylacinus* (Santacrucian) and *Thylacinus cynocephalus* (Tasmanian wolf or thylacine, extinct in historical times; Engelman and Croft 2014).

The Fitzcarrald crocodyliforms, although not the focus of this paper, include two non-eusuchian oreinirostral sebecids, an advanced gavialoid and several caimanine species, representing a mosaic of distantly related taxa and most snout morphotypes (Salas-Gismondi *et al.* 2007). Among sebecids, the medium-sized *Langstonia huilensis* and the huge-sized *Barinasuchus arveloi* (Paolillo and Linares 2007) were predators at different trophic levels and probably of terrestrial habits (e.g. Langston 1965). They might have compensated for the apparent scarcity of mammalian predators in South America, as has been claimed for 'terror birds' (phorusrhacids; Croft 2006). Furthermore, due to the average high temperature and low range of variation in tropical regions, the physical

activity of (supposedly) cold-blooded sebecids could have approached that of a warm-blooded mammal.

Although the mammalian fauna essentially consists of terrestrial taxa, most of the recovered crocodyliforms are aquatic. As at La Venta, *Gryposuchus* (cf. *G. colombianus*) is the only gavialoid species discovered in Fitzcarrald. Among caimanines, the record includes cranial remains of *Mourasuchus* and *Purussaurus*, as well as isolated teeth of the enigmatic taxon *Balanerodus longimus* (Salas-Gismondi *et al.* 2007). Snout morphological disparity is a consistent feature among crocodylian faunas of South America during the Miocene (Riff *et al.* 2010). Such disparity further supports resource variety and abundance in the aquatic environments of the Pebas system (Hoorn *et al.* 2010). Proposed diets for some Fitzcarrald species are piscivorous (*Gryposuchus*), durophagous (*Balanerodus longimus*) and filter feeding (*Mourasuchus*) (Langston 1965).

FAUNAL COMPARISONS AND PALAEOGEOGRAPHY

Middle Miocene localities in South America are rare, especially within the intertropical area. Strictly speaking, the one locality to which Fitzcarrald can be compared in both time and a low-latitude geographical position is La Venta in Colombia. Quebrada Honda in Bolivia, although coeval (Laventan SALMA), is located just at the edge of the Tropic of Capricorn and is faunistically different from La Venta (and Fitzcarrald as seen further in the section) due apparently to isolating mechanisms separating low- and high-latitude faunas, as observed by Croft (2007). The Acre (Brazil) and Urumaco (Venezuela) assemblages, on the other hand, although also located at low latitudes, are younger (Late Miocene, Huayquerian SALMA; Pascual and Díaz Gamero 1969; Marshall *et al.* 1983; Cozzuol 2006; Sánchez-Villagra and Aguilera 2006) than Fitzcarrald and La Venta and do not belong to the Pebas megawetland system but to the fluvio-tidal Acre system instead (e.g. Wesselingh and Salo 2006; Hoorn *et al.* 2010). The spatial configuration of the Acre system is more similar to that of modern Amazonia than that of the Pebas system; in fact, the onset of the Amazon fan and the eastern drainage of the proto-Amazon River started at this moment, culminating with the full establishment of the Amazon River around 7 Ma (e.g. Hoorn *et al.* 2010). Consistently, we would expect Acre and Urumaco to be faunistically different to La Venta and the Fitzcarrald local fauna (as shown below). Cozzuol (2006) concluded that the Acre and Urumaco amniote faunas were taxonomically closer to the Mesopotamian faunal assemblage from Uruguay and Argentina (Huayquerian SALMA, Late Miocene) than to the La Venta fauna, despite the greater

geographical distance of the former. The faunistic differences between Acre/Urumaco and La Venta are in agreement with that mentioned above (i.e. a lacustrine Pebas system vs a fluvio-tidal Acre system), but the resemblances between the former and high-latitude faunas would furthermore suggest that the isolating mechanisms between low and middle/high latitudes lasted up to the end of the Middle Miocene. Thus, these isolating mechanisms separating low–middle/high latitude might have disappeared together with the Pebas system and the Parianian Sea, leading to the connection of previously disconnected continental areas (see Hoorn *et al.* 2010; Roddaz *et al.* 2010; Boonstra *et al.* 2015).

