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Early Oligocene caviomorph rodents from Shapaja, Peruvian Amazonia

by

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with 6 text-figures, 1 table and 3 appendices

Abstract

The rodent record during the late Eocene – early Oligocene interval is poorly known in South America. Our team's recent fieldwork in Peruvian Amazonia allowed for the discovery of five new fossil-bearing localities in a single stratigraphic section at Shapaja (Tarapoto area, San Martín Department), considered as early Oligocene by mammalian biostratigraphy. Here, we describe the caviomorph material from Shapaja, which documents 17 distinct taxa (with the co-occurrence of four to seven caviomorph taxa in a single level) representing at least three of the four extant superfamilies. Eight taxa are new to science: *Kichkasteiromys raimondii* nov. gen. et sp. and *Shapajamys labocensis* nov. gen. et sp. (Erethizontoidea), *Selvamys paulus* nov. gen. et sp. and *Mayomys confluens* nov. gen. et sp. and *T. mayoensis* nov. gen. et sp. (superfamily indet.). These diversified caviomorph faunas constitute the most equatorial Paleogene record of this group. The taxa from Shapaja are not documented in other low-, mid- and high-latitudes Paleogene localities, except for *Eoincamys*. This genus is otherwise only found at Santa Rosa (Peruvian Amazonia, ?late Eocene/early Oligocene), thereby indicating a close temporal window for the Shapaja localities.

Keywords: systematics, biostratigraphy, Tinguirirican, Peru, South America

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1. Introduction

From the Eocene onward, caviomorph rodents (Caviomorpha WOOD, 1955) are a significant component of most South American mammalian communities. Nowaday, this clade is represented by ~255 species (WILSON & REEDER 2005), distributed among four superfamilies (i.e., Cavioidea, FISCHER DE WALD-HEIM 1817, Chinchilloidea, BENNETT 1833, Octodontoidea, WATERHOUSE 1839, and Erethizontoidea, BONAPARTE 1845). In addition, it displays a wide range of ecomorphological adaptations including terrestrial, cursorial, fossorial, scansorial, arboreal, and semiaquatic abilities (WILSON & GEIGER 2015). Caviomorphs are widely spread through South America and beyond, with notably the octodontoids, which have a natural distribution area ranging from the Tierra del Fuego up to the Greater Antilles and Central America, and were introduced in the Old World in the last centuries (for a review, see CARTER & LEON-ARD 2002). Erethizontoids also display a remarkable distribution in having colonised Nearctic regions of North America (e.g., UPHAM & PATTERSON 2015). For the Neogene (and especially the Miocene), numerous localities, usually yielding abundant caviomorph specimens and species-rich assemblages, were discovered at the South American scale: in Argentina (e.g., Santa Cruz Formation (Fm., SCOTT 1905), Sarmiento Fm. (VUCETICH et al. 2010a), Monte Hermoso Fm. (DESCHAMPS et al. 2012)), Bolivia (e.g., Quebrada Honda, CROFT et al. 2011), Brazil (e.g., Brazilian Acre, KERBER et al. 2017), Chile (e.g., Laguna del Laja, FLYNN et al. 2008), Colombia (e.g., La Venta, WALTON 1997), Ecuador (on the vicinity of Nabón, ANTHONY 1922), Peru (e.g., FITZCARRALD & CON-TAMANA, TEJADA-LARA et al. 2015, ANTOINE et al. 2016), Uruguay (e.g., Arazati Beach, RINDERKNECHT et al. 2011) and in Venezuela (e.g., Urumaco Fm., e.g., CARRILLO & SÁNCHEZ-VILLAGRA 2015). The Miocene fossil record of caviomorphs has proven that this rodent group was highly diversified at that time, with notably a wide array of body sizes, locomotor adaptations and feeding behaviors (similar to extant species, CANDELA et al. 2012), already recorded as early as the late early Miocene (Colhuehuapian and Santacrucian South American Land Mammal Ages (Salmas)).

The fossil record of caviomorphs throughout the Deseadan Salma (late Oligocene) is also substantial documented, with 18 localities across South America but a single one, poorly documented, in the West Indies (from the Lares Limestone at Puerto Rico, Greater Antilles, Vélez-Juarbe et al. 2014). It is worth noting that until recently, most of Deseadan localities (14/18) were primarily reported at high (Argentina) to mid (Bolivia, Brazil, and southern Peru) latitudes. Only four localities document Deseadan caviomorphs at low latitudes: Lircay (Peru, HARTEN-BERGER et al. 1984) and CTA-73, CTA-61 and CTA-32 (Contamana, Peruvian Amazonia, ANTOINE et al. 2016, 2017, BOIVIN et al. 2017a). Two Deseadan localities are particularly famous for yielding abundant caviomorph fossils: Cabeza Blanca in Argentina (e.g., WOOD & PATTERSON 1959, VUCETICH et al. 2015a and references therein) and Salla in Bolivia (HOFF-STETTER & LAVOCAT 1970, HARTENBERGER 1975, LAVOCAT 1976, PATTERSON & WOOD 1982). In the Neotropics, 16 localities document pre-Deseadan caviomorphs. Ten are reported from the Contamana area (Peruvian Amazonia), in deposits dating from the late middle Eocene (Barrancan Salma, ANTOINE et al. 2012, 2016, 2017, BOIVIN et al. 2017b). These localities from Peruvian Amazonia so far record the earliest representatives of caviomorphs (stem Caviomorpha, ANTOINE et al. 2012, 2016, 2017, BOIVIN et al. 2017b), as well as the probable earliest stem members of the octodontoids (e.g., *Eoespina* sp., BOIVIN et al. 2017b, see ARNAL & VUCETICH, 2015a) and cavioids (e.g., *Eobranisamys javierpradoi* BOIVIN et al. 2017b). Four other pre-Deseadan localities document caviomorphs from the early Oligocene (Tinguirirican SALMA and subsequent unnamed interval): Termas del Flaco (Tinguiririca, Chile, Wyss et al. 1993, Flynn et al. 2003, BERTRAND et al. 2012), La Cantera (Argentina, VUCETICH et al. 2010b), the San Sebastián Fm. at Puerto Rico (Greater Antilles, Vélez-Juarbe et al. 2014), and Santa Rosa (Peru, FRAILEY & CAMPBELL 2004). FRAILEY & CAMPBELL (2004) proposed a late Eocene age for the locality of Santa Rosa. However, considering the entire mammalian fauna of that locality, and taking into account the new fossil data assembled in recent years, notably from (bio)geographically close localities from Peruvian Amazonia, Santa Rosa is most likely earliest Oligocene in age (i.e., documenting the Tinguirirican SALMA, SHOCKEY et al. 2004, CROFT et al. 2008, VUCETICH et al. 2010b, 2015b, ANTOINE et al. 2012, 2017, KAY 2015, but see GOIN & CANDELA 2004, BOND et al. 2015). Termas del Flaco (Tinguiririca fauna) is the type locality of the Tinguirirican (Wyss et al. 1993, FLYNN et al. 2003), whereas La Cantera appears to be slightly younger, i.e., intermediate in age between the Tinguirirican and Deseadan SALMAs (~29 Ma, VUCETICH et al.

2010b). The San Sebastián Fm. at Puerto Rico, which had yielded only one caviomorph incisor, is posterior to ~27 Ma, and considered late early Oligocene in age (Vélez-Juarbe et al. 2014). The earliest erethizontoid comes from Santa Rosa (Eopululo wigmorei FRAILEY & CAMPBELL, 2004), and the earliest non-ambiguous chinchilloid (Eoviscaccia frassinettii BERTRAND et al. 2012) from Termas del Flaco. Santa Rosa is the pre-Deseadan locality from Peruvian Amazonia which has so far yielded the most diverse rodent fauna (including more than 300 specimens documenting 17 species, FRAILEY & CAMPBELL 2004, see BOIVIN et al. 2017b regarding a possible synonymy between Eoespina/Eosachacui), followed by CTA-27 (177 specimens assigned to five species, e.g., ANTOINE et al. 2012, BOIVIN et al. 2017b). Finally, few caviomorph teeth collected from the upper Juruá River in Brazil (Foz do Breu and Cachoeira São Salvador localities, Solimões Fm., RIBEIRO et al. 2013, KERBER et al. 2017) would be late Eocene/early Oligocene in age. Although these specimens are no stratigraphically-constrained, they are assigned to *Eoincamys* sp. and cf. *Eobranisamys* sp. These two genera were named at Santa Rosa (FRAILEY & CAMPBELL 2004) and close allies of *Eobranisamys* were further recognised in CTA-27 and CTA-66 (late middle Eocene, Contamana, ANTOINE et al. 2016, BOIVIN et al. 2017b).

Since 2012, our paleontological surveys in the Tarapoto area, situated in Peruvian Amazonia (San Martín Department, Text-fig. 1A), have allowed for the discovery of five new fossil-bearing localities (TAR-01, TAR-13, and TAR-20–22) in the vicinity of the Shapaja village (Text-fig. 1B), yielding rich assemblages including plants, invertebrates, and numerous vertebrate taxa. All of them are considered to be early Oligocene in age (KLAUS et al. 2017), based on mam-



Text-fig. 1. Geographic location and stratigraphy of the Shapaja localities (Peru, early Oligocene, Tinguirirican SALMA). A: location map of the Tarapoto area (star symbol) in Peru. The other Paleogene localities yielding caviomorphs (circle symbols) are mapped (red: pre-Deseadan, yellow: Deseadan). Scale bar: 100 km. B: location map of the outcrops in the Tarapoto area (San Martín Department). Scale bar: 1 km. C: synthetic stratigraphic units of the Shapaja Paleogene sequence, including ro-dent-yielding localities TAR-21, TAR-13, TAR-22 and TAR-01. Owing to the uncertain stratigraphic position of TAR-20, this locality is not included. Fm.: Formation.

malian biostratigraphy, depositional environment sequence, and stratigraphic correlation in the northern Peruvian foreland (see Material and Methods section).

The primary purpose of the present work is to describe and compare the specimen-rich caviomorph material found in the new fossil-bearing localities from Shapaja (TAR-01, TAR-13, and TAR-20–22). These new rodent communities document the northernmost Paleogene caviomorph record at the South American scale. The interest of that study is double: i. to highlight and substantiate the Amazonian caviomorph record during the considered time interval and ii. to further our understanding of the morphological evolution of caviomorphs during their earliest adaptive radiation.

2. Material and methods

The rodent fossils studied in the present work originate from a short stratigraphic section on a road cut located about 12 km southeast of Tarapoto City (San Martín Department, Peru), near the small village of Shapaja (Text-fig. 1B). Five new localities (TAR-01, TAR-13, TAR-20, TAR-21, and TAR-22) are documented around the confluence between the Mayo and Huallaga rivers (6° 34' 59" S -76° 16' 53.15" W, Text-fig.1C). These fossil-bearing levels were originally mapped as belonging to the late Oligocene - early Miocene Chambira Fm., without any chronostratigraphic or biostratigraphic constraints (SAN-CHEZ FERNÁNDEZ et al. 1997). Fine-grained floodplain deposits are dominating in the Shapaja section, which better matches the underlying "Upper Pozo (shale) Member" (Mb.) as detailed by HERMOZA et al. (2005) and synthesised by RODDAZ et al. (2010). In sharp contrast with the fully fluvial medium- to coarse-grained deposits of the Chambira Fm. (see HERMOZA et al. 2005, ANTOINE et al. 2016), this shale-dominated member is further characterised by a shallow marine/littoral component with a strong tidal influence (RODDAZ et al. 2010), retrieved below and beteen TAR-13 and TAR-21 localities, which have yielded marine/estuarine myliobatid rays. There are no disconformities in the concerned sequence, but a gradational change from tidally-influenced fine sandstones (TAR-21 and TAR-13) to fluvial micro-conglomeratic lenses intercalated with floodplain fine deposits (TAR-22 and TAR-01). We therefore consider the Shapaja fossiliferous section as a whole to be part of the marine-influenced Upper Pozo Shale Mb., hypothesised as documenting the late Eocene - early

Oligocene interval in the northern Peruvian foreland (RODDAZ et al. 2010, ANTOINE et al. 2016).

The fossil content of the Shapaja localities encompasses plants, charophyte oogones, crabs, molluscs, chondrichthyans, osteichthyans, lissamphibians, chelonians, squamates, crocodylomorphs, and mammals (including metatherians, xenarthrans, South American native ungulates (i.e., small pyrothere, astrapotheres, and notungulates), and caviomorph rodents), the study of which is under progress. KLAUS et al. (2017) recently studied the crab remains from TAR-01 and assigned them to the Neotropical freshwater family Trichodactylidae. The biostratigraphic age of the Shapaja assemblages, as hypothesised aside from caviomorphs, is Oligocene and most likely early Oligocene, based on the co-occurrence of a minute bonapartherioid polydolopimorphian marsupial (TAR-21) and of a proto-hypsodont argyrolagoid polydolopimorphian marsupials (TAR-21, TAR-20, and TAR-01). Such an assemblage is similar to those recorded in the early Oligocene localities of La Cancha and La Cantera (GOIN et al. 2010). TAR-01 also yields an armored xenarthran of enigmatic affinities (cf. Yuruatherium) close to a taxon only documented in Santa Rosa (CIANCIO et al. 2013). The presence of a smallsized pyrothere (from TAR-21 up to TAR-01), and of a brachydont/mesodont archaeoyracid notoungulate (TAR-22) also pleads for a pre-Deseadan age. The biostratigraphic contribution of rodents studied here is discussed in the section 'Age of the Shapaja localities and biostratigraphic implications' of this present work (see p. 48), pending results of chemostratigraphic and chronostratigraphic analyses.

The fossil material of each locality was collected by in situ wet screening of the sediments (1 and 2 mm mesh sizes): ~440 kg for TAR-01 (2012, 2013, and 2015), ~20 kg for TAR-13 (2012), ~135 kg for TAR-20 (from 2014 to 2016), ~73 kg for TAR-21 (from 2012 to 2016), and ~214 kg for TAR-22 (from 2014 to 2016). All the fossil specimens described in this paper (exclusively isolated teeth) are permanently stored in the paleontological collections of the 'Museo de Historia Natural, Universidad Nacional Mayor de San Marcos' (MUSM), Lima, Peru.

The terminology used here for the rodent dentition follows the nomenclature proposed by BOIVIN & MARIVAUX in BOIVIN et al. (2017a). Upper case letters are used for the upper dentition (dP: for decidual premolar, P: for premolar, M: for molar) and lower case letters for the lower dentition (dp: for decidual premolar, p: for premolar, m: for molar). In this study,

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several new species are described. The association between the holotype and the other material attributed to these new species is based on several points: i. a similar size, ii. a similar crown heigh, and iii. a similar occlusal pattern (bunolophodonty/lophodonty, taeniodonty/non-taeniodonty, and obliquity, length, and presence/absence of loph(-id)s). The lower and upper molars of *Eoincamys* cf. pascuali sharing a very similar dental pattern (p. 29), they were distinguished by the number and position of the roots. Indeed, regarding the studied material, there are four roots on the lower molars and three on upper molars. On the lower molars, the roots are placed at the four corners of the teeth, the root below the hypoconid being the largest. For upper molars, there are two labial roots and one large lingual root. The caviomorph taxa used for comparison in this study are listed in Appendix S1. For more information regarding the taxa cited in comparison sections (institutions, references used), refer to Appendix S1. When the fossils from Shapaja localities are compared with several taxa, the latter are primarily listed according to their chronostratigraphic order (from oldest to youngest) and then alphabetically. The dental measurements are given in Appendix S2. The hypsodonty index of a tooth (HI, JANIS 1986) equals its crown height (H) divided by its anteroposterior length (ML). With this hypsodonty index (H/ ML), teeth with a HI <1 are considered as brachydont, those with a HI = 1 are considered as mesodont, and those with a HI > 1 are considered as hypsodont. "Subhypsodonty" designates an intermediary condition between the mesodonty and hypsodonty. Depending on specimens, photographs were taken with two scanning electron microscopes (SEM): HITA-CHI S 4000 and HITACHI S 4800.

Institutional abbreviations

FMNH, Field Museum of Natural History, Chicago, USA, LACM, Los Angeles County Museum, Los Angeles, USA, MOZ-PV, Museo Provincial de Ciencias Naturales "Dr. Prof. Juan A. Olsacher", Zapala, Argentina, MUSM, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima, Peru, PU, Princeton University, Princeton, USA (but specimens are today deposited at the Yale Museum of Natural History, New Haven, USA), UM, Université de Montpellier, Montpellier, France.

Other abbreviations

FAD, First Appearance Datum, Fm., Formation, Hb, maximum labial crown height, Hg, maximum lingual crown height, Hh, hypostria/id height, HIb, hypsodonty index (calculated from Hb), HIg, hypsodonty index (calculated from Hg), LAD, Last Appearance Datum, ML, maximum anteroposterior length, MW, maximum labiolingual width, S, south, SALMA, South American Land Mammal Age, TAR, Tarapoto (here Shapaja), W, west.

3. Systematic palaeontology

Order Rodentia BOWDICH, 1821 Infraorder Hystricognathi TULLBERG, 1899 Parvorder Caviomorpha WOOD, 1955

Superfamily Erethizontoidea BONAPARTE, 1845

Kichkasteiromys nov. gen.

Type species: Kichkasteiromys raimondii nov. sp. Species content: only the type species. Derivation of name: from the Quechua kichka, spine, in reference to the spines of the erethizontids. Generic diagnosis: as for the type and only known species.

Kichkasteiromys raimondii nov. sp.

(Text-fig. 2D, Appendix S2)

Derivation of name: in honor of ANTONIO RAIMONDI, who described the first fossils of San Martín Department in Peru, found at Juan Guerra, near TAR-21.

Holotype: MUSM 2925, right M1 or M2 (Text-fig. 2D). Deposited in the MUSM, Lima, Peru.

Type locality: TAR-21, Shapaja, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Diagnosis (based on a single tooth): Small-sized rodent characterised by brachydont teeth. Differs from all Palaeogene and Miocene erethizontoid genera (except Palaeosteiromys and Microsteiromys) in being smaller in size. Differs from all erethizontoid species (except Protosteiromys medianus) with non-taeniodont upper molars in having a more lingually situated lingual protoloph. Differs from Eopululo, Palaeosteiromys, Plesiosteiromys, Protosteiromys, Eosteiromys and cf. Microsteiromys sp. (from MD-67, Madre de Dios, Peru) in having upper molar more transverse in outline. Differs from Palaeosteiromys and cf. Microsteiromys sp. in having a weaker and shorter lingual protoloph on upper molar. Differs from Eopululo, ?Protosteiromys sp. (from Salla), Hypsosteiromys and Steiromys detentus in showing upper molar with a well-defined pentalophodont pattern (or with a longer metaloph for some specimens of S. detentus), from Plesiosteiromys in displaying a longer protoloph and a third transverse crest, and in having a less extensive hypoflexus labiomesially, from *Eosteiromys* in having a longer



Text-fig. 2. Scanning electron microscope images (in occlusal view) of fossil caviomorph teeth from TAR-22 (A-C, F, M, O-S, U-W, Y,), TAR-21 (D, I, K-L, N, T, X), TAR-13 (E, J, Z), TAR-20 (G-H). (A-B) Selvamys paulus nov. gen. et sp. (C) Caviomorpha indet. 3. (D Kichkasteiromys raimondii nov. gen. et sp. (E) Adelphomyinae indet. (F) Caviomorpha indet. 2. (G-N) Eoincamys valverdei nov. sp. (O-Y) Eoincamys parvus nov. sp. (Z) ?Eoincamys sp. (A) MUSM 2960, right M2 (holotype), (B) MUSM 3340, right M1 or 2, (C) MUSM 3439, p4 or m1?, (D) MUSM 2925, right M1 or M2 (holotype), (E) MUSM 2968, right lower molar, (F) MUSM 3438, m1 or 2, (G) MUSM 3334, right P4, (H) MUSM 3336, left M1, (I) MUSM 2943, left ?M2, (J) MUSM 2969, right M3, (K) MUSM 2947, right M1 (holotype), (L) MUSM 2948, right M1, (M) MUSM 3429, left M3, (N) MUSM 2952, right p4 or m1, (O) MUSM 3430, left dp4, (P) MUSM 3432, left m1, (Q) MUSM 3433, left m2, (R) MUSM 2962, right m3, (S) MUSM 3434, right P4, (T) MUSM 2950, left M1, (U) MUSM 3436, left M2, (V) MUSM 3437, left M3, (W) MUSM 2963, right P4, (X) MUSM 2951, right M1 (holotype), (Y) MUSM 2965, left M3, (Z) MUSM 2970, left upper molar, . The underlined letters indicate the reversed teeth. Scale bar: 1 mm.

protoloph and a third transverse crest, from *Parasteiromys* in developing a strong and complete mure, from *Steiromys duplicatus* in displaying a shorter metaloph, from cf. *Microsteiromys* sp. in having a metaloph labially connected to the metacone, from *Branisamyopsis* and *Neosteiromys* in having a lingual protoloph (even reduced) and a less developed labial wall.

Description: The MUSM 2925 M1 or M2 (Textfig. 2D) is low-crowned and wider than long with rounded corners. Labially, the paracone and mesostyle are the most distinct tubercles, and they are well separated (mesial mesoflexus (i.e., mesoflexus sensu WOOD & PATTERSON 1959, PATTERSON & WOOD 1982, CANDELA 1999, BOIVIN et al. 2017a, b, open labially). The metacone is faintly differentiated, being crestiform and merged with its long anterior arm. The lingual cusps are crestiform, especially the protocone, which is particularly pinched and very lingual in position. This cusp is mesially labiolingually oriented and distally longitudinally directed. It displays a long and arcuate anterior arm, in continuity with the anteroloph. Due to the configuration of the protocone and its anterior arm, the anteroloph appears very long. The latter extends labially, being labiolingually straight, and it ends at the base of the mesial aspect of the paracone, thereby generating a very thin notch between both structures. The protocone displays a short posterior outgrowth, distally oriented and ending abruptly. The lingual protoloph is faintly developed, but complete (i.e., it reaches the mure) at this degree of wear. At a more advanced degree of wear, it is probably thicker and strongly connected to the mure. A long and markedly oblique protoloph (labial part) links the paracone to the lingual protoloph spur. Distolingually, the hypocone occupies a position slightly more labial than the protocone. It displays a well-defined but short and oblique anterior arm, which ends its course at the same level than the lingual extremity of the labial protoloph. The protoloph and anterior arm of the hypocone are linked by a short and longitudinal mure, occupying a very lingual position. Because of the mure position, the hypoflexus is reduced and only slightly proverse. The third transverse crest is long, labiolingually complete, and it links the mesostyle to the mesial extremity of the anterior arm of the hypocone. This crest, parallel to the protoloph, is constricted just before its connection with the anterior arm of the hypocone. This suggests that this third crest primarily consists of a very long mesoloph, plus a very short, spur-like mesolophule. The paracone is isolated from the labial end of the anteroloph and from the mesostyle. MUSM 2925 has a long and curved labiodistal enamel wall, formed by the small and crestiform metacone, a long anterior arm, a short posterior arm, and the posteroloph. That long wall reaches the posterior arm of the mesostyle and it is lingually linked to the hypocone. A well-defined metaloph, stemming from the metacone, and as strong as the other transverse crests, extends lingually, parallel to the mesoloph and protoloph (slightly oblique). At the level of the middle line of the crown, it turns backwardly to connect the posteroloph. Contrary to the mesial flexi, both distal flexi (distal mesoflexus (i.e., metaflexus sensu CANDELA 1999, BOIVIN et al. 2017a, b) + lingual part of the posteroflexus and labial part of the posteroflexus) are labially closed and they form fossettes.

Comparisons: That M1 or M2 from TAR-21 (MUSM 2925) is brachydont and slightly wider than

long. It displays weakly oblique lophs, long protoloph and third transverse crest, a mure occupying a very lingual position, and a well-developed metaloph that links the posteroloph. This suite of characters strongly suggests erethizontoid affinities. The morphology and proportions of MUSM 2925 of Kichkasteiromys raimondii nov. gen. et sp. is reminiscent to those of the upper molar of Palaeosteiromys amazonensis BOIVIN et al., 2017a from the late Oligocene of Contamana, Peru (CTA-32) and those of cf. Microsteiromys sp. from the early middle Miocene of Madre de Dios, Peru (MD-67, ANTOINE et al. 2013), notably in having both the protoloph and third transverse crest slightly oblique, and a strong metaloph. On MUSM 2925, the metaloph is labially connected to the metacone like on upper molars of Palaeosteiromys, but contrary to the MUSM 1975 M3 of cf. Microsteiromys sp. from MD-67. However, MUSM 2925 differs from the upper molars of Palaeosteiromys and from the upper molar of cf. Microsteiromys sp. from MD-67 in being more transverse, and in displaying a weaker and more lingually situated lingual protoloph. The latter character is unusual among other erethizontoid species with non-taeniodont upper molars and it is only find on the MACN A 52-111 M1 attributed to Protosteiromys medianus (WOOD & PATTERSON 1959: fig. 30A). In addition, and with the notable exception of Microsteiromys jacobsi WALTON, 1997 from the late middle Miocene of La Venta, Colombia (the upper teeth of which are not known), all other species of erethizontoids have larger teeth. MUSM 2925 from TAR-21 is more transverse than upper molars of Eopululo, Plesiosteiromys BOIVIN et al., 2017a (CTA-61, Peru, late Oligocene), *Protosteiromys* (Амеднімо, 1903) (Sarmiento Fm., Argentina, late early Oligocene - late Oligocene), and *Eosteiromys* Амеднию, 1902 (Sarmiento Fm., Argentina, early Miocene). MUSM 2925 also differs from (i) *Eopululo*, ?*Protosteiromys* sp. (Salla, Bolivia, late early Oligocene – late Oligocene, CANDELA 2000), Hypsosteiromys Ameghino, 1902 (Sarmiento Fm., Argentina, early Miocene), and Steiromys detentus Ameghino, 1887 (Santa Cruz Fm., Argentina, early Miocene) in exhibiting a pentalophodont pattern (or with a longer metaloph for some specimens of *S. detentus*), (ii) from *Plesiosteiromys* in displaying longer protoloph and third transverse crest, and in having a less extensive hypoflexus labiomesially, (iii) from *Eosteiromys* in having a longer protoloph and third transverse crest, (iv) from *Parasteiromys* AMEGHINO, 1903 (Sarmiento Fm., Argentina, early Miocene) in developing a strong and complete mure,

(v) from *Steiromys duplicatus* AMEGHINO, 1887 (Santa Cruz Fm., Argentina, early Miocene) in displaying a shorter metaloph, and (vi) from *Branisamyopsis* CAN-DELA, 2003 (Sarmiento and Pinturas Fm., Argentina, early Miocene) and *Neosteiromys* CANDELA, 2004 (Andalhuala Fm., Argentina, late Miocene) in having a lingual protoloph (even reduced) and a less marked labial wall.

Shapajamys nov. gen.

Type species: *Shapajamys labocensis* nov. sp. Species content: only the type species. Derivation of name: from the Peruvian Shapaja village from the vicinity of which the type-locality TAR-01 was found. Generic diagnosis: as for the type species.

Shapajamys labocensis nov. sp.

(Text-fig. 3A–I, Appendix S2)

Derivation of name: from the Spanish "*La Boca*", confluence, as the confluence between the Mayo River and the Huallaga River occurs near the aplomb of the type locality TAR-01.

Holotype: MUSM 2995, right M2 (Text-fig. 3H). Deposited in the MUSM, Lima, Peru.

Referred material: In addition to the holotype (MUSM 2995) – MUSM 2971, left dp4 (Text-fig. 3A), MUSM 2972, fragment of a right ?p4, MUSM 3341, fragment of a left lower molar, MUSM 2973, left m1 (Text-fig. 3B), MUSM 2974–2975, fragment of right m1s, MUSM 2976, fragment of a left m2, MUSM 2978–2980, fragments of right m2s, MUSM 2981, left m2 (Text-fig. 3C), MUSM 2977, right m3 (Text-fig. 3D), MUSM 2982, fragment of a left dP4, MUSM 2983, left dP4 (Text-fig. 3E), MUSM 2984, right P4 (Text-fig. 3F), MUSM 2985–2986, fragments of left upper molars, MUSM 2987–2991, fragments of right upper molars, MUSM 2987–2991, fragments of right upper molars, MUSM 2992, right upper molar, MUSM 2993–2994, left M1s (Text-fig. 3G), MUSM 2996, left M3 (Text-fig. 3I).

Type locality: TAR-01, Shapaja, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Diagnosis: Small-sized rodent characterised by brachydont and non-taeniodont teeth. Differs from all Palaeogene and Miocene erethizontoid genera (except *Kichkasteiromys, Palaeosteiromys,* and *Microsteiromys*) in being smaller. Differs from all erethizontoids in having a dp4 with a narrower trigonid and a curved hypolophid (not straight). Differs from *K. raimondii* in displaying a more curved anteroloph, less oblique protoloph and third transverse crest, and more open mesial mesoflexus and hypoflexus on upper molars. Differs from *Protosteiromys medianus* in having a more oval-shaped hypoflexid and no alignment of the ectolophid with the protoconid on lower molars. Differs

from *Protosteiromys asmodeophilus* and *Eosteiromys homogenidens* in having more rectilinear and transverse second cristid and hypolophid on lower molars. Differs from *E. homogenidens* in having a dp4 with a thicker and straighter metalophulid II. Differs from *Parasteiromys* in having upper molars with a mure. Differs from cf. *Microsteiromys* sp. in having labiolingually wider upper molars, and less oblique protoloph and third transverse crest on upper cheek teeth.

Description: The MUSM 2971 dp4 (Text-fig. 3A) is brachydont and much longer than wide (long axis mesiodistal), with a talonid wider than the trigonid. MUSM 2971 is hexalophodont and non-taeniodont. The five main cuspids/stylids (i.e., metaconid, protoconid, mesostylid, entoconid, and hypoconid) are small, but still recognisable (cuspate). The metaconid is slightly more distal than the protoconid, while the entoconid is lingually opposed to the hypoconid. There are many accessory cuspids (or cuspid-like structures): an anteroconid-like cuspid in the middle of the circular metalophulid I, a cuspid in the centre of the anteroflexid, a mesoconid-like cuspid on the mesial ectolophid, and a minute enamel swelling on the lingual part of the posteroflexid. The small metaconid is connected to the well-marked and slightly lingually displaced protoconid: mesially via a long and well-curved metalophulid I, and distally via a thick and slightly oblique (i.e., linguodistally oriented) metalophulid II (labiolingually complete posterior arm of the protoconid). The accessory cuspid in the centre of the anteroflexid displays two cristulids, one labial (free) and another lingual, the latter reaching the distal flank of the metalophulid I, near the metaconid. This accessory cuspid and both cristulids form a short and low transverse neolophid within the anteroflexid. Lingually, a small and isolated mesostyle, as large as the metaconid, occurs around the middle of the lingual margin. Labially, the mesial ectolophid corresponds to a mesoconid-like cuspid associated with two cristulids stemming from that neocuspid-like enamel swelling. The first cristulid is longitudinal, forwardly directed and connected to the base of the distal aspect of the protoconid. The second is longer, linguodistally directed, and it joins the distal ectolophid. The latter is short, but complete, almost longitudinal and centrally situated. From the mesial and distal ectolophid junction, a long and well-defined mesolophid extends linguomesially and links the mesostylid. The large entoconid displays short and slightly distinct anterior and posterior arms. Nevertheless, these arms neither

reach the posterior arm of the mesostylid mesially nor the lingual end of the posterolophid distally, respectively. The well-marked hypolophid links the entoconid with the distal ectolophid. The hypolophid is arcuate (convex). The crestiform hypoconid displays an anterior arm, which is lingually oriented, thin and slightly low but complete (linked to the distal ectolophid-hypolophid junction, non taeniodont pattern). The hypoconid has an anterior outgrowth, markedly long, running mesiolabially and involving a noticeable labial constriction of the hypoflexid. The posterolophid is long and curved, notably in its lingualmost part (small radius of curvature). Except for the paraflexid, which is closed lingually (metalophulid I connected to the metaconid) and thus forming a parafossettid, other flexids remain open lingually, and they are large and deep.

The m1–3s (Text-fig. 3B–D) are brachydont and they share the same dental structure, characterised by a tetralophodont pattern, the absence of taeniodonty, and by flexids labiolingually extended, notably the hypoflexid. The m1s (e.g., Text-fig. 3B) are smaller and more mesiodistally elongated than the m2-3s (Text-fig. 3C–D). The trigonid of m1–2s equals the talonid in width or it is slightly narrower, contrary to the m3 (Text-fig. 3D) in which the trigonid is wider. The cuspids/stylids are not well differentiated, as they are crestiform and included within the strong cristids, which in addition display thick enamel layers. On all lower molars, the metalophulid I is long, transverse and strongly connected to the labiolingually aligned metaconid and protoconid. The metaconid is distally prolonged by its posterior arm, connected to a small mesostylid. The protoconid displays a long and strong posterior arm, extending distolingually in its labial part then lingually, to connect a short and thin neomesolophid, stemming from the mesostylid. The second transverse cristid is thus composite, formed by two cristids (i.e., posterior arm of the protoconid and neomesolophid), clearly recognisable on MUSM 2973 (Text-fig. 3B) and 2981 (Text-fig. 3C), but less distinct on other lower molars (e.g., MUSM 2977, Text-fig. 3D). On these molars, the second transverse cristid seems to only consist of a very long posterior arm of the protoconid, linking the protoconid to the metaconid (= metalophulid II). Some lower molars (MUSM 2973, 2975, and 2976) have an accessory cristulid on the anteroflexid, which is connected to the lingual part of the second transverse cristid. On MUSM 2973 (Text-fig. 3B), this cristulid is also mesi-

ally linked to the metaconid. The entoconid may develop anterior and posterior arms, but the latters are still well separated from the mesostylid (or its posterior arm) and from the lingual end of the posterolophid. Thus, on all lower molars, the mesoflexid and metaflexid are lingually open contrary to the anteroflexid (= anterofossettid). The hypolophid is roughly transverse and parallel to the second transverse cristid, except on MUSM 2981 (Text-fig. 3C) where it is slightly curved. The ectolophid is strongly variable in length and direction. Indeed, it is usually complete (i.e., linking the posterior arm of the hypoconid to the labial extremity of the hypolophid) and well marked. Nevertheless, on one molar (MUSM 2981), it is limited to a very low and short cristulid stemming from the labial extremity of the hypolophid, involving the confluence of the mesoflexid with the hypoflexid. Moreover, the ectolophid can be oblique (MUSM 2973-2975, e.g., Text-fig. 3B) or almost longitudinal, as on MUSM 2977. The hypoconid has an anterior arm, either strong (e.g., MUSM 2973 and 2977) or low and pinched in its middle part. Accordingly it may be composed of two cristulids, with a mesial one from the hypolophid-ectolophid junction and a distal one from the hypoconid (e.g. MUSM 2974 and 2981, Text-fig. 3C). The hypoconid also displays an anterior outgrowth, mesiolabially oriented, which can be strong and long, but without involving a mesiodistal constriction of the hypoflexid. The posterolophid is long and well curved, and it never connects to the entoconid lingually. The anterofossettid, mesoflexid and metaflexid are wide, mesiodistally extended. The same is true for the hypoflexid, which is also labiolingually expensive (wide labial aperture).