To test this scenario, the taxonomic composition of Fitzcarrald was compared with those of La Venta (Colombia), Quebrada Honda (Bolivia), Acre (Brazil) and Urumaco (Venezuela) because of their temporal and geographical position, and because of their well-sampled nature and availability of revised faunal lists. To test the effect of latitude on faunal distribution, we also compared Fitzcarrald with the Middle Miocene localities Collón-Curá and El Petiso in Argentina and Río Cisnes in Chile, all located more than 30 degrees south of Fitzcarrald. The Early Miocene primate-yielding locality MD-61 ('Pinturan' biochronological unit; Marivaux *et al.* 2012) and early Middle Miocene locality MD-67 (Colloncuran SALMA; Antoine *et al.* 2013), from the Madre de Dios sub-Andean Zone of south-eastern Peru, were not formally included in this comparison because of their low species diversity (seven mammalian taxa in both localities). Faunal similarities were assessed using the Simpson coefficient (SC; Simpson 1960). Minimum similarity (SC_{\min}) includes shared taxa at the generic level; maximum similarity (SC_{\max}) assumes that taxa not identified to generic level could pertain to any of the genera present in the compared faunas (Table 3).

The results show that the Fitzcarrald mammal fauna strikingly resembles the La Venta fauna (Kay *et al.* 1999), with at least 11 genera of non-primate terrestrial mammals in common (at least 18 if we consider taxa unidentifiable to the generic level but possibly representing shared taxa). As a matter of fact, faunal similarity between Fitzcarrald and La Venta is above 60% ($SC_{\min} = 64.7$, $SC_{\max} = 81.8$). Similarity is lower between Fitzcarrald and Acre ($SC_{\min} = 41.2$, $SC_{\max} = 45.5$), Fitzcarrald and Quebrada Honda ($SC_{\min} = 11.8$, $SC_{\max} = 27.3$), and almost negligible when compared with Urumaco ($SC_{\min} = 5.9$, $SC_{\max} = 22.7$), with only one genus in common (*Urumacotherium*). When compared with the selected high-latitude faunas, Fitzcarrald shares at least four genera with Collón-Curá locality (*Megathericulus*, *Theosodon*, *Acarechymys* and *Drytomomys*; $SC_{\min} = 23.5$, $SC_{\max} = 27.3$) and two genera with the Río Cisnes locality (*Megathericulus*

TABLE 3. Shared genera and suprageneric taxa of non-primate terrestrial mammals recorded in South America.

Fitzcarrald mammal fauna	Early Middle Miocene (Friasian SALMA)			Late Middle Miocene (Laventan SALMA)			Late Miocene	
	Collón Curá†	Río Cisnes‡	La Venta†	Quebrada Honda†	El Petiso§	Acre¶	Urumaco**	
Sparassodonta	*	*	*	*			*	
Xenarthra								
Borhyaenoidea indet.								
Cingulata								
<i>Borestermma</i>			X			X		
<i>Neoglyptatelus</i>			X			X		
<i>Parapropalaeophlophorus</i>								
Pilosa								
<i>Urumacotherium</i>						X	X	
<i>Megathericulus</i>	X	X	*					
Megalonychidae indet.			*			*		
Myodontidae indet.			*	*		*	*	
Astrapotheria				?			?	
<i>Xenastrapotherium</i>			X			X		
<i>Granastrapotherium</i>			X					
Toxodontidae								
<i>Pericotodon</i>			X		*			
<i>Miocochilus</i>			X	X				
Litopterna								
cf. <i>Theosodon</i>	X		X	?				
cf. <i>Tetramerorhinus</i>			?					
' <i>Scleromys</i> '			X			X		
<i>Drytomomys</i>	X		X					
Potamarchinae indet.			*			*		
<i>Potamarchus</i>					*	X		
<i>Prodolichotis</i>			X					
<i>Acarechimys</i>	X	X	X	X				
Octodontoidae indet.	*	*	*	*	*			
<i>Neoeplema</i>						X		

TABLE 3. (Continued)

Fitzcarrald mammal fauna	Early Middle Miocene (Friasian SALMA)		Late Middle Miocene (Laventan SALMA)		Late Miocene		
	Collón Cura [†]	Río Cisnes [‡]	La Venta [†]	Quebrada Honda [†]	El Petiso [§]	Acre [¶]	Urumaco ^{**}
Minimum number of shared genera	4	2	11	2	0	7	1
Maximum number of shared taxa	6	4	18	6	3	10	5
Minimum (SC _{min}) and maximum (SC _{max}) value of Faunal similarity	23.5–27.3	11.8–18.2	64.7–81.8	11.8–27.3	0–13.6	41.2–45.5	5.9–22.7

x, genera shared between Fitzcarrald and other localities.