The most complete dP4 (MUSM 2983, Textfig. 3E) is damaged, corroded and worn (the other dP4, MUSM 2982, is a fragment of a distal part). MUSM 2983 is oval and longer than wide (long axis mesiodistal). Although the corrosion obscures occlusal morphology, the cusps/styles are incorporated within the crests. The curved anteroloph runs far mesially to the protoloph, and it connects to the paracone labially, thereby closing the paraflexus (= parafossette). There is an accessory cusp or crestule on the labial part of the parafossette, linked to the anteroloph. The paracone is roughly labially opposed to the protocone, and linked to the latter via a long and slightly oblique labial protoloph (labiomesially directed), and a short but strong lingual protoloph (= non taeniodont pattern). The mure and strong ante-

rior arm of the hypocone are labiomesially directed, and they form together a long and oblique crest, almost continuing the labial protoloph. Labially, the mesostyle displays a long anterior arm, reaching the posterior arm of the paracone. Both structures close the mesial mesoflexus labially (= mesial mesofossette). On the two dP4s, the third transverse crest consists of two crests: a long mesoloph from the mesostyle and a short mesolophular spur from the mure-anterior arm of the hypocone complex. On MUSM 2983, the third transverse crest is more transverse than the oblique labial protoloph. On MUSM 2983, the metacone and labial end of the posteroloph are broken and not observable. In contrast, on the MUSM 2982 fragment, this part is preserved: the metacone is crestiform and entirely subsumed within the curved posteroloph. The very short posterior arm of the mesostyle is separated from this metacone-posteroloph complex by a thin and shallow notch. On both dP4s, there is a well defined and moderately long longitudinal crest, which is connected distally to the posteroloph, and mesially free on the more distal flexus (distal mesoflexus + posteroflexus). This crest could be a residual metaloph.

The MUSM 2984 P4 (Text-fig. 3F) is characterised by a rounded occlusal outline, and by a hypocone occupying a more labial position than the protocone. MUSM 2984 is a virtually pristine tooth, with well-recognisable cusps, except the metacone, which is undifferentiated and probably subsumed within the labial and well-curved part of the posteroloph. There are four main transverse crests (i.e., anteroloph, protoloph, third transverse crest, and posteroloph) plus a very short cuspid-like crestule (relic of the metaloph?) on the mesial flank of the metacone-posteroloph complex. The anteroloph is curved and divided into two crests separated by a very thin and shallow furrow: a lingual one connected to the protocone (anterior arm of the protocone) and a labial one, which is labially free and slightly oriented labiodistally. The protocone also displays a posterior outgrowth, of moderate length, and a strong posterior arm (= lingual protoloph) reaching the protoloph (labial portion). The latter, well developed and slightly oblique, extends from an isolated, well-defined, and elevated paracone to the mure, which is slightly grooved in its middle part. The mure and anterior arm of the hypocone are aligned, forming a long and slightly oblique crest (distolingually directed). Labially, the mesostyle is far distally located with respect to the paracone, thereby generating a wide labial aperture of the mesial mesoflexus.

The third transverse crest corresponds to a long and sinuous mesolophule stemming from the mure-anterior arm of the hypocone complex, and extending toward the mesostyle, but without connection with this style. The curved and thick metacone-posteroloph complex is almost merged with the mesostyle, and thus the more distal flexus (distal mesoflexus + posteroflexus) forms a fossette. Within this fossette, a small and isolated enamel swelling coincides probably with a relictual metaloph. That swelling could correspond to a partial fusion and/or rest of the link between the metaloph and the posteroloph (the distal crestule observed on the MUSM 2983dP4, Text-fig. 3E). The flexi are narrow and deep.

The upper molars are brachydont. The M1s (MUSM 2993 and 2994, e.g., Text-fig.3G) are slightly mesiodistally elongated or subquadrate, while the M2 (MUSM 2995, Text-fig. 3H) and the M3 (MUSM 2996, Text-fig. 3I) are subrectangular, being slightly wider than long. The four main cusps (i.e., paracone, protocone, metacone, and hypocone) and the mesostyle are cuspate, well differentiated from the rather thin main transverse crests. On M1 and M2, the hypocone is located directly distal to the protocone while on M3 the hypocone is more labially positioned. On all three loci, the metacone is smaller than other cusps, whereas the paracone dominates (especially on M2-3). The four main transverse crests (i.e., anteroloph, protoloph, third transverse crest, and posteroloph) are particularly long. The protocone is crestiform, oblique in position, and it displays a strong posterior outgrowth, potentially long, notably on M2 and M3 (without involving a mesiodistal constriction of the hypoflexus yet). The transverse anteroloph extends labially from the protocone and ends at the base of the paracone. The paraflexus remains generally widely open labially, except on MUSM 2993 (Textfig. 3G) where it is almost closed. The long protoloph extends from the paracone to the long mure, either longitudinal or slightly directed mesiolabially. All the upper molars are non-taeniodont: a lingual protoloph connects the protocone to the protoloph-mure junction. The lingual protoloph is thick on M1s and thinner on M2. On M3, even if complete, the lingual protoloph is much thinner and lower. The difference of wear between the M2-3s, which are pristine, and the more worn M1s can explain at least partly the variation of development of the lingual protocone. Labially, the mesostyle is often well separated from the paracone (or its posterior arm) by a large notch,



Text-fig. 3. Scanning electron microscope images (in occlusal view) of fossil caviomorph teeth from TAR-01. (**A**–**I**): *Shapajamys labocensis* nov. gen. et sp. (**J**–**P**): *Eoincamys* cf. *pascuali*. (**Q**–**R**): Chinchilloidea indet. (**A**): MUSM 2971, left dp4, (**B**): MUSM 2973, left m1, (**C**): MUSM 2981, left m2, (**D**): MUSM 2977, right m3, (**E**): MUSM 2983, left dP4, (**F**): MUSM 2984, right P4, (**G**): MUSM 2994, left M1, (**H**): MUSM 2995, right M2 (holotype), (**I**): MUSM 2996, left M3?, (**J**): MUSM 3490, right dp4, (**K**): MUSM 3492, right m1, (**L**): MUSM 3294, left m2, (**M**): MUSM 3297, right m3, (**N**): MUSM 3296, right m2, (**O**): MUSM 3299, left M1, (**P**): MUSM 3300, right M2, (**Q**): MUSM 3506, dentary fragment, (**R**): MUSM 3507, dentary fragment. The underlined letters indicate the reversed teeth. Scale bar: 1 mm.

but they can be linked with wear. On pristine upper molars (MUSM 2995 and 2996, Text-fig. 3H–I), the third transverse crest is thinner and/or lower in its labial part before its connection with the mesostyle, and as such, it predominantly corresponds to a mesolophule. In contrast, on MUSM 2994 (Text-fig. 3G), the mesoloph dominates, connected to a short mesolophular spur. On MUSM 2993, the continuous third transverse crest is composed of one crest (either a mesoloph or a mesolophule, or both fusioned). The third transverse crest is roughly parallel to the protoloph and the labiomesial obliquity of both crests is variable: it is particularly marked on MUSM 2987, 2994 and 2996, whereas both crests are almost transverse on MUSM 2993 and 2995. Distally, the posteroloph is mesiodistally constricted before its connection with the hypocone, and both structures can be even separated by a thin and shallow furrow (MUSM 2994

and 2996). Although the metacone is smaller than the mesostyle, it is well recognisable and isolated on fresh upper molars, whereas it is incorporated within the posteroloph on worn teeth (i.e., metacone-posteroloph complex). The metacone is separated from the mesostyle by either a thin notch or an accessory cusplike structure (MUSM 2996, Text-fig. 3I). From the metacone occurs a variably developed metaloph. It is usually long and lingually connected to the posteroloph (in its middle part), or shorter and almost limited to the lingual flank of the metacone as on MUSM 2985 and 2993. Thus, according to the configuration of the metaloph, the posteroflexus can be entirely confluent with the distal mesoflexus or only in part and generating a small and oval posterofossette. The flexi are deep and rather extended.

Remark: the association between the lower and upper teeth and between the deciduous and permanent teeth attributed to Shapajamys is based on several points: i. a similar size, ii. a similar crown heigh, and iii. a similar occlusal pattern. The latter is characterised by non-taeniodonty, recognisable cusp(-id)s (i.e., buno-lophodonty), loph(-id)s slightly oblique (except sometimes for the labial protoloph on upper teeth), a second cristid on lower molars and a third crest on upper teeth well-developed and complete, and a presence of a metaloph (even reduced) or a rest of its connection with the posteroloph on upper teeth. The MUSM 2971 dp4 shows a non-taeniodont pattern with well-developed transverse cristids as on lower molars attributed to Shapajamys. Moreover, lower molars and upper teeth of *Shapajamys* display features typical of erethizontoids (see below). MUSM 2971 has a hexalphodont pattern with a neolophid on the anteroflexid, a structure finding in some erethizontoids (see below).

Comparisons: By its brachydonty, non-taeniodonty, extended flexi(-ds), rounded P4, pentalophodont upper molars with a well-developped metaloph, and very weak obliquity of loph(-id)s, *Shapajamys labocensis* nov. sp. exhibits strong erethizontoid affinities. In most species of this superfamily, the mesoflexid is more labiolingually extended than the hypoflexid (across three quarters of the width of the occlusal surface, e.g., VUCETICH & CANDELA 2001, but sometimes it can be less). Even if it is not the case on the material from TAR-01 (both flexids have roughly a similar labiolingual expansion), the prominent development of the flexids is a feature found in some erethizontoids (like in *Protosteiromys*). Moreover, like on MUSM

2971, some erethizontoids (Branisamyopsis, ?Eosteiromys sp. nov. (CANDELA, 2002), and Steiromys) show accessory structures on the anteroflexid on their dp4s, forming a neolophid. Among erethizontoids, Shapajamys is closer to Kichkasteiromys raimondii nov. sp. from TAR-21, Palaeosteiromys, Protosteiromys, Eosteiromys homogenidens Ameghino, 1902 and cf. Microsteiromys sp. (MD-67), in having non-taeniodont and pentalophodont upper molars, with a well-developped metaloph, and a complete mure. Shapajamys is markedly smaller than all erethizontoid species except K. raimondii, Palaeosteiromys, Microsteiromys jacobsi and cf. Microsteiromys sp., which are slightly smaller. Contrary to Protosteiromys medianus (AMEGHINO, 1903), S. labocensis does not show an ectolophid aligned with the protoconid on lower molars, and the hypoflexid is more oval than triangular. Shapajamys differs from Protosteiromys asmodeophilus WOOD & PATTERSON, 1959 and *E. homogenidens* in having more rectilinear and transverse second cristid and hypolophid on lower molars. The MUSM 2971 dp4 of Shapajamys has a thicker and straighter metalophulid II than in dp4 of E. homogenidens. Besides, the trigonid of MUSM 2971 is narrower than in the dp4 of *E. homogenidens* and of all other erethizontoids in general. Shapajamys labocensis have lower molars with a hypoflexid more labiolingually extended than Microsteiromys jacobsi. Shapajamys labocensis differs from Palaeosteiromys and cf. Microsteiromys sp. in having labiolingually wider upper molars, and less oblique protoloph and third transverse crest. In addition to its larger size, S. labocensis has a more curved anteroloph, less oblique protoloph and third transverse crest, and more open mesial mesoflexus and hypoflexus on upper molars than K. raimondii. Parasteiromys is distinguishable from all other genera in having upper molars without mure. On upper molars (notably on MUSM 2996), the transverse lophs are long, as it is also observed in the non-erethizontoid Draconomys VUCETICH et al., 2010b from the early Oligocene of La Cantera, Argentina. However, the lower molar pattern of Shapajamys from TAR-01 does not match that of Draconomys. In lower molars of Shapajamys, the second transverse cristid is complete, the posterior arm of the metaconid is more developed and connected to a mesostylid, the posterolophid is more curved, and the flexids are larger than in Draconomys. Like in S. labocensis and in some erethizontoids, the dp4s of the dasyproctid *Eobranisamys* FRAILEY & CAMPBELL, 2004 and of the chinchilloid Branisamys HOFFSTETTER &

LAVOCAT, 1970 (according to KRAMARZ et al. 2013) also display accessory structures/a neolophid between the first two cristids. However, these taxa have no extended flexi(-ds) and their upper molars are taeniodont contrary to *S. labocensis*. Lastly, a particularity of *S. labocensis*, absent in all other compared species, is the unusual configuration of the hypolophid, which is curved instead of being straight.

Superfamily Octodontoidea WATERHOUSE, 1839 Family Echimyidae Subfamily Adelphomyinae

Gen. et sp. indet.

(Text-fig. 2E, Appendix S2)

Referred material: MUSM 2968, fragment of a right lower molar (Text-fig. 2E).

Locality: TAR-13, Shapaja, San Martín Department, Peru. Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Description: MUSM 2968 (Text-fig. 2E) is a small fragment of a large right lower molar, in which two oblique cristids, with thick enamel layers, can be recognised: the mesialmost fragment of cristid corresponds to the labial part of the metalophulid I, and the distal one, longer, is the central and diagonal cristid. Its occlusal plan is flat. The metalophulid I is enlarged in its lingual part, probably coinciding with an inflated metaconid. The central cristid is massive, linguodistally directed, and extending from the protoconid to probably end around the entoconid-lingual extremity of the posterolophid. Due to the fragmentary state of this tooth, the entoconid is not preserved. Nevertheless, with its distal position, the central cristid must correspond to a hypolophid. The anterior arm of the hypoconid is strong and complete, and separates the metaflexid from the hypoflexid.

Comparisons: Although very fragmentary, the small preserved part of MUSM 2968 indicates that this lower tooth was non-taeniodont, and displayed oblique and thick cristids incorporating the cuspids, conditions which are primarily found in adelphomyine echimyids (Octodontoidea). Among Palaeogene and Miocene adelphomyines, MUSM 2968 recalls *Ethelomys* (WOOD & PATTERSON, 1959) (Sarmiento Fm., Argentina, late early Oligocene – late Oligocene) and *Adelphomys* AMEGHINO, 1887 (Pinturas and Santa Cruz Fm., Argentina, early Miocene) in showing a trilophodont pattern, a connection between the metalophulid I and the protoconid, a strongly oblique hypolophid, and in having a complete anterior arm of the hypoconid. Stichomys AMEGHINO, 1887 (Santa Cruz Fm., Argentina, late early Miocene) also shows these characters but some specimens attributed to that genus display a complete second transverse cristid or rests of that cristid. MUSM 2968 differs from (i) Deseadomys WOOD & PATTERSON, 1959 (Sarmiento Fm., Argentina, late early Oligocene – late Oligocene), *Xylechimys* PATTERSON & PASCUAL, 1968 (Sarmiento Fm., Argentina, late early Oligocene – late Oligocene) and Prostichomys KRAMARZ, 2001a (Sarmiento and Pinturas Fm., Argentina, early Miocene) in developing a trilophodont pattern, (ii) *Eodelphomys* FRAILEY & CAMPBELL, 2004 (Santa Rosa, Peru, ?late Eocene/ early Oligocene) and Ricardomys WALTON, 1997 (La Venta, Colombia, late middle Miocene) in having a connection between the metalophulid I and the protoconid, (iii) Quebradahondomys CROFT et al., 2011 (Quebrada Honda, Bolivia, late middle Miocene) and Ricardomys in displaying a central diagonal cristid, very oblique and composed of the hypolophid rather than the posterior arm of the protoconid, and (iv) Paradelphomys PATTERSON & PASCUAL, 1968 (Sarmiento Fm., Argentina, early Miocene) in having a strong and complete anterior arm of the hypoconid. This fragmentary tooth does not allow for a generic or specific assignment.

Family indet.

Mayomys nov. gen.

Type species: Mayomys confluens nov. sp.

Species content: only the type species.

Derivation of name: from the Peruvian Mayo River, which flows near the type locality.

Generic diagnosis: as for the type species.

Mayomys confluens nov. sp.

(Text-fig. 4A-S, Appendix S2)

Derivation of name: from the Latin *confluens*, confluent, in reference to the junction of the Mayo and Huallaga Rivers, occurring near the type locality.

Holotype: MUSM 3183, left M2 (Text-fig. 4R). Deposited in the MUSM, Lima, Peru.

Referred material: In addition to the holotype (MUSM 3183) – MUSM 2997–3015 and 3440–3354, left dp4s, MUSM 3016–3037, right dp4s (Text-fig. 4A–B, F), MUSM 3038, right p4 (Text-fig. 4G), MUSM 3039–3059 and 3355, left m1s (Text-fig. 4C), MUSM 3060–3072 and 3356, right m1s (Text-fig. 4H), MUSM 3073–3088, left m2s (Text-fig. 4D), MUSM 3089–3097 and 3357, right m2s (Text-fig. 4I), MUSM 3098–3108, left m3s (Text-fig. 4E), MUSM 3109–3117 and 3358–3359, right m3s (Text-fig. 4J),

MUSM 3118–3138, left dP4s, MUSM 3139–3156, right dP4s (Text-fig. 4K, O), MUSM 3157, left ?P4 (Text-fig. 4P), MUSM 3158–3171 and 3360–3361, left M1s (Text-fig. 4L, Q), MUSM 3172–3182, right M1s, MUSM 3183–3188, 3441–3449 and 3362–3363, left M2s (Text-fig. 4M), MUSM 3450–3460, right M2s, MUSM 3461–3471, left M3s (Text-fig. 4N, S), MUSM 3472–3485, right M3s.

Type locality: Tarapoto TAR-01, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Diagnosis: Small-sized rodent characterised by brachydont teeth and a normal replacement of decidual teeth (dp4s/dP4s). Differs from most Miocene octodontoids in showing thinner loph(-id)s. Differs from Acaremys in having lower crowned teeth. Differs from *Eoespina/Eosachacui* in displaying dp4 with a mesial wall including the mesostylid, from Dudumus in showing a weaker mesolophid and a well-curved metalophulid I on dp4, from *Plesiacarechimys* in having dp4 with a shorter metalophulid I, and from *Protacaremys* in having dp4 characterised by a narrower trigonid. Differs from Paulacoutomys in having a p4 with a wider trigonid and a posterior arm of the protoconid, which does not reach the lingual edge of the tooth, from *Platypittamys* in having a p4 with a longer posterior arm of the protoconid, from Galileomys, Platypittamys, Acaremys, and Sciamys in having a complete and strong hypolophid on p4. Differs from Draconomys, Acarechimys leucothea, Ethelomys, Galileomys baios, Sallamys pascuali and most Miocene octodontoids in having a longer posterior arm of the metaconid, and in the presence of a mesostylid and a neomesolophid (only on some lower molars). Differs from *Eoespina/Eosachacui* and *Eosallamys* in having a poorly distinct mesostylid on lower molars. Differs from Galileomys, Acaremys, Dudumus, Caviocricetus, Prospaniomys, Protacaremys, and some specimens of Acarechimys in having a protoconid and a hypoconid less mesiodistally compressed on lower molars. Differs from Plesiacarechimys in having a dP4 more elongated mesiolabially. Differs from Eoespina/Eosachacui, Eosallamys, Draconomys, and Plesiacarechimys in having upper molars without metaloph (or residual metaloph, except for one teeth). Differs from Draconomys, Eosallamys, and Miocene species of Galileomys in having less transversely elongated upper molars. Differs from *Eoespina/Eosachacui* in displaying upper molars with more extensive flexi (notably the mesial mesoflexus), and from ?Vallehermosomys merlinae in having a M3 with a wider distal mesoflexus. Differs

from Sallamys pascuali in displaying a third crest always connected from the anterior arm of the hypocone. Differs from Sallamys pascuali, Platypittamys, and most Miocene octodontoids (e.g., Caviocricetus or *Dudumus*) in showing a mesostyle more mesially positioned and smaller with respect to Miocene octodontoids on upper teeth. Differs from Acaremys murinus and Pseudoacaremys in having a more persistent first and last labial flexi on upper molars. Differs from Prospaniomys cf. P. priscus and Protacaremys denisae in having a less oblique protoloph on upper molars. Differs from *Caviocricetus* in having a more developed second transverse cristid on lower molars, and less elevated and enlarged cusp(-id)s, notably the labial ones on upper teeth, and the lingual ones on lower teeth. **Description:** The dp4s (Text-fig. 4A–B, F) are longer

than wide, with a trigonid narrower than the talonid. The entoconid is the largest and tallest cuspid. The latter and the protoconid are well differentiated contrary to the crestiform metaconid and hypoconid. A small mesostylid is usually connected to the long and strong posterior arm of the metaconid, and thus, it is faintly differentiated from these two structures (i.e., metaconid and its posterior arm). The mesostylid is well recognisable only on three dp4s (MUSM 2998, 3018, and 3025). On MUSM 3025, it is small and well defined at the distal extremity of the posterior arm of the metaconid. On MUSM 2998 and 3018 (Text-fig. 4B), the mesostylid is strongly connected to the posterior arm of the metaconid, but it is large and elevated. On all dp4s, the mesostylid is separated from the entoconid by a more or less developed notch, except on one tooth (MUSM 3000) where both cuspids are linked. The protoconid displays two permanent connections: a lingual one with a short and curved metalophulid I, which extends lingually to the metaconid, and a distal one with the low mesial extremity of the mesial ectolophid. The distal part of the mesial ectolophid is not longitudinal contrary to the mesial one, but oblique (i.e., distolingually directed), and connects to the distal ectolophid, which is aligned with it or being more longitudinal. Because of the configuration of these mesial structures, all dp4s are characterised by a long and circular mesial wall, which extends from the lingual margin of the tooth to the labial one. It is formed by the mesial ectolophid, the protoconid, the metalophulid I, the metaconid, its posterior arm and the mesostylid in the majority of cases. The dp4s are particularly variable in terms of size and development plus orientation of the posterior arm of the protoconid



Text-fig. 4. Scanning electron microscope images (in occlusal view) of fossil caviomorph teeth from TAR-01. (A–S): *Mayomys confluens* nov. gen. et sp. and (T–H'): *Tarapotomys mayoensis* nov. gen. et sp. (A): MUSM 3020, right dp4, (B): MUSM 3018, right dp4, (C): MUSM 3040, left m1, (D): MUSM 3075, left m2, (E): MUSM 3099, left m3, (F): MUSM 3017, right dp4, (G): MUSM 3038, right p4, (H): MUSM 3060, right m1, (I): MUSM 3089, right m2, (J): MUSM 3109, right m3, (K): MUSM 3141, right dP4, (L): MUSM 3159, left M1, (M): MUSM 3158, left M2, (N): MUSM 3461, left M3, (O): MUSM 3139, right dP4, (P): MUSM 3157, fragmentary left P4?, (Q): MUSM 3158, left M1, (R): MUSM 3303, left M2 (holotype), (S): MUSM 3462, left M3, (T): MUSM 3302, right dp4, (U): MUSM 3303, right p4, (V): MUSM 3304, left m1, (W): MUSM 3309, left m2, (X): MUSM 3315, right m3, (Y): MUSM 3310, right m2, (Z): MUSM 3307, left dP4, (E'): MUSM 3319, left P4, (F'): MUSM 33499, right M2, (H'): MUSM 3502, right M3. The underlined letters indicate the reversed teeth. Scale bar: 1 mm.

and mesolophid. The posterior arm of the protoconid either reaches the lingual margin of the tooth (and can be connected to the metaconid, = metalophulid II) or it is shorter and backwardly oriented. The mesolophid is sometimes complete, extending from the mesial ectolophid-distal ectolophid junction to the mesostylid, but it can also be short (in most specimens), reduced to a cuspid-like or even absent. On MUSM 3005, 3016 and 3018 (Text-fig. 4B), secondary cristulids connect the posterior arm of the protoconid to the mesolophid. On all dp4s, a well-marked and roughly transverse hypolophid joins the large entoconid with the distal ectolophid. Besides, the hypoconid always displays a long anterior outgrowth and a thin but complete anterior arm, reaching the hypolophid-distal ectolophid junction (i.e., non-taeniodont pattern). The hypolophid, hypoconid, its anterior arm and a strong and well-curved posterolophid (ending far from the entoconid), isolate an expansive metaflexid, further characterised by a wide lingual opening.

The MUSM 3038 p4 (Text-fig. 4G) is slightly shorter than the dp4s, with a trigonid comparatively wider than the talonid. MUSM 3038 is tetralophodont with thin and straight cristids, except the wellcurved posterolophid. By its large surface, strong elevation and isolation, the entoconid is the most differentiated cuspid. The metalophulid I is transverse, connected lingually to a metaconid elevated but crestiform, and labially to a protoconid more distinct and distal and lower than the metaconid. The latter displays a long posterior arm, the elevation of which decreases mesiodistally. There is no apparent mesostylid on the lingual margin of the tooth. That stylid is probably entirely subsumed within the posterior arm of the metaconid, well separated from the entoconid by a wide furrow. The protoconid shows a long and slightly oblique posterior arm, but the latter does not reach the lingual margin of the tooth and it remains lingually free. Thus, the anteroflexid and mesoflexid are confluent, and they form a flexid lingually open between the posterior arm of the metaconid and the entoconid. The ectolophid, oblique, connects the protoconid to a long and well-marked hypolophid, stemming from the entoconid. The hypoconid displays a complete anterior arm (i.e., non-taeniodont pattern), a short anterior outgrowth labially directed, and a long curved posterior arm (i.e., posterolophid), reaching the distal base of the entoconid. The metaflexid is the most extended flexid.

The m1s (Text-fig. 4C, H) are clearly smaller than m2s (Text-fig. 4D, I), and the m3s (Text-fig. 4E, J)

roughly equal m2s in size. On m1s, the trigonid is as wide as the talonid, while on m3s, it is often narrower than the latter. The relative width of the trigonid is more variable on m2s. The shape of m3s is extremely variable: they can be long, and with a more or less rounded posterolophid. The occlusal pattern is similar from m1 to m3, and strongly reminiscent of that of p4. Molars differ from p4s in having a wider trigonid comparatively to the talonid. The molars have salient cuspids and thin cristids. On the less worn lower molars, the protoconid and entoconid are clearly cuspate contrary to the metaconid, hypoconid, and mesostylid, which are crestiform. The latter is small and merged with the long and strong posterior arm of the metaconid. A transverse or slightly mesially convex metalophulid I connects the metaconid to the protoconid. The second transverse cristid is highly variable in terms of orientation, composition, and development. Indeed, it can be transverse or slightly oblique, continuous or discontinuous, and sometimes linking the lingual edge of the tooth. However, the second transverse cristid is always composed of a long posterior arm of the protoconid, lingually free or not, connected to the metaconid-posterior arm of the metaconid-mesostylid complex (= metalophulid II), or linked to a short neomesolophid. The latter is present or absent, sometimes reduced to a cuspid-like structure (e.g., MUSM 3109 (Text-fig. 4J) and 3114), and it can be disconnected to the mesostylid. The second cristid can bear an accessory cristulid, forwardly oriented and reaching the metalophulid I (MUSM 3081 and 3093). When the second transverse cristid is complete, the three lingual flexids (i.e., anteroflexid, mesoflexid, and metaflexid) are roughly equal in surface, while when the second cristid is incomplete, the confluent anteroflexid and mesoflexid form a larger flexid than the metaflexid. The MUSM 3109 m3 (Textfig. 4J) shows a peculiar configuration of the mesial cristids and cuspids. On that tooth, the metaconid is separated from the metalophulid I by a deep notch on the mesial edge of the tooth, but it remains connected to the metalophulid I via a more internal and secondary cristid. On all lower molars, the elevated and large entoconid, usually bearing poorly differentiated arms (i.e., anterior and posterior), is connected to the crestiform hypoconid via a well-marked, roughly transverse hypolophid and a thinner but complete anterior arm of the hypoconid (i.e., non-taeniodont pattern). The distolingually directed ectolophid links the protoconid to the hypolophid-anterior arm of the hypoconid junction. In addition to its anterior arm, the hypoconid displays also an anterior outgrowth and a wellcurved posterior arm (i.e., posterolophid), remaining lingually free. The anterior outgrowth of the hypoconid can be long and always directed labially, an orientation which never involves a mesiodistal constriction of the triangular hypoflexid.

The dP4s are longer than wide with rounded corners (Text-fig. 4K, O). Some dP4s are either trapezoidal or more rectangular, but others have a more oval occlusal outline, with well-arcuate anteroloph (mesially convex) and posteroloph (distally convex). All dP4s are brachydont, tetralophodont, non-taeniodont, and with thin crests. The protocone is mesiolingually-distolabiallly pinched, and labially and lingually continued by its anterior arm and posterior outgrowth, respectively. These three structures (i.e., protocone, its anterior arm and posterior outgrowth) form a long, curved and mesial crest. The latter remains labially free at any wear stages and sometimes involved a small mesiodistal constriction of the subtriangular hypoflexus. The isolated paracone is the largest labial cusp. It is connected to a labial protoloph, without anterior or posterior arms. The labial protoloph is well marked, long and transverse or slightly oblique, whereas the lingual protoloph, which connects the protocone to the labial protoloph, is thinner, shorter and always oblique (labiodistally directed). The long mure is rarely longitudinal and often labiomesially directed. It may be aligned with the strong anterior arm of the hypocone. Labially, the mesostyle is more or less differentiated (well-defined on some specimens, or indistinct on some others), well separated from the paracone (except with strong wear), but always merged with the posteroloph, strongly connected to the hypocone. There is neither differentiated metacone on the curved mesostyle-posteroloph complex nor any traces of metaloph. The third transverse crest is usually clearly disconnected to the mesostyle, or otherwise, it reaches the lingual aspect of this style. So, this crest corresponds to a mesolophule. The latter is variably developed: either long, short, or reduced to a spur on the anterior arm of the hypocone. In some specimens (e.g., MUSM 3122 and 3141 (Textfig. 4K)), it is poorly connected to that crest. Depending on the development of the third transverse crest, both mesoflexi (i.e. mesial and distal ones) are more or less confluent.

MUSM 3157 (Text-fig. 4P) is considered as a mesiolingual fragment of a P4. A round and small hypofossette is recognisable and at least delimited by a thick protocone-posterior outgrowth of the protocone complex, a thin lingual protoloph, the lingual end of the labial protoloph, and a longitudinal mure.

Like the dP4s, upper molars show rounded corners in occlusal view. The M1–2s are usually quadrate. Nonetheless, some teeth are more mesiodistally elongated. In both cases, the M2s (Text-fig. 4M, R) are larger than M1s (Text-fig. 4L, Q), and the hypocone on M2s is often smaller and more labial in position. The reduction of the hypocone and its labial displacement are more pronounced on M3s (Text-fig. 4N, S). The shape of M3s varies from heart-shaped to round, and some teeth present more angular corners. All upper molars are brachydont, tetralophodont, and with thin crests and salient cusps/styles. The paracone, which can display anterior and posterior arms, is well defined and it dominates over other cusps. The well-marked anteroloph extends labially from a crestiform protocone, and often remains labially free. But, on some upper molars (usually worn or more pristine as: MUSM 3185 (Text-fig. 4M) and 3451), the anteroloph joins the paracone (or its anterior arm), thereby closing the paraflexus labially. The anteroloph is roughly transverse on M1–2s and often more curved on M3s. The protocone also displays a long posterior outgrowth, notably on M2s, in which it generates a wide mesiodistal constriction of the hypoflexus. The labial protoloph is long, transverse, or only slightly oblique. It extends from the lingual aspect of the paracone to the mure. In many cases, the latter is longitudinal or slightly mesiolabially directed, aligned with the oblique anterior arm of the hypocone, notably on M1s. Most upper molars are non-taeniodont but there are some exceptions. Indeed, the lingual protoloph may be low and thin, disconnected to the labial protoloph-mure junction, or even lacking (MUSM 3164), which involves a partial or complete confluence of the paraflexus with the hypoflexus (i.e., pseudo-taeniodont or taeniodont pattern). A curved posteroloph connects the hypocone to the mesostyle, which is well separated from the paracone and usually faintly differentiated from the posteroloph. On that mesostyle-posteroloph complex, the metacone is either lacking or undifferentiated, except on some M3s (MUSM 3462 (Text-fig. 4S) and 3480). The metacone is probably subsumed within the distal transverse crest in the majority of cases. The third transverse crest is well marked and always longer than the midline of the tooth width. Like on the dP4s, it corresponds to a mesolophule, stemming from the anterior arm of the hypocone. In most cases, it reaches the lingual flank of the mesostyle, merging with it with wear. A lingual accessory crestule (spur), backwardly oriented, may occur on the mesolophule (e.g., MUSM 3174 and 3454). Besides, a short and forwardly oriented crest connects to the posteroloph on MUSM 3455. A small cusp occurs on the most distal flexus of MUSM 3472. Both structures may represent a residual metaloph. A metaloph is present only on two M3s (Text-fig. 4N): on MUSM 3480, it is very short and developed from the metacone while on MUSM 3461, it is reduced to a cusp in the middle of the most distal flexus. Thus, the latter corresponds to the confluence of the distal mesoflexus with the posteroflexus, which can be also confluent with the mesial mesoflexus.

Remark 1: It is worth noting that MUSM 3183 (Textfig. 4R) and 3185 (Text-fig. 4M), both identified as M2, although displaying a similar dental pattern, are clearly distinct in occlusal outline, thus suggesting the existence of two morphs (morph 1 and 2, respectively). A wide range in the occlusal outline shape is observed in the material reported here, with many intermediate outline shapes, MUSM 3183 and MUSM 3185 being the two extremes. Lastly, the morphological variation on the other loci (dP4s, dp4s, and lower molars) also appears rather continuous. Accordingly, we consider that all the material reported here documents a single taxon.

Remark 2: the association between the two permanent premolars (the MUSM 3038 p4 and the MUSM 3157 ?P4) and the other teeth attributed to Mayomys is based on several points: i. a similar size, ii. a similar crown heigh, and iii. a similar occlusal pattern. The MUSM 3157 ?P4 shows a non-taeniodont pattern with a complete lingual protoloph, the usual condition of dP4s and upper molars of Mayomys. In contrast, the other taxa from Shapaja and with a similar size with Mayomys (E. parvus, T. subandinus and T. mayoensis) have taeniodont P4s. As the lower molars of *Mayomys*, the MUSM 3038 p4 is non-taeniodont and tetralophodont with lophids slightly oblique, a reduced second cristid and posterior arm of the metaconid, and whithout mesostylid. We attribute the great number of deciduous premolar (43 dp4s et 39 dP4s) comparatively to the number of pemanent premolars (1 p4 and 1 P4) in *Mayomys* to a probable predator selection (more juveniles killed than adults).

Comparisons: By its low-crowned and tetralophodont upper teeth, generally non-taeniodont, with moderately expanded flexi(-ds), absence of laminar pattern and of strong obliquity of loph(-id)s, this set of isolated teeth described here likely documents an octodontoid. The dP4s of many extinct octodontoids (e.g., Acaremys murinus Ameghino, 1887, 'Acaremys' preminutus BORDAS, 1939 (a potential junior synonym of Protacaremys prior AMEGHINO, 1902, see ARNAL & VUCETICH 2015b), Caviocricetus lucasi VUCETICH & VERZI, 1996, Dudumus ruigomezi Ar-NAL et al., 2014, Prospaniomys cf. P. priscus (ARNAL & KRAMARZ 2011), and Prostichomys bowni KRAMARZ, 2001a) are mesiodistally elongated and tetralophodont, as observed in the dP4s identified for this new taxon. Teeth referred to Mayomys confluens nov. gen. et sp. do not show loph(-id)s with a strong obliquity (even absence of obliquity), contrary to the condition characterising teeth of adelphomyine octodontoids.