* , suprageneric taxa shared (i.e. species unidentifiable at generic level but that could pertain to the same taxon).

?, questionable occurrence.

Faunal similarities have been measured using the Simpson Coefficient, SC = (number of shared genera/number of genera in the smaller fauna) × 100.

Minimum number of genera recorded in Fitzcarrald is 17.

Number of taxa including specimens not identifiable at the generic level is 22.

†Data from Bostelmann *et al.* (2012).

‡Data from Villafañe *et al.* (2008).

§Data from Cozzuol (2006).

¶Data from Sanchez-Villagra and Aguilera (2006).

**Data from Sanchez-Villagra and Aguilera (2006).

and *Acarechimys*; $SC_{\min} = 11.8$, $SC_{\max} = 18.2$). No genera are common between the Fitzcarrald and El Petiso localities ($SC_{\min} = 0$, $SC_{\max} = 13.6$), although the presence of *Pericotaxodon* and a 'Dolichotinae sp. small' has been suggested for the latter. As already mentioned by Croft (2007), neither of the SC values (SC_{\min} and SC_{\max}) has to be regarded as the more 'conservative' option considering the temporal and geographical ranges of the faunas included in the comparison. For instance, the minimum SC value between Fitzcarrald and Collón-Curá ($SC_{\min} = 23.5$) is likely to be more accurate (considering the significant age and geographical disparity); on the other hand, the maximum SC value between Fitzcarrald and Quebrada Honda ($SC_{\min} = 27.3$) is probably more applicable as they are closer in age and location. In any case, minimum and maximum SC values between Fitzcarrald and both Quebrada Honda and Collón Curá are pretty similar (this of course, without considering the obvious inaccuracies of the fossil record and the degree to which the sampling time and methods used could alter these values). Only one genus identified in Fitzcarrald has been reported in the Middle–Late Miocene Argentinian faunas of Lower Arroyo Chasicó and Upper Arroyo Chasicó (the large dinomyid *Drytomomys*; see revised faunistic list in Croft 2007). Similarly, only one genus is common between Fitzcarrald and the Middle–Late Miocene fauna of the Aisol Formation in central Argentina (Forasiepi *et al.* 2011): the macrauchenid *Theosodon*, found in the lower section of this formation.

These results show that, as part of the same dominant system, Fitzcarrald and La Venta share greater similarities with each other than with localities situated geographically or temporally outside the Pebas system. Thus, the isolating mechanisms noticed by Croft (2007) between the Middle Miocene localities La Venta and Quebrada Honda could be related, at least in part, to the presence of the large Pebas lacustrine complex (Tejada-Lara *et al.* 2015). The Pebas system might therefore have represented an environmental and/or geographical barrier, most likely isolating northern South America (Venezuela, Colombia, Peru, western Brazil and northern Bolivia) from southern areas (southern Bolivia, Chile and Argentina) during the Middle Miocene (Wesselingh and Salo 2006; Tejada-Lara *et al.* 2015). The ecological and geographical barriers generated by the Pebas system seem to have played a stronger role than the time itself as Fitzcarrald is more similar with asynchronous but equivalent-latitude Acre than with coeval but middle-latitude Quebrada Honda. Similarly, Quebrada Honda shares more faunistic similarities with asynchronous but high-latitude faunas than with coeval but Pebas-dominated La Venta and Fitzcarrald. The isolating mechanisms associated with the existence of the Pebas megawetland could have come to an end with its disappearance in the Late Miocene. This may explain why

localities such as Acre and Urumaco share greater faunal similarities with Mesopotamian faunas in Argentina and Uruguay than with La Venta (Cozzuol 2006), in spite of their greater geographical distance.

Fitzcarrald aquatic vertebrates document freshwater and deltaic environments, with probable marine incursions, as is described for areas farther to the north (e.g. Wesselingh *et al.* 2002; Boonstra *et al.* 2015). The Fitzcarrald crocodyliform fauna closely resembles the Middle Miocene La Venta fauna, although no other coeval fauna has been described comprehensively. *Langstonia huilensis* and *Balanerodus logimus* are currently known only from La Venta and Fitzcarrald, whereas gavialoids are represented by several species in the Late Miocene localities Acre and Urumaco (Cozzuol 2006; Sanchez-Villagra and Aguilera 2006). In Fitzcarrald and La Venta, the same species of *Gryposuchus* (i.e. *G. colombianus*) is probably the sole gavialoid taxon (Langston and Gasparini 1997; Salas-Gismondi *et al.* 2007). At the generic level, Fitzcarrald, La Venta, Acre and Urumaco share remains of *Purusaurus* and *Mourasuchus*. These two taxa show a wide geographical range and were apparently successful during the Late Miocene, judging from the gigantic sizes attained (Bocquentin-Villanueva *et al.* 1989; Riff *et al.* 2010).