Among Palaeogene octodontoids, the dental pattern of *M. confluens* is particularly reminiscent of that characterising *Platypittamys brachyodon* WOOD, 1949 (Sarmiento Fm., Argentina, late Oligocene), notably in having a complete or reduced second transverse cristid, with a dominant posterior arm of the protoconid, non-taeniodont and completely tetralophodont upper molars. However, M. confluens differs from P. brachyo*don* in having a longer posterior arm of the protoconid on p4, and in displaying a hypolophid on p4. Other taxa also show a reduction of the second transverse cristid, which is moderate in Draconomys verai (a potential octodontoid, VUCETICH et al. 2010b but see ARNAL et al. 2014), Galileomys baios VUCETICH et al., 2015 (Sarmiento Fm., Argentina, late early Oligocene - late Oligocene) and Sallamys quispea SHOCKEY et al., 2009 (Moquega Fm., Peru, late Oligocene), and more pronounced in Acarechimys leucothea Vu-CETICH et al., 2015 (Sarmiento Fm., Argentina, late early Oligocene - late Oligocene), Ethelomys loomisi (WOOD & PATTERSON, 1959) and Sallamys pascuali HOFFSTETTER & LAVOCAT, 1970 (Salla, Bolivia, late early Oligocene - late Oligocene). Nevertheless, the lower molars of Mayomys show a long posterior arm of the metaconid, even if it is inclined on the distal flank of the metaconid (on pristine teeth), whereas in D. verai, A. leucothea, E. loomisi, G. baios, P. brachyodon, and Sallamys, it is short or absent (as well as in Migraveramus beatus PATTERSON & WOOD, 1982, and ?Protacaremys adilos (VUCETICH et al., 2015a)). In these taxa, the metaconid is very crestiform and often connected with an accessory cristid (i.e., metaconid cristid/spur), sometimes linked to the second transverse cristid (no neomesolophid), and other accessory

cristulids may occur on the metalophulid I. Conversely, lower molars of *Eoespina/Eosachacui*, *Eosalla*mys FRAILEY & CAMPBELL, 2004 (Santa Rosa, Peru, ?late Eocene/early Oligocene) and Paulacoutomys Vu-CETICH et al., 1993a (Tremembé Fm., Brazil, late early Oligocene – late Oligocene) display a long posterior arm of the metaconid like in Mayomys, but the mesostylid is more distinct in Eoespina/Eosachacui and *Eosallamys* (poorly visible in *Paulacoutomys* due to the advanced wear of the specimen). The p4 of Mayomys (MUSM 3038) is very similar in morphology to that of *Paulacoutomys*, but its trigonid is wider, and the posterior arm of the protoconid does not reach the lingual edge of the tooth contrary to what it is observed in Paulacoutomys. The upper molars of Mayomys also recall those of ?Vallehermosomys merlinae (La Cantera, Argentina, late early Oligocene, VUCE-TICH et al. 2010b) and *Eoespina/Eosachacui*, notably by their rounded occlusal outline and by the presence of a curved posteroloph. The distal mesoflexus of the M3 attributed to ?Vallehermosomys merlinae is smaller than that of M3s of *Mayomys*. As in upper molars of Mayomys, the development of the lingual protoloph is variable in *Eoespina/Eosachacui*, in which some teeth are fully taeniodont. Nevertheless, upper molars of Eoespina/Eosachacui display less expanded flexi, notably the mesial mesoflexus, than in Mayomys, and some of them have a relictual metaloph. The mesial wall of dp4 is sometimes prominently developed in *Eoespina*/ Eosachacui, but it does not include a well-separated mesostylid contrary to what it is observed on dp4 of Mayomys. The upper molars of Eosallamys and Draconomys are strongly labiolingually widened compared to those of Mayomys. Besides, they show a complete or relictual metaloph, not observed (i.e., lost) on upper molars of Mayomys. As for Mayomys, upper teeth of Sallamys are tetralophodont, but their third crest is often disconnected from the anterior arm of the hypocone, and often lingually linked to the posteroloph. Mayomys also differs from Sallamys and Platypittamys in having upper molars bearing a more mesial mesostyle.

Basically, *Mayomys* exhibits a dental pattern similar to some Miocene octodontoids, such as *Acarechimys* AMEGHINO, 1887 (Argentina, Bolivia, Chile, Colombia and Peru, late early Oligocene – middle Miocene), *Acaremys* AMEGHINO, 1887 (Sarmiento, Pinturas and Santa Cruz Fm., Argentina, early Miocene), *Caviocricetus* VUCETICH & VERZI, 1996 (Sarmiento, Chinchinales and Cerro Bandera Fm.,

Argentina, early Miocene), Dudumus ARNAL et al., 2014 (Sarmiento Fm., Argentina, early Miocene), Galileomys VUCETICH & KRAMARZ, 2003 (Sarmiento and Pinturas Fm., Argentina, late early Oligocene late early Miocene), Prospaniomys AMEGHINO, 1902 (Sarmiento Fm., Argentina, early Miocene), and Protacaremys AMEGHINO, 1902 (Sarmiento and Collón Cura Fm., Argentina, early Miocene - middle Miocene). This is particularly shown in the tetralophodonty, the non-taeniodonty, the presence of roughly transverse loph(-id)s, a reduction of the second transverse cristid, and in the hypoflexus labiolingually shorter than both the protoloph and third transverse crest. Besides, some Miocene genera (e.g., Acaremys, Galileomys, Prostichomys, and Sciamys AMEGHINO, 1887) show a strong mesial wall on dp4, like in Mayomys. Nevertheless, the lower molars of Mayomys have persistent flexids, notably the anteroflexid. This feature is more frequent in Palaeogene genera than in Miocene ones, which show a higher crown and where flexids reduce fastly with wear (more slightly in the Miocene genus *Dudumus*, yet). The teeth of *Mayomys* show thinner loph(-id)s than in most Miocene genera. Moreover, like in some Palaeogene octodontoids (see paragraph above), these Miocene genera have a crestiform metaconid often connected with metaconid cristid/spur, usually connected to the second transverse cristid (absence of neomesolophid and mesostylid, and weak development or absence of posterior arm of the metaconid). On lower molars of Mayomys, the protoconid and hypoconid are clearly less mesiodistally compressed than in Acaremys, Caviocricetus, Dudumus, Galileomys, Prospaniomys, Protacaremys, and most specimens of Acarechimys. p4s of Mayomys display a strong and complete hypolophid contrary to Acaremys and Galileomys (in Sciamys as well), in which the hypolophid is reduced, partly fused with the posterolophid, or entirely absent. Mayomys differs from *Dudumus* in showing a weaker mesolophid and a wellcurved metalophulid I on dp4, and in displaying a mesostyle smaller and more mesially positioned on upper teeth. In Mayomys, the protoloph and third transverse crest are parallel or slighly divergent (U-shaped protoloph-third transverse crest complex). In contrast, in Dudumus (as in most Miocene octodontoids, such as *Acaremys* or *Caviocrietus*) the mesostyle is strongly cuspate (cusp-like style) and clearly distally displaced, which involves a marked divergence between the protoloph and the third transverse crest (V-shaped protoloph-third transverse crest complex), and therefore a larger mesial mesoflexus (wide labial opening) and a smaller distal mesoflexus. The upper molars of Miocene species of Galileomys are more elongated transversely than those of *Mayomys*. The latter also differs from *Caviocrietus* in having a more developed second transverse cristid on lower molars, and less elevated and enlarged cusps, notably the labial ones on upper teeth, and the lingual ones on lower teeth. On lower molars of Acaremys and Protacaremys, labially, the second transverse cristid occupies a more distal position, and as such, it could be interpreted as a mesolophid. Mayomys displays more persistent first and last labial flexi on upper molars than Acaremys murinus and Pseudoacaremys ARNAL & VUCETICH, 2015b (Santa Cruz Fm., Argentina, early Miocene). Mayomys has also a smaller dP4 than Acaremys murinus and a lower crown than the representatives of Acaremys in general. Mayomys differs from Protacaremys in having dp4 characterised by a narrower trigonid. In *Prospaniomys* cf. P. priscus (Sarmiento Fm., Argentina, early Miocene) and Protacaremys denisae VUCETICH et al., 1993b (Collón Cura Fm., Argentina, middle Miocene), the protoloph is more oblique than in M. confluens. Mayomys differs from Plesiacarechimys koenigswaldi VUCE-TICH & VIEYTES, 2006 (Collón Cura Fm., Argentina, middle Miocene) in having a dP4 more mesiolabially elongated, upper molars without metaloph (or residual metaloph, except for few teeth), and in having dp4 characterised by a shorter metalophulid I. Mayomys differs from Caviocricetus, Dudumus, Plesiacarechimys, Prospaniomys, Protacaremys and Spaniomys in having a normal replacement of its dp4s/dP4s.

To sum up, *Mayomys confluens* nov. gen. et sp. is characterised by a very peculiar dental pattern among Octodontoidea. Indeed, it shares dental features with pre-Deseadan taxa (*Eoespina/Eosachacui* and ?*Vallehermosomys merlinae*) but also with Deseadan (*Platypittamys, Paulacoutomys*, etc.) and even Miocene taxa (e.g., *Dudumus*). However, *Mayomys* appears have several dental characters more primitive than Deseadan and Miocene octodontoids: a metacone sometimes still present, a small mesostyle proximal to the paracone, a third crest usually straight on upper teeth, and a posterior arm of metaconid still long on lower molars.

Remark: The MUSM 2892dP4 found at CTA-61 (see BOIVIN et al. 2017a) and assigned to an octodontoid indet. (BOIVIN et al. 2017a: fig. 5M) is very close in size and morphology (notably by the shape of the occlusal outline, the development of flexi, and thinness of crests) to *Mayomys confluens* from TAR-01. However, the third transverse crest is complete on MUSM 2892, whereas it has a weak connection with the mesostyle, or is clearly disconnected to that style in *Mayomys*. Thus, MUSM 2892 from CTA-61 is provisionally re-assigned to aff. *Mayomys* sp.

Selvamys gen. nov.

Type species: *Selvamys paulus* nov. sp. Species content: only the type species. Derivation of name: from the Spanish *selva*, forest. Generic diagnosis: as for the type species.

Selvamys paulus nov. sp.

(Text-fig. 2A–B, Appendix S2)

Derivation of name: from the Latin *paulus,* small, in reference to the size of the species.

Holotype: MUSM 2960, right M2 (Text-fig. 2A). Deposited in the MUSM, Lima, Peru.

Referred material: in addition to the holotype (MUSM 2960) – MUSM 3340, right M1 or 2 (Text-fig. 2B).

Type locality: TAR-22, Shapaja, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Diagnosis: very tiny rodent characterised by brachydont and bunolophodont teeth. Differs from all other caviomorphs (except *Loretomys*) in being very smallsized. Upper molars tetralophodont and non-taeniodont. Differs from *Loretomys* in having a hypoflexus lingually opened on upper molars and a labiolingually wider M2, differs from *Galileomys* in having lower-crowned upper molars, a lingual protoloph more transverse, and a hypoflexus more labiolingually extended.

Description: The MUSM 2960 M2 (Text-fig. 2A) and MUSM 3340 (Text-fig. 2B) are damaged at the level of their hypocone. MUSM 2960 also shows many digestion marks, notably in its lingual part. Both are brachydont, tetralophodont with thin crests, and non-taeniodont. MUSM 2960 is transversely widened, whereas MUSM 3340 is more quadrate. The anteroloph is quite short, ending directly mesial to the lingual aspect of a cuspate paracone. The less worn molar MUSM 2960 bears a small enamel swelling in its labialmost extremity, likely to indicate the presence of a minute parastyle. The latter is separated form the paracone by a shallow furrow. The protocone is mesially canted and labiolingually pinched. It displays a well-marked anterior arm and a long posterior outgrowth, thereby appearing crescentiform. The long

posterior outgrowth of the protocone is linguodistally oriented, which involves a mesiodistal constriction of the lingual opening of the hypoflexus. On MUSM 2960, the protoloph is long, slightly oblique, and parallel to the anteroloph, whereas it is more transverse on MUSM 3340. On both teeth, it extends from the paracone to the mure, which is markedly long, low, oblique, and not aligned with the more transverse and short anterior arm of the hypocone. The posterior arm of the protocone (= lingual protoloph) is thick, slightly labiodistally directed, and strongly connected to the protoloph-mure junction. Labially, the distal cusp is interpreted here as a mesostyle, which is distally displaced. On MUSM 2960, this cusp is connected to the third transverse crest, linking lingually the mesial extremity of the short anterior arm of the hypocone. On MUSM 3340, the mesostyle is connected to a short and low crestule, almost indiscernible and interpreted here as being a mesoloph. This tooth also displays a short mesolophule stemming from the anterior arm of the hypocone, unlinked to the mesoloph. On MUSM 2960, the mesostyle bears a short and low posterior arm. Molars have neither metacone nor metaloph. The posteroloph, markedly curved with respect to the anteroloph, is strongly linked to the hypocone. On MUSM 2960, the posteroloph and the short posterior arm of the mesostyle are almost connected at their base but distinct at their tip (presence of a shallow notch). On MUSM 3340, (more worn) the posteroloph is strongly linked to the mesostyle. Contrary to the labial protoloph, mesiolabially oriented or transverse, the third transverse crest is distolabially oriented on both teeth. The third transverse crest, protoloph, and long mure isolate a mesiodistally extended and U-shaped mesial mesoflexus, further characterised by a very large labial opening, especially on MUSM 2960. In contrast, the paraflexus and distal mesoflexus are narrower and less widely open labially. Besides, the markedly long protoloph and third crest coincide with strongly labiolingually developed labial flexi.

Comparisons: By its small size, brachydonty, weak crest obliquity, absence of laminar pattern, tetralophodonty (i.e., absence of metaloph), non-taeniodonty, mesostyle distally displaced and mesiodistally narrow, and labially open paraflexus and distal mesoflexus, MUSM 2960 and MUSM 3340 likely document a single and distinctive octodontoid. Indeed, many Palaeogene and Miocene octodontoids also display these characters. Nevertheless, *Selvamys* differs from

all these taxa (except *Loretomys* BOIVIN et al., 2017a, and Acarechimys minutissimus (AMEGHINO, 1887)) by its very small size. Selvamys differs from Loretomys in having a hypoflexus lingually opened on upper molars and a labiolingually wider M2. In octodontoids, the latter feature is unusual (as in A. minutissimus, Dudumus or Caviocricetus), but found in Galileomys. However, MUSM 2960 and MUSM 3340 are lower-crowned than the upper molars of Galileomys, the lingual protoloph is more transverse and the hypoflexus is more labiolingually extended in *Selvamys* than in Galileomys. As on the upper teeth of Dudumus or Caviocricetus, the third crest of upper molars of Sel*vamys* is either complete or reduced. In latter case, the mesolophule is dominant and it is not linked to the mesostyle (or a short mesoloph).

Chinchilloidea BENNETT, 1833 Family indet.

Gen. et sp. indet.

(Text-fig. 3Q–R, Appendix S2)

Referred material: MUSM 3506–3507, dental fragments (Text-fig. 3Q–R).

Locality: TAR-01, Shapaja, San Martín Department, Peru. Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Description: Despite their very fragmentary nature, both specimens document a large species, which is the largest taxon to be recorded at TAR-01. Given their poor state of preservation, it is impossible to determine if these fragments document upper or lower molars. The two fragments have a pronounced crown height with broken roots. Moreover, their lophs (or lophids) form laminated lobes, especially MUSM 3506 (Text-fig. 3Q). On this tooth, two loph(-id)s are recognisable. They delimit an open flexus or flexid (probably the hypoflexus or hypoflexid). One of these loph(-id)s is mesiodistally thin. The thickness of the second cannot be assessed because only one of its margins is preserved. The latter shows a thick enamel layer, whereas the thin loph(-id) has almost no enamel layer on the flexus/id wall, and a very thick enamel on its other margin. Both loph(-id)s are very close together because of a very narrow flexus(-id).

MUSM 3507 (Text-fig. 3R) is a fragment of either a right lower or a left upper cheek tooth. Three loph(-id)s are recognisable on this tooth. Two of them are weakly connected to the margin of the tooth. They might have been linked to the other margin as well. The third loph(-id), close to the other, remains distinct.

Comparisons: The high crown, laminar occlusal pattern and heterogeneous thickness of the enamel layer (thicker on the leading edges than on the trailing edges, KRAMARZ et al. 2013) suggest chinchilloid affinities. Owing to their strong heterogeneous thickness of the enamel layer, they probably document a taxon distinct from the chinchilloid Scleromys AMEGHINO, 1887 (included "Scleromys", Argentina, Brazil, Colombia, Peru, late Oligocene – middle Miocene) or the alleged chinchilloid Branisamys (KRAMARZ et al. 2013). There is no strong interprismatic cement on the flexus/ids of both specimens from TAR-01, thereby precluding a referral to Neoepiblemidae KRAGLIEV-ICH, 1926 for these fragments. The occlusal configuration of MUSM 3507 does not correspond to that of the cephalomyid Cephalomys AMEGHINO, 1897 (for lower teeth at least, Sarmiento Fm., Argentina and Salla, Bolivia, late early Oligocene - late Oligocene) and Soriamys KRAMARZ, 2001b from the early Miocene of Sarmiento Fm., Argentina (for the superfamilial assignation of the cephalomyids as chinchilloids, see Vucetich 1985, 1989, Dozo 1995, Vucetich et al. 1999, KRAMARZ 2001b, but see KRAMARZ 2005). This fragmentary tooth recalls some teeth of Garridomys KRAMARZ et al., 2013 (Cerro Bandera Fm., Argentina, early Miocene) and Eoviscaccia Vu-CETICH, 1989 (Sarmiento, Chichinales, and Cerro Bandera Fm., Argentina, Lacayani, Bolivia, Termas del Flaco, Chile, early Oligocene – early Miocene) at a medium degree of occlusal wear. It is strikingly reminiscent of the MOZ-PV-944 m1 attributed to Garridomys (KRAMARZ et al. 2013). However, the first flexus/id seems to be longer on MUSM 3507 than on MOZ-PV-944 and the difference in enamel thickness of MUSM 3506 is stronger than in Garridomys (and *Eoviscaccia*). Besides, a thin interprismatic cement and marked difference in enamel thickness characterising the specimens of TAR-01 also recall the morphology of some dinomyids (e.g., Arazamys RINDERKNECHT et al., 2011).

Superfamily ?Chinchilloidea BENNETT, 1833 Family indet.

Genus Eoincamys FRAILEY & CAMPBELL, 2004

Type species: *Eoincamys pascuali* FRAILEY & CAMPBELL, 2004.

Species content: the type species and *Eoincamys ameghinoi* FRAILEY & CAMPBELL, 2004, *Eoincamys valverdei* nov. sp., *Eoincamys parvus* nov. sp., and *Eoincamys* cf. *pascuali* (this work).

Geographic and stratigraphic distribution: Shapaja, Pozo Fm., Upper Shale Mb. (TAR-21, TAR-22, TAR-13 and TAR-01, early Oligocene), San Martín Department, Peru, Santa Rosa LACM 6289, mapped as "Yahuarango Fm." (?late Eocene/early Oligocene), Ucayali Department, Peru.

Remark: *Eoincamys* is already documented in Santa Rosa (Peru, ?late Eocene/early Oligocene, FRAILEY & CAMPBELL 2004). *Eoincamys* was originally assigned to the Dasyproctidae BONAPARTE, 1938 (Cavioidea, FRAILEY & CAMPBELL 2004). However, a revision of the content of that family would be necessary, inasmuch as several extinct genera considered as dasyproctids (e.g., Branisamys and Incamys HOFFSTETTER & LAVOCAT, 1970) show morphological affinities with chinchilloids, thereby raising the question of their suprageneric assignation (KRAMARZ et al. 2013, Vu-CETICH et al. 2015a). Eoincamys tends to have taeniodont upper and lower teeth, and some species of that genus display an increase in the crown height (see below), two features characterising most of chinchilloids, but also some cavioids (e.g., Neoreomys AMEGH-INO, 1887, Australoprocta KRAMARZ, 1998) and some octodontoids (e.g., Protadelphomys AMEGHINO, 1902). However, *Eoincamys* has a peculiar pattern (strong obliquity and tendency to be tetralophodont, with the reduction of the second transverse cristid and third transverse crest on lower and upper molars, respectively), which is commonly found in extinct and extant chinchilloids (Eoviscaccia, Scleromys, Garridomys, Drytomomys Anthony, 1922 (sensu Candela & NASIF 2006), Chinchilla BENNETT, 1829, and Lagidium MEYEN, 1833). This pattern also characterises Chambiramys sylvaticus BOIVIN et al., 2017a (superfamily indet.), the dasyproctid Microscleromys WALTON, 1997, and the octodontoid *Protadelphomys*. Nevertheless, from our personnal observation, the first two taxa would be potentially representatives of chinchilloids. Otherwise, Eoincamys clearly differs from Protadelphomys in having p4s and lower molars with a strong mesostylid, whereas the latter is lacking in *Protadelphomys* (a feature characterising octodontoids). So, *Eoincamys* would be best classified among the chinchilloids. A phylogenetic analysis would be necessary to assess this hypothesis.

Eoincamys valverdei nov. sp.

(Text-fig. 2G-N, Appendix S2)

Derivation of name: in honour of the geologist Roberto L. Valverde, who performed the first Cenozoic section of the Huallaga basin.

Holotype: MUSM 2947, right M1 (Text-fig. 2K). Deposited in the MUSM, Lima, Peru.

Referred material: In addition to the holotype (MUSM 2947) – MUSM 2952, right p4 or m1 (Text-fig. 2N), MUSM 2941, fragment of a left lower molar, MUSM 2942, fragment of a right lower molar, MUSM 3334, right P4 (Text-fig. 2G), MUSM 2944, 3335 and 3428, fragments of left upper molars, MUSM 2945–2946, fragments of right upper molars, MUSM 3336, left M1 (Text-fig. 2H), MUSM 2948, right M1 (Text-fig. 2L), MUSM 2943, left ?M2 (Text-fig. 2I), MUSM 2969, right M3 (Text-fig. 2J), MUSM 3429, left M3 (Text-fig. 2M).

Type locality: TAR-21 (MUSM 2941–2948 and 2952), Shapaja, San Martín Department, Peru.

Other localities: TAR-13 (only for MUSM 2969), TAR-22 (MUSM 3428–3429) and TAR-20 (MUSM 3334–3336), Shapaja, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Diagnosis: Small-sized rodent characterised by strongly oblique loph(-id)s, and moderately highcrowned and pseudo-taeniodont upper molars. Differs from *Eoincamys ameghinoi* and *E. pascuali* in having a distinct metacone, a short metaloph and higher-crowned upper molars, differs from E. ameghinoi in having larger teeth and upper molars with a shorter mesoloph, differs from *E. pascuali* in having a mesoloph not connected lingually to the posteroloph, differs from Chambiramys sylvaticus in being larger and in having more subsquare upper molars, from Incamys *bolivianus* in being smaller, in having a more oblique protoloph, more persistent flexi, and in displaying a deeper hypostria, differs from all species of *Scleromys*, Protadelphomys latus, Microscleromys paradoxalis and Microscleromys cribriphilus in having a well-defined metaloph on upper molars, differs from all species of Scleromys, M. paradoxalis and M. cribriphilus in having teeth characterised by thinner and less laminated loph(id)s.

Description: The MUSM 2952 p4 or m1 (Textfig. 2N) is worn and eroded. This tooth is longer than wide with a talonid wider than the trigonid. With wear, the cuspids, notably the hypoconid, are faintly visible, forming dentine platforms surrounded by thick enamel layers. Mesiolingually, a crestiform metaconid displays a strong but short posterior arm, reaching a well-developed anterior arm of the entoconid. There is neither distinct mesostylid nor neomesolophid. Labially, the massive protoconid shows a thick but short posterior arm, firstly linguodistally oriented, then more lingually directed. From the metaconid, a very short and slightly curved metalophulid I extends labiodistally to

reach the lingual extremity of the posterior arm of the protoconid. The configuration of the metalophulid I (arcuate, concave) with respect to the protoconid and metaconid generates a small mesial fovea. The enlarged entoconid is linked to the protoconid via a strong hypolophid, labiomesially oriented, and a more longitudinal but still oblique ectolophid, joining the posterior arm of the protoconid. Due to the pattern of the mesial cristids, the mesoflexid and a part of the anteroflexid are confluent, forming an anterior fossettid. Centrally, the hypoconid has a thick and short anterior arm, which links the hypolophid-ectolophid junction. The hypoconid displays a strong, long and mesiolabially oriented anterior outgrowth, but which remains well separated from the protoconid, thereby involving a wide labial opening of the deep and labiolingually extended hypoflexid. With wear, the posterolophid appears particularly thick and it strongly links the entoconid and the hypoconid, forming a massive and crescentiform platform of dentine. The posteroflexid is then closed lingually, appearing as a small and shallow posterofossettid.

Both fragments of lower molars (MUSM 2941 and 2942) are labiodistally broken. The metalophulid I, hypolophid, metaconid, mesostylid and a part of the protoconid are recognisable on both dental fragments. On MUSM 2942, a mesiolingual part of the posterolophid is preserved. These teeth have a flat occlusal surface with poorly differentiated cuspids, which are included in the cristids. However, the mesostylid is particularly strong and well defined on MUSM 2942. Both lower molar fragments are characterised by cristids having a marked obliquity: the protoconid is crestiform and tends to be aligned with the ectolophid and the hypolophid, thus forming a long and diagonal cristid, notably on MUSM 2942. The metalophulid I, connected to the protoconid, is very short and thin on MUSM 2942 and thicker on MUSM 2941 (more worn). The mesiodistally pinched metaconid is disconnected from the very thin metalophulid I on MUSM 2942, contrary to MUSM 2941. The mesostylid is connected to a very short but strong posterior arm of the metaconid. On MUSM 2942, there is no second transverse cristid, whereas on MUSM 2941, the mesostylid displays a short neomesolophid, mesially directed toward the metalophulid I but lingually free. Moreover, on MUSM 2941, a very tiny posterior arm of the protoconid (reduced to a spur) develops from the lingual flank of the protoconid-ectolophid complex. The mesiolingual part of the posterolophid, preserved on MUSM 2942, is parallel to the hypolophid.

The MUSM 3334 P4 (Text-fig. 2G) has a rounded occlusal outline. It is labiolingually asymmetrical with a higher lingual crown (HIg = 0.83 and HIb = 0.32). In addition to being blunt, this tooth is much worn, as indicated by the extremely low labial cown and the worn occlusal surface. Two well-marked crests with thick enamel layers are distinct. The thicker one is convex and lingually situated. It may be formed by the fusion of a short anteroloph (its labial extremity does not reach the buccal margin of the tooth) and two twinned cusps, the protocone and hypocone, corresponding to wide plates of dentine. There is no recognisable posteroloph. The latter was probably posterior and connected to the hypocone, but it has disappeared with wear and/or due to the blunting of the tooth. On the labial margin, the cusps/styles (paracone and mesostyle) are not distinct from the labial protoloph and the third transverse crest, respectively. Both crests are parallel and strongly oblique (i.e., mesiolabially directed). They are labially separated by a thin mesial mesoflexus and lingually connected via a short and longitudinal mure. The paracone, labial protoloph, mure, third transverse crest, and mesostyle form a labial "U-shaped" crest contiguous with the lingual convex one (i.e., there is no hypoflexus).

Like P4, the upper molars exhibit a noticeable labiolingual asymmetry regarding crown height (i.e., unilateral hypsodonty, for less worn molars, HIg ranges between 1.04–1.22 and HIb between 0.50–0.56). Considering the maximum width (i.e., width of the total crown), well-preserved upper molars (MUSM 2943, 2947, 2948, 2969, 3336 and 3429, Text-fig. 2H– M) are wider than long, but if only the occlusal width is considered, MUSM 2947 (Text-fig. 2K) is slightly more elongated mesiodistally. The cusps/styles are incorporated in massive crests, characterised by thick enamel layers. The crestiform protocone and the hypocone are roughly mesiodistally aligned on M1s (MUSM 2947, 2948 and 3336), whereas the hypocone is more labial on the MUSM 2943 ?M2 and even more on M3s (MUSM 2969 and 3429, Text-fig. 2J, M). M2-3s are also characterised by a more rounded occlusal outline and by a smaller hypocone than M1s. Like on P4 (Text-fig. 2G), the crest obliquity is particularly well marked: the protocone, its anterior arm and its posterior outgrowth are aligned, and they form a long and slightly curved crest directed linguodistally. That oblique crest is labially connected to the anteroloph, which is clearly shorter and more transverse. Mesiolabially, the paracone displays short and weakly marked anterior and posterior arms, the anterior one being well separated from the labial extremity of the anteroloph on the less worn teeth. On MUSM 2947 and 3429 (Text-fig. 2K, M), from the paracone, a strong and oblique labial protoloph extends distolingually and tapers lingually, especially on MUSM 2947. On the latter, it connects to the labial flank of a very short mure, reduced to a cusp-like crest, linking distally the mesial extremity of the long and oblique anterior arm of the hypocone. On MUSM 3429, the mure is not discernible from the labial protoloph. On MUSM 2948 (Text-fig. 2L), MUSM 2969 (Textfig. 2J) and MUSM 3336 (Text-fig. 2H), the labial protoloph, mure and anterior arm of the hypocone are merged and aligned due to wear and they form a long, strong, and diagonal (central) crest, linking the paracone to the hypocone. On MUSM 2943, 2947 and 2948, the lingual protoloph is divided into two very short crestules, on the distal flank of the protocone, and on the mesial flank of the mure, respectively. These two crestules remain disjoint, thereby involving a small, narrow confluence of the paraflexus with the hypoflexus (i.e., pseudo-taeniodont pattern). On the MUSM 2969 M3, there is no lingual protoloph, and thus the hypoflexus and the furrow-like, deep paraflexus are confluent (i.e., taeniodont pattern). Labially, the well developed mesostyle has short but strong arms (except the anterior one on MUSM 2948, faintly distinct). Its sloped anterior arm reaches the base of the posterior arm of the paracone, so that the mesial mesoflexus remain opened labially (presence of a marked notch). The posterior arm of the mesostyle is connected to a small metacone, well-defined on MUSM 2947 (Text-fig. 2K), and linked distolingually to the posteroloph. The latter is connected to the hypocone on MUSM 2943, but both structures are usually separated by a notch, narrower on MUSM 2948 and 3429 than on MUSM 2947 and 2969. MUSM 2947 and 2948 display a short metaloph, stemming from the metacone and running mesiolingually. The metaloph is absent on other upper molars. This crest ends abruptly, without any connection on MUSM 2948. On MUSM 2943, 2947, 2948 and 3429, the third crest is limited to a strong mesoloph. The latter is very short on MUSM 2943, of medium-length on MUSM 2947 and 2948, and long on MUSM 3429. On MUSM 2947 (Text-fig. 2K), the mesoloph is slightly mesiolingually oriented and lingually free, whereas it

is backwardly directed and lingually connected to the metaloph on MUSM 2948 (Text-fig. 2L), MUSM 2969 (Text-fig. 2J) and MUSM 3429 (Text-fig. 2M). MUSM 3336 displays a thick posterior crest, which probably corresponds to the fusion between the mesoloph and the posteroloph due to wear. On MUSM 2947 and 2969, in addition to that crest, there is a mesolophular spur on the anterior arm of the hypocone, which is absent on MUSM 2948. That crestule is labially free and very short on MUSM 2947, whereas it is longer and connected to the mesoloph on MUSM 2969. On the least worn upper molars (except MUSM 2943), the posteroloph displays a short and roughly longitudinal crestule (rest of a lingual connection of the metaloph with the posteroloph or neostructure?). On MUSM 2947 and 2948, that crestule ends mesially near to the lingual extremity of the mesoloph and metaloph, whereas it is connected to the mesoloph on MUSM 3429, and to the mesoloph-mesolophule on MUSM 2969. That crestule stemming from the posteroloph is longer and more mesiolingually directed on MUSM 2947 than on MUSM 2948. With the configuration of the posterior crests, both mesoflexi and posteroflexus are confluent on MUSM 2947 (Text-fig. 2K). On MUSM 2948 (Text-fig. 2L), the distal mesoflexus is divided into two parts: one slighly extended and limited by the mesoloph and metaloph, and another confluent with the mesial mesoflexus and posteroflexus. On MUSM 3429 (Text-fig. 2M), the mesial mesoflexus is confluent with the posteroflexus, contrary to the distal mesoflexus forming a small and rounded distal mesofossette. On MUSM 2969 (Textfig. 2J), three small, but deep, distolabial fossettes correspond to the mesial mesoflexus, the lingual part of the posteroflexus and the confluence of the labial part of the latter with the distal mesoflexus.

Comparisons: These isolated specimens from TAR-21 are morphologically reminiscent of teeth of *Eoincamys*, and they are therefore referred to that genus. This is particularly shown in the marked obliquity of loph(-id)s, the tendency to develop a taeniodont pattern, the presence of a reduced second transverse cristid on lower molars, the transverse occlusal outline of upper molars, and the presence on these latter of a reduced third transverse crest, consisting of a dominant mesoloph disconnected from the anterior arm of the hypocone. Nevertheless, this material has very distinctive features, which motivates the erection of a new species: *E. valverdei* nov. sp. The upper molars of *E. valverdei* show intermediate characters between

Eoincamys ameghinoi and E. pascuali regarding the obliquity of lophs and the configuration of the distal crests (i.e., third transverse crest, metaloph and posteroloph). Indeed, in upper molars of *E. ameghinoi*, the mesoloph is long, transverse or with its lingual end slightly directed backwardly. On most upper molars attributed to *E. valverdei*, the mesoloph is shorter and with a lingual extremity either slightly backwardly directed or distolingually oblique. In addition, on M1–2s, the mesoloph is not connected to the posteroloph but it is very close to the short crestule stemming from the posteroloph. In *E. pascuali*, the mesoloph is distolingually oblique but always lingually connected to the posteroloph (via perhaps a short crestule stemming from the posteroloph). The teeth of *E. valverdei* equal in size those of *E. pascuali*, being larger than those of *E. ameghinoi* (Appendix S3). On upper molars from TAR-21, there are a distinct metacone and a short metaloph, lacking in *E. ameghinoi* and E. pascuali. Moreover, upper molars of E. valverdei are higher-crowned than those of *E. ameghinoi* and E. pascuali. Upper molars of Chambiramys sylvaticus (CTA-61, Contamana, Peru, late Oligocene) and Incamys (Sarmiento Fm., Argentina, Salla, Bolivia, late early Oligocene–late Oligocene) are as high-crowned as those of *E. valverdei*. Moreover, they show comparable occlusal patterns with upper molars of *E. valverdei*, notably in the loph obliquity and in the arrangement of the distal crests with the mesoloph, either reduced, free, or connected to the metaloph or to the posteroloph via a short crestule. Contrary to *E. valverdei*, the mesoloph can be also connected on the anterior arm of the hypocone on some specimens of C. sylvaticus and Incamys. Nevertheless, E. valverdei differs from C. sylvaticus in being larger and in having more subsquare upper molars, from *Incamys* in being smaller, in having a more oblique protoloph, more persistent flexi, and in displaying a deeper hypostria. Among Miocene taxa, many display a strong obliquity of loph(-id)s, develop a taeniodont pattern, have a reduced second transverse cristid on lower molars and a reduced third transverse crest on upper molars (e.g., Scleromys, Protadelphomys, or Microscleromys) but none have a well-defined metaloph stemming from a metacone on their upper molars. Microscleromys paradoxalis WALTON, 1997 (La Venta, Colombia, late middle Miocene) and some specimens of Scleromys quadrangulatus KRAMARZ, 2006 (Pinturas Fm., Argentina, late early Miocene) have a mesoloph lingually free and an expansion of the posteroloph, which can correspond to the third distal crestule stemming from the posteroloph as that observed on MUSM 2947–2948. Nevertheless, teeth of *E. valverdei* are characterised by thinner and less laminated loph(id)s than teeth of *Scleromys* and *Microscleromys*. They are also smaller than teeth of *Scleromys*, and larger than those of *Microscleromys*.