Simpson's Stratum 2 migrants are recorded only by hystricognath rodents, with at least three dinomyids (*Drytomomys aequatorialis*, '*Scleromys*' *schurmanni* and *Potamarchus murinus*), a dolichotine cavioid (*Prodolichotis* cf. *pridiana*), a neoepiblemid (*Neoepiblema* sp.) and octodontoids (*Acarechimys* sp. and two unidentified octodontoids). Of these, *Drytomomys aequatorialis*, *Scleromys* cf. '*S.*' *schurmanni* and *Prodolichotis pridiana* have previously been recorded in the Middle Miocene, while *Potamarchus murinus* has Late Miocene records in Argentina, Brazil and Venezuela. *Neoepiblema* has been recorded in the Late Miocene of Brazil and Argentina, and *Acarechimys* is known from Early to Middle Miocene faunas from Argentina, Colombia, Bolivia and Chile. The presence of *Potamarchus* and *Neoepiblema* in Fitzcarrald (*in situ* and together with typical Middle Miocene taxa; see Table 1) represents the FADs of these genera.

No post-GABI element or specimen referable to a taxon of North American affinity was found stratigraphically *in situ* during the 2005–2007 expeditions. However, dozens of mineralized remains of the so-called 'Simpson's Stratum 3' migrants were handpicked floating on river banks (Antoine *et al.* 2007). They comprise the cervids *Odocoileus* and *Mazama*, the tayassuid suiform *Tayassu*, the tapirid perissodactyl *Tapirus*, an aquatic mustelid and an indeterminate elephantoid (fragmentary tusk). Native Pleistocene–Holocene taxa such as the large rodent *Hydrochoerus*, as well as the extinct giant *Glyptodon* (armoured armadillo-relative) and cf. *Eremotherium* (ground sloth), were also identified from float specimens.

SUMMARY AND CONCLUSIONS

The Fitzcarrald local fauna represents an important contribution to the knowledge of South American tropical faunas because it records a time period otherwise known in tropical South America by only one species-rich vertebrate locality, La Venta in Colombia. Moreover, the Middle Miocene interval is particularly interesting because molecular studies identify it as the epoch when the primary diversification of modern lineages now distributed in Amazonia occurred (Hoorn *et al.* 2010). Additionally, the basic phylogenetic composition of modern neotropical rainforests (Jaramillo *et al.* 2006), as well as humid climate conditions sufficient to sustain a rainforest (Kaandorp *et al.* 2003), seems to have been present at least since the Middle Miocene. Therefore, in terms of climate and vegetation, modern Amazonia seems to have been established by at least the Middle Miocene (in the areas not long-covered by the Pebas megawetland).

Although the Fitzcarrald area was sampled for a short period of time (field missions from 2005 to 2007 for less than a month each), the diversity of its mammal fauna is not negligible, including at least 24 taxa (22 terrestrial and two aquatic). The presence of taxa known from other localities at disparate epochs (early Middle, late Middle and Late Miocene) highlights: (1) our still patchy knowledge on the evolutionary and biogeographical history of South American mammals; (2) the importance of tropical localities for improving our understanding of these aspects for several clades; and (3) the biased nature of our knowledge towards the southern cone of the continent. More missions to the Fitzcarrald area and other localities in tropical South America are certainly needed to recover more material and substantiate these ideas.

The Fitzcarrald mammal fauna is more similar to the coeval La Venta fauna of Colombia (and even with the younger Acre fauna in Brazil) than to the coeval but mid-latitude fauna of Quebrada Honda in Bolivia. This pattern coincides with the occurrence of the Pebas system during the Middle Miocene, which might have created isolating environmental conditions between northern and southern South America. With a peak in the uplift of the Andes and the subsequent disappearance of the Pebas megawetland in the Late Miocene (e.g. Hoorn *et al.* 2010), the Acre system presumably reunited continental areas previously isolated by the Pebas megawetland.

Tropical localities, with their unique assemblages (the mixing of early offshoots, as well as FADs and LADs of various taxa), are crucial places to elucidate the evolution of mammalian faunas in South America. In this sense, the Fitzcarrald fauna provides important data that help piece

together the phylogenetic history and biogeography of South American mammals and the evolution of Amazonia.

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