To sum up, in displaying a metaloph and a metacone, and in being higher-crowned than teeth of *E. ameghinoi* and *E. pascuali*, these isolated teeth from TAR-21 are referred here to a new species of *Eo*-*incamys*: *E. valverdei* nov. sp.

Eoincamys parvus nov. sp.

(Text-fig. 2O–Y, Appendix S2)

Derivation of name: from the Latin *parvus*, small, in reference to the small size of the referred teeth and of the concerned species.

Holotype: MUSM 2951, right M1 (Text-fig. 2X). Deposited in the MUSM, Lima, Peru.

Referred material: in addition to the holotype (MUSM 2951) – MUSM 3430, left dp4 (Text-fig. 2O), MUSM 2966, fragment of a right dp4, MUSM 3431, fragment of a right lower molar, MUSM 3432, left m1 (Text-fig. 2P), MUSM 3433, left m2 (Text-fig. 2Q), MUSM 2962, right m3 (Text-fig. 2R), MUSM 2963, 3337 and 3434, right P4s (Text-fig. 2S, W), MUSM 2949, fragment of a a right upper molar, MUSM 3435, right upper molar, MUSM 2960, left M1 (Text-fig. 2T), MUSM 3436, left M2 (Text-fig. 2U), MUSM 2965 and 3437, left M3s (Text-fig. 2V, Y).

Type locality: TAR-21 (for MUSM 2949–2951), Shapaja, San Martín Department, Peru.

Other localities: TAR-20 (only for MUSM 3337), and TAR-22 (for MUSM 2962–2966 and 3430–3437), Shapaja, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Diagnosis: Small-sized rodent characterised by strongly oblique loph(-id)s, and moderately highcrowned and taeniodont upper teeth. Differs from *E. valverdei* and *E. pascuali* in being smaller. Differs from *E. valverdei* in having M1–2s with a mure completely undifferentiated from the labial protoloph and the anterior arm of the hypocone, a metacone more separated from the posteroloph, and in lacking the lingual protoloph, the mesolophule, and metaloph, differs from *E. ameghinoi* and *E. pascuali* in having higher-crowned upper teeth, a metacone on upper molars, and a metaloph on M3.

Description: Two dp4s are referable to this taxon: MUSM 2966 and 3430 (Text-fig. 2O). MUSM 2966 is a fragment of dp4 (talonid), on which the mesostylid, distal part of the mesolophid, distal ectolophid, hypolophid, and posterolophid are recognisable. MUSM 3430 is a dp4 slightly broken at the level of the metaconid (Text-fig. 2O). The cristids are thin. The metaconid is more posteriorly located than the protoconid. Both cuspids are connected by a mesial and convex mesolophid I, and more distally by a well-marked second transverse cristid. The mesostylid develops two short arms: an anterior one connecting to the metaconid (or its posterior arm) and a posterior one, which remains well separated from the entoconid. The mesolophid extends lingually to the mesostylid from a straight and distolingually oblique ectolophid (mesial part). The mesial ectolophid and the protoconid are not connected. Therefore the mesial ectoflexus remains labially open. The isolated and well-defined entoconid is mesially located with respect to the crestiform hypoconid and connected to a long hypolophid, which joins the distal ectolophid. Entoconid and hypolophid are weakly connected on MUSM 2966 (the least worn dp4), and more strongly on MUSM 3430. The hypoconid is faintly distinct (mesiolabially from its anterior outgrowth and distolingually from the posterolophid), which generates a long, strongly curved distal cristid. On MUSM 2966, there is no anterior arm of the hypoconid, and thus the metaflexid and hypoflexid are fully confluent (i.e., taeniodont pattern). On MUSM 3430, a very short and low cristulid links the mesial flank of the hypoconid to the distal flank of the hypolophid-ectolophid junction, thereby involving a partial (but almost complete) confluence between the metaflexid and the hypoflexid (i.e., pseudo-taeniodont pattern).

MUSM 3431 corresponds to an anterior fragment of lower molar, MUSM 2962 (Text-fig. 2R) to a heavily worn, eroded and slightly broken m3, and MUSM 3432-3433 to complete lower molars (m1 (Textfig. 2P) and m2 (Text-fig. 2Q), respectively). MUSM 2962 (Text-fig. 2R) presents the labiolingual pinch of the talonid characteristic of m3s. All lower molars are brachydont, tri- to tetralophodont, taeniodont and with a marked obliquity of cristids. Their occlusal plan is flat and the cuspids are incorporated within the cristids. The protoconid, forming a large platform of dentine with wear, is connected to the metaconid via a transverse and complete metalophulid I. The protoconid, ectolophid, and labial part of the hypolophid tend to be aligned. They form a long and diagonal central cristid (linguodistally oriented), whereas the lingual part of the hypolophid, incorporing a small

entoconid, is short, roughly transverse or linguomesially directed (on MUSM 2962). The metaconid and its posterior arm are fused, poorly distinct and slightly connected to the anterior arm of the mesostylid. With wear, the posterior arm of the metaconid and the anterior arm of the mesostylid are fused like on MUSM 2962, where the small mesostylid is also linked to the entoconid. The second transverse cristid is reduced to a short neomesolophid (MUSM 3433) or a neomesolophid spur (MUSM 2962, 3431, and 3432) stemming from the mesostylid. There is no posterior arm of the protoconid except on MUSM 3433, where a very short spur, labially free, runs from the central cristid (= ectolophid + protoconid). Also, with wear, the metaconid, protoconid, entoconid, and mesostylid are connected via cristids, thereby forming a lingual wall. They isolate an anterior fossettid that corresponds to the confluence between the anteroflexid and the mesoflexid. The posterolophid is entirely merged with the hypoconid and its anterior outgrowth, usually forming a well-curved posterior cristid separated from the entoconid. However, on MUSM 2962, the posterolophid is very short and its lingual extremity reaches the distal flank of the hypolophid, at the level of the junction of its two parts (i.e., lingual and labial parts). There is no anterior arm of the hypocone and thus the metaflexid is confluent with the hypoflexid.

The P4s are mesodont (HIg between 1.05 and 1.15). In occlusal view, their crown is transverse and oval in occlusal outline (Text-fig. 2S, W). The anteroloph, protocone, and its posterior outgrowth form a long crest, connected to the long anterior outgrowth of the hypocone and thereby forming the mesiolingual margin of the tooth. The labial end of the anteroloph reaches the mesial flank of the paracone, involving the labial closing of the paraflexus. Besides, there is no posterior arm of the protocone. Accordingly, the most anterior flexus is a fossette, corresponding to the confluence of the paraflexus with the hypoflexus (i.e., taeniodont pattern). The mure and the very short anterior arm of the hypocone are thin, linked (more weakly on MUSM 3434 than on other P4s), aligned, and forming a sub-longitudinal crest (slightly oblique). The latter is connected to the lingual extremity of the protoloph, which is oblique and much thicker than the anterior arm of the hypocone-mure complex. On MUSM 2963 (Text-fig. 2W), the protoloph is very thick in its labial part, and in continuity with the massive but faintly visible paracone (not well-defined with respect to the labial protoloph). On MUSM

3434 (Text-fig. 2S), the protoloph is thinner and the paracone is clearly less inflated than on MUSM 2963. On the least worn P4s (MUSM 2963 and 3434), the posteroloph is divided into two parts separated by a tiny furrow: a very short lingual one connected to the hypocone, and a long labial one which is completely fused with a very long and mesiolingually-distolabially pinched metacone. On MUSM 2963, a small mesostyle is present (absent on other P4s), isolated between the paracone and the metacone (presence of narrow and shallow notches separating the mesostyle from the two main labial cusps). The mesostyle displays a very short and low mesoloph on that tooth. There is no trace of mesolophule on the anterior arm of the hypocone on the three P4s. On MUSM 2963, two other low crestules (a labial one and a more lingual one) on the anterior flank of the metacone-labial posteroloph complex probably correspond to the rests of a metaloph. Neither these crestules nor the mesoloph are linked, thus generating the confluence of the mesial mesoflexus with the distal mesoflexus and the posteroflexus. On other P4s, these flexi are fully confluent due to the absence of metaloph, mesoloph, and mesolophule.

The MUSM 2949 and 2964 tooth fragments correspond to mesiolingual portions of upper molars. Other upper molars are complete (Text-fig. 2T-V, X-Y). These upper molars have a similar pattern than that characterising P4s (i.e., high-crowned, taeniodont, crests strongly oblique (especially the protoloph), and metacone distinct on pristine teeth, Text-fig. 2S, W). Besides, the upper molars develop a small but well-defined mesostyle like on the MUSM 2963 P4. However, contrary to P4s, upper molars are characterised by a long and strong posterior outgrowth of the protocone, which does not connect to the hypocone (the latter has no anterior outgrowth). The hypoflexus, markedly proverse (sub-longitudinal), remains open lingually far distally. In the absence of a lingual protoloph (i.e., taeniodont pattern), the hypoflexus is confluent with the paraflexus. Mesially, the anteroloph is labially more separated from the paracone than on P4s (at least for the first stages of wear), and as such, the hypoflexus-paraflexus complex is labiolingually open. MUSM 2950 (Text-fig. 2T) exhibits a discontinuous anterior crest, characterised by a small notch situated between the anteroloph and the anterior arm of the protocone, a notch lacking on other upper molars. On less worn upper molars, the mesostyle is strongly isolated from the paracone as observed on P4s. On MUSM 2951 (Text-fig. 2X), a very thin and shallow notch occurs between the mesostyle and the metacone-posteroloph complex, whereas on P4s (e.g., MUSM 2950 and 2965), both structures are clearly more separated. The MUSM 2965 M3 (Textfig. 2Y) does not develop any mesoloph, contrary to MUSM 2950, 2951, 3436 and 3437. On these teeth, the mesoloph is turned backwardly and, on MUSM 2950 and 2951, it is connected to a short crestule, forwardly oriented and stemming from the posteroloph. On MUSM 2950 (Text-fig. 2T), that crestule is longer than on MUSM 2951 (Text-fig. 2X) and subdivided into two very short crestules. With wear, the mesoloph tends to fuse with the posteroloph, as on MUSM 3435 and 3437. Compared to P4s, the metacone is more reduced on the molars. MUSM 2965 is the only upper molar with a crestule occurring on the flank of the metacone-posteroloph complex, probably corresponding to a residual metaloph. The posteroloph is more strongly connected to the hypocone on MUSM 2965 than on MUSM 2950, 2951 and the MUSM 2963 and 3434 P4s.

Comparisons: These upper molars referred to Eoin*camys parvus* nov. sp. have basically a similar occlusal pattern than those of *E. valverdei*. In *E. parvus*, the labial protoloph, mure, and anterior arm of the hypocone are aligned like in E. valverdei, but they are undifferentiated, thereby forming a continuous, slightly arcued, and diagonal central crest. *Eoincamys parvus* differs substantially from *E. valverdei* in lacking the lingual protoloph (i.e., fully taeniodont pattern), the mesolophule and metaloph on M1-2s. However, upper molars of *E. parvus* bear a well-defined metacone as in E. valverdei, but this labiodistal cusp is more separated from the posteroloph in *E. parvus* than in E. valverdei. Moreover, on M1-2s of E. parvus, as observed in *E. valverdei*, there is a short crestule stemming from the posteroloph and forwardly oriented. That crestule is longer on MUSM 2950 (Textfig. 2T) than on MUSM 2951 (Text-fig. 2X) and subdivided into two tiny crestules. However, contrary to *E. valverdei*, in *E. parvus* there is a lingual connection between the mesoloph and the posteroloph, probably via that short crestule. In E. ameghinoi and E. pas*cuali*, there is neither metaloph nor distinct metacone. In *E. pascuali*, the mesoloph has a lingual connection with the posteroloph probably via a short crestule like in E. parvus. With respect to E. ameghinoi and *E. pascuali*, upper molars of *E. parvus* are much higher-crowned, a condition which is roughly similar

to that observed in *E. valverdei*. Finally, *E. parvus* is characterised by small teeth, equal in size (or slightly larger than) those of *E. ameghinoi*, and smaller than *E. valverdei* and *E. pascuali* (Appendix S3).

Eoincamys cf. pascuali

(Text-fig. 3J–P, Appendix S2)

Referred material: MUSM 3489 and 3364, fragments of left dp4s, MUSM 3490, right dp4 (Text-fig. 3J), MUSM 3491 and 3365, fragments of left m1s or 2s, MUSM 3492, right m1 (Text-fig. 3K), MUSM 3493–3295, fragments of left m2s (Text-fig. 3L), MUSM 3296, right m2 (Text-fig. 3N), MUSM 3297, right m3 (Text-fig. 3M), MUSM 3298, fragment of a left M1, MUSM 3299, left M1 (Text-fig. 3O), MUSM 3300, right M2 (Text-fig. 3P).

Locality: TAR-01, Shapaja, San Martín Department, Peru. Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Description: There are three dp4s recovered for this taxon. MUSM 3364 is mesially and distally broken, MUSM 3489 is damaged on its lingual margin, and MUSM 3490 (Text-fig. 3J) is slightly broken on its mesial part. These dp4s have a flat occlusal plan with cristids characterised by thick enamel layers. Because of their inclusion within cristids, the cuspids/stylids are almost indistinct. The curved metalophulid I and the roughly transverse metalophulid II are both lingually and labially connected to the metaconid and protoconid, and isolate a narrow anteroflexid. On MUSM 3490, the metalophulid I has a tiny spur in its middle part, backwardly oriented. Lingually, the mesostylid displays a long and strong posterior arm and a very short anterior arm, linked to a long and strong posterior arm of the metaconid. The mesial and distal ectolophids are not distinguishable as they are aligned, thereby forming a long and oblique cristid (i.e., linguodistally directed (diagonal)). The labial end of this cristid is weakly connected to the protoconid on MUSM 3490 and 3489, whereas both structures are separated by a wide notch on MUSM 3364. The hypolophid is almost in continuity with this diagonal ectolophid cristid and lingually connected to the entoconid. On MUSM 3490 (Text-fig. 3J), the entoconid is mesially and distally separated by thin furrows from the posterior arm of the mesostylid and the lingual end of the posterolophid, respectively. On MUSM 3489 and 3364, the entoconid is also free from the posterolophid, but linked to the mesostylid. On three dp4s, there is no mesolophid on the ectolophids. However, the mesostylid displays a neomesolophid, variable in length. On MUSM 3490, it is longer and labiomesially oriented, where its labial extremity reaches the distal margin of the metalophulid II. Together with the metaconid, its posterior arm, the metalophulid II, the mesostylid, and the neomesolophid, they isolate a small fossettid. On MUSM 3489 and 3364, the neomesolophid is shorter, and thus, the mesial mesoflexid is fully confluent with the distal one. On MUSM 3490, a small, isolated and lingual cuspid occurs between the neomesolophid and the hypolophid, unlike on MUSM 3489 and 3364 where it lacks. There is no anterior arm of the hypoconid or rest of that cristid on three dp4s, the furrow-like metaflexid and hypoflexid are entirely confluent (i.e., taeniodont pattern). The hypoconid is merged with its anterior outgrowth and the posterolophid, generating a long and curved cristid.

Considering about the root organisation (see chapter 2: Material and Methods), eight lower molars and three upper molars have been identified. The m1 (Text-fig. 3K) is shorter and more squared than m2 (Text-fig. 3L, N). The m3 (Text-fig. 3M) is rectangular, like m2, but smaller. For the upper molars, compared to the M1s, the hypocone on M2 is located more labially with respect to the protocone. The lower and upper molars are characterised by brachydont crowns, faintly distinct cusp(id)s, massive crests and cristids with thick enamel layers, a tetralophodont pattern, taeniodonty and furrow-like flexi(ds), which tend to be closed, constricted or even divided with wear (MUSM 3492 and 3299, Text-fig. 3K, O, respectively). On the less worn lower molars, the most distal flexid, corresponding to the confluence between the metaflexid and the hypoflexid, is the most persistent flexid. Indeed, it is still lingually and labially open (i.e., transversely open) contrary to other flexids. The lower and upper molars also have strongly oblique loph(-id) s, notably for the first three cristids of lower molars and the last three crests of upper molars. Even if the posterolophid and anteroloph are curved, their labial or lingual part tend to be parallel with other loph(-id) s. The second transverse cristid and third transverse crest are short and reduced to a neomesolophid and a mesoloph, linked labially to the metalophulid I and lingually to the posteroloph, respectively. Besides, the hypolophid is aligned with the ectolophid and the protoconid on lower molars, and the protoloph tends to be aligned with the mure and anterior arm of the hypocone on upper molars.

Comparisons: The peculiar pattern (tetralophodonty, taeniodonty, strong obliquity and reduction

of the second transverse cristid and third transverse crest) of lower and upper molars is also found in *Eo*incamys, Chambiramys sylvaticus, Protadelphomys and many chinchilloids (Eoviscaccia, Scleromys, Garridomys, and Drytomomys). By its low crown, small size, persistent flexi(-ds), and the absence of metacone and metaloph on upper molars, the morphology of these isolated teeth from TAR-01 unambiguously recall the dental pattern of *Eoincamys pascuali*. However, lower molars of *E. pascuali* differ on their mesial part, notably in showing a metalophulid I usually not connected to the protoconid, and in displaying a neomesolophid never linked labially to the metalophulid I. The latter feature is also found in other species of *Eoincamys* (i.e., *E. ameghinoi*, *E. parvus*, and *E. valverdei*). These teeth from TAR-01 are smaller than those of *E. ameghinoi* and *E. parvus*, and they roughly equal in size those of E. pascuali and E. valverdei (Appendix S3). The TAR-01 specimens differ from teeth of *E. ameghinoi* in having more oblique crests on upper molars, notably the mesoloph, from teeth of *E. parvus* and *E. valverdei* in being lower crowned and in lacking the metacone and metaloph on upper molars. With wear, in Protadelphomys (Sarmiento Fm., Argentina, early Miocene), flexi(-ds) are less persistent than on teeth from TAR-01, notably the most mesial flexus (i.e., confluence between the hypoflexus and the paraflexus) on upper molars, which is rapidly closed. The same is true for the posteroflexus, which disappear quickly with wear. Contrary to the material from TAR-01, lower molars of *Protadelphomys* are trilophodont, with a very large metaconid (perhaps fused with a lingual part of the second cristid?) and sometimes with a very short posterior arm of the protoconid. The TAR-01 teeth differ from teeth of C. sylvaticus in having a stronger obliquity of lophids on lower molars, less mesiodistally elongated upper molars, a continuous third transverse crest always strongly lingually connected to the posteroloph, and in the absence of metaloph or rest of this crest. Chinchilloids (except the alleged chinchilloid *Branisamys*) are characterised by an enamel layer heterogeneously thick: it is typically thicker on the leading edges than on the trailing edges in cheek teeth (KRAMARZ et al. 2013). This feature is quite tenuous on teeth from TAR-01, like in Scleromys where it is only insinuated (KRAMARZ et al. 2013). Like in Scleromys and Drytomomys, the flexi(-ds) of the TAR-01 teeth are more persistent at an advanced stage of occlusal wear than in *Eoviscaccia* and *Garridomys*. However, contrary to Scleromys and Drytomomys (and other chinchilloids in general), the teeth of TAR-01 are low-crowned.

?Eoincamys sp.

(Text-fig. 2Z, Appendix S2)

Referred material: MUSM 2970, left upper molar (Text-fig. 2Z).

Locality: TAR-13, Shapaja, San Martín Department, Peru. Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Description: MUSM 2970 is a fragment of a large left upper molar (Text-fig. 2Z). This worn and eroded fragment lacks the protocone, the hypocone and almost all the anteroloph. Its labial margin is also heavily damaged. This tetralophodont tooth shows highly oblique and massive crests with very thick enamel layers. Despite the wear and fragmentary nature of this tooth, it seems that the cusps are entirely subsumed within the crests. The anteroloph and protoloph are connected at mid-crown width by a longitudinal crestule (probably strong) that divides the paraflexus into two parts. This crestule is probably a neostructure because it is too labially placed to correspond to a posterior arm of the protocone. The mure is very oblique and aligned with the anterior arm of the hypocone. The protoloph is also labiomesially directed, but less oblique than the mure-anterior arm of the hypocone complex. The hypocone is connected distally to a transverse and long posteroloph, curved labially and continuing mesiolabially to connect to the mesostyle. There is neither differentiated metacone nor metaloph. The strong third transverse crest corresponds to a mesoloph stemming from the mesostyle and extending linguodistally, then turning backwardly, and joining the posteroloph. The latter and the mesoloph isolate an oval distal mesofossette.

Comparisons: The pattern of MUSM 2970 closely resembles that of upper molars of *Eoincamys pascuali*, *Scleromys, Protadelphomys, Incamys menniorum* VU-CETICH et al., 2015 (Sarmiento Fm., Argentina, late early Oligocene–late Oligocene), and some specimens of *Incamys bolivianus* HOFFSTETTER & LAVOCAT, 1970 from the late early Oligocene – late Oligocene of Salla, Bolivia (i.e., strongly oblique crests with a labial protoloph aligned with the mure and anterior arm of the hypocone, mesoloph connected to the posteroloph, and no mesolophule). Like on MUSM 2970, some specimens of *E. pascuali* and *Scleromys* display a labial neocrestule linking the anteroloph with the protoloph. Although fragmentary, the estimated size of MUSM 2970 was probably close to that of *Incamys*

menniorum and *Protadelphomys*. However, the flexi of MUSM 2970 appear more persistent, notably the distal mesofossette, than in *Incamys*, *Scleromys*, and *Protadelphomys*. That tooth might document either a new species of *Eoincamys* or a close ally, substantially larger than all other species known for that genus (i.e., *E. ameghinoi*, *E. parvus*, *E. pascuali*, and *E. valverdei*). Pending new material, we leave it in open nomenclature.

Superfamily indet. Family indet.

Tarapotomys nov. gen.

Type species: Tarapotomys subandinus nov. sp. **Species content:** the type and Tarapotomys mayoensis nov.

Derivation of name: from Tarapoto, the Peruvian town in the vicinity of which TAR-21 was discovered.

Generic diagnosis: Small-sized rodent characterised by variably developed lingual protoloph and anterior arm of the hypoconid on upper and lower teeth, respectively (taeniodont, pseudo-taeniodont, and non-taeniodont patterns) and mesodont upper teeth, differs from *Eoincamys pascuali* and *Incamys* in being smaller in size, from Pozomys, Eoincamys, and Incamys in having less transverse upper molars, differs from Po*zomys* and *Eoincamys* in having higher-crowned upper molars, from Incamys in having lower-crowned upper molars, from Eoincamys pascual, Scleromys, Garridomys, Protadelphomys, Drytomomys, and Microscleromys in having less oblique crests on upper molars, from Vallehermosomys mazzonii in having less transverse crests on upper molars, from ?Vallehermosomys mer*linae* in having more closely appressed mesostyle and paracone, and as such a third transverse crest closer to the protoloph, from Drytomomys in having connected hypocone and posteroloph, from Neoreomys in having a metaloph usually more reduced, from Pozomys and *Eoespina/Eosachacui* in showing a reduced second transverse cristid on lower molars, from Deseadomys, Galileomys, Leucokephalos, Llitun, Platypittamys, Sallamys, and Xylechimys by the presence or the stronger development of the posterior arm of the metaconid, and having a neomesolophid and a mesostylid on lower molars.

Tarapotomys subandinus nov. sp.

(Text-fig. 5A–G, Appendix S2)

Derivation of name: from the Latin *sub*, beneath and *andinus*, Andean, in reference to the location of Tarapoto in the Subandean Zone. Holotype: MUSM 2939, right M2 (Text-fig. 5D). Deposited in the MUSM, Lima, Peru.

Referred material: In addition to the holotype (MUSM 2939) – MUSM 2929, fragment of a right lower molar, MUSM 2930, right m2, MUSM 2931, right m3 (Text-fig. 5G), MUSM 2932, fragment of a left dP4, MUSM 2933, left dP4 (Text-fig. 5A), MUSM 2934, fragment of a right ?P4, MUSM 2935–2936 and 2961, right P4s (Text-fig. 5B, E–F), MUSM 3339, left upper molar, MUSM 2937, right M1 (Text-fig. 5C), MUSM 2938, left M2.

Type locality: TAR-21, Shapaja, San Martín Department, Peru.

Other locality: TAR-22 (only for MUSM 2961), Shapaja, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Diagnosis: Differs from *T. mayoensis* in possessing slightly smaller teeth, dP4s with a less developed metaloph, P4 with a third transverse crest, non-taeniodont lower and upper molars, and in showing upper molars with longer protoloph and third transverse crest.

Description: MUSM 2930 and 2931 are complete whereas MUSM 2929 is an anterior fragment of lower molar on which a distal part of the metalophulid I, a short neomesolophid, the ectolophid, and a part of the hypolophid and of the posterolophid are recognisable. The MUSM 2930 m2 is eroded, more worn, larger and longer than the MUSM 2931 m3 (Text-fig. 5G). MUSM 2930 and 2931 are brachydont. The cristids are massive with thick enamel layers. The cuspids/stylids are faintly differentiated, as they are incorporated in the ends of the transverse cristids. On MUSM 2931, the entoconid is the most recognisable lingual cuspid owing to its large surface and the development of strong anterior and posterior arms. Labially, the protoconid and hypoconid are well recognisable, but due to advanced wear, these two cuspids appear as large pits of dentine, surrounded by thick enamel. The metaconid is lingually opposed to the protoconid, while the entoconid is more mesially situated than the hypoconid. The metaconid is faintly differentiated from its short but strong posterior arm, which is distally linked to a very small mesostylid. The metalophulid I, transverse, links the crestiform metaconid to the protoconid. The second transverse cristid, limited in its lingual part, consists of a short neomesolophid stemming from the mesostylid and labially free. This neomesolophid is coalescent with the metalophulid I due to wear (like on MUSM 2930). Given the free labial extremity of the neomesolophid, the anteroflexid is confluent with the mesoflexid.

There is no posterior arm of the protoconid. A long and thick ectolophid extends from the protoconid to the labial extremity of the hypolophid. The ectolophid is mesiolabially directed, whereas the hypolophid is more transverse, both having a similar length. On MUSM 2931 (Text-fig. 5G), the anterior arm of the entoconid and mesostylid are almost linked, so that the anteroflexid-mesoflexid remains nearly open lingually. Moreover, the posterior arm of the entoconid is well separated from the lingual extremity of the posterolophid, and thus, the metaflexid remains open lingually. In contrast, on MUSM 2930, the anteroflexid-mesoflexid and metaflexid are both closed lingually. Centrally, the short and strong anterior arm of the hypoconid extends mesially to join the ectolophid-hypolophid junction (i.e., non-taeniodont pattern). The mesiodistally pinched hypocone displays a long anterior outgrowth directed labially, so that the hypoflexid is nearly transverse or slightly retroverse and linguolabially well extended. The hypoconid is strongly linked to the posterolophid, both structures appearing in continuity due to wear.

MUSM 2933 is a complete dP4 (Text-fig. 5A), whereas MUSM 2932 corresponds to a less worn fragment of dP4 preserving only the anteroloph, a mesial part of the protoloph, the mure, and the anterior arm of the hypocone. These dP4s (at least MUSM 2933) have a trapezoidal occlusal outline, with the labial margin longer than the lingual one. Compared with MUSM 2933, the anteroloph is more differentiated on MUSM 2932, stemming from a very large and well-defined protocone. On both dP4s, the anteroloph is labially linked to the paracone, and thus the paraflexus is closed labially. From the paracone, the labial protoloph extends lingually and it strongly connects to the mure. The labial protoloph is very thick. Its lingual branch (or posterior arm of the protocone) is thin but complete, projecting lingually and straightly, to connect to the protocone. On MUSM 2932, the mure is oblique and aligned with the oblique anterior arm of the hypocone, whereas on MUSM 2933, the mure is longitudinal. On MUSM 2933 (Text-fig. 5A), the well curved posteroloph develops a tiny median spur, connecting a longitudinal cuspid-like crestule on the most distal flexus (distal mesoflexus + posteroflexus). That structure may correspond to a residual metaloph. On MUSM 2933, with wear, the mesiodistally enlarged posteroloph incorporates the metacone and extends mesially (via probably a strong anterior arm of the metacone) to reach a well-marked mesostyle, thereby



Text-fig. 5. Scanning electron microscope images (in occlusal view) of fossil caviomorph teeth from TAR-21 (A–E, G–H, I–J, O, V–X), TAR-22 (F), TAR-13 (N), TAR-20 (K–M, P–T, U). (A–G): *Tarapotomys subandinus* nov. gen. et sp. (H): aff. *Tarapotomys* sp. (I–T): cf. *Tarapotomys* sp. (U–X): Caviomorpha indet. 1. (A): MUSM 2933, left dP4, (B): MUSM 2935, right P4, (C): MUSM 2937, right M1, (D): MUSM 2939, right M2 (holotype), (E): MUSM 2936, right P4, (F): MUSM 2961, right P4, (G): MUSM 2931, right m3, (H): MUSM 2940, right upper molar, (I): MUSM 2927, left m1, (J): MUSM 2926, left m2, (K): MUSM 3330, left m3, (L): MUSM 3328, right m1 (reversed), (M): MUSM 3327, left m1, (N): MUSM 2967, left m1, (O): MUSM 2928, left m2, (P): MUSM 3329, left m2, (Q): MUSM 3331, right dP4, (R): MUSM 3332, right M1, (S): MUSM 3333, left M2, (T): MUSM 2911, left M3, (U): MUSM 2909, left dp4, (V): MUSM 2924, left P4, (W): MUSM 2923, right dP4, (X): MUSM 2913, left dp4. The underlined letters indicate the reversed teeth. Scale bar: 1 mm.

closing the distal mesoflexus + posteroflexus labially. Although MUSM 2933 is slightly labially broken, the mesostyle appears weakly connected to the paracone, and the mesial mesoflexus forms a mesial mesofossette. The third transverse crest, stemming from the mesostyle, extends lingually and connects to the mure-anterior arm of the hypocone junction (= mesoloph? or at least a dominant mesoloph). On MUSM 2933, the anteroloph, protoloph, and third transverse crest are short and more transverse than on MUSM 2932. On MUSM 2933, given the shortness of the anteroloph, protoloph, and third transverse crest, the hypoflexus is labiolingually developed. On both teeth, the hypoflexus is widely open lingually.

Four P4s are attributed to this new taxon (MUSM 2934–2936 and 2961). MUSM 2935 (Textfig. 5B), 2936 (Text-fig. 5E) and 2961 (Text-fig. 5F) are complete, whereas MUSM 2934 is a labial tooth fragment on which the protocone is missing. P4s are mesodont-subhypsodont (HIg between 0.88 and 1.20). The round occlusal outline of these P4s derives from a long, curved crest, which results from the fusion between the anteroloph, protocone and its long posterior outgrowth, hypocone, posteroloph, and mesostyle. With the connection between the posterior outgrowth of the protocone and hypocone, the hypoflexus is closed lingually. Although the protocone, hypocone, and mesostyle are crestiform, and participate to the formation of that long and circular crest, they are well recognisable. On the less worn P4 (MUSM 2961, Text-fig. 5F), the hypocone displays a long, strong and longitudinal anterior outgrowth, extending mesially to connect to the posterior outgrowth of the protocone. The outgrowths of these two lingual cusps are merged together at their base, but they remain faintly disconnected at their top (presence of shallow and narrow notches). On all P4s, the paracone is the most distinct cusp due to its large surface, its high elevation, and its complete or partial isolation. Indeed, on MUSM 2935 and 2961, the paracone is separated, mesially and distally, from the labial end of the anteroloph, and from the mesotyle, respectively, whereas on MUSM 2934 and 2936, the paracone is connected to the labial extremity of the anteroloph. Moreover, on MUSM 2936, the paracone is almost linked to the mesostyle, both structures being separated by a very thin and shallow notch. On MUSM 2934, these structures are more separated. On MUSM 2934–2936, there is no lingual protoloph, thereby involving the confluence between the paraflexus and the

hypoflexus. On MUSM 2961, a short and very low crestule could be a rest of that crest. That crestule connects to the flank of the labial protoloph, not to the protocone but more labially on the distal flank of the anteroloph. As that crestule is very low, the paraflexus is confluent with the hypoflexus. The labial protoloph is short and roughly transverse on MUSM 2935, 2936 and 2961, whereas it is slightly more oblique on MUSM 2934. It extends lingually from the paracone, and reaches a short and longitudinal mure. The third crest is variably developed in the four specimens. It is strong and complete (i.e., extending from the mesostyle to the anterior arm of the hypocone) on MUSM 2934, whereas it is reduced to a mesolophule or mesolophular spur, stemming from the anterior arm of the hypocone, on MUSM 2935 (Text-fig. 5B), 2936 (Text-fig. 5E) and 2961 (Text-fig. 5F). On MUSM 2935, the mesolophule is oblique and connected to a spur (rest of a metaloph?), which is not linked to the mesostyle, but more distally to the metacone (entirely undifferentiated from the posteroloph). On MUSM 2961, it extends labially from the mure, but it does not reach the large mesostyle. On MUSM 2936, the mesolophule is shorter (mesolophular spur), much lower than on MUSM 2935, and it remains labially free. No P4 has a differentiated metacone. A strong anterior arm of the hypocone, extending from the hypocone (MUSM 2936) or from its labial aspect (MUSM 2934 and 2935), connects to the mure. On MUSM 2961, a short crestule occurs from the third transverse crestmure junction, it is backwardly oriented and weakly connected to the posteroloph. That crestule could be a rest of the anterior arm of the hypocone very labial in position. All flexi are very deep.

Upper molars are mesodont with their crown higher lingually than labially. The less worn upper molar (MUSM 2937, Text-fig. 5C) has a HIg equal to 1.05 and a HIb equal to 0.45. They are characterised by a tetralophodont pattern, and have rounded corners. The teeth interpreted as M2 are subsquare (Text-fig. 5D), whereas the MUSM 2937 M1 is slightly more transversely developed (Text-fig. 5C). M2s are also larger and have their hypocone occupying a more labial position than on M1s. Only the paracone and mesostyle are well cuspate, the other cusps being crestiform. The protocone is aligned with its anterior arm (i.e., lingual part of the anteroloph) and its posterior outgrowth, so that they form a massive complex directed distolingually, contary to the labial part of the anteroloph, which is more

transverse. As the posterior outgrowth of the protocone is very long and backwardly oriented, the lingual opening of the narrow hypoflexus is mesiodistally constricted. Labially, the paracone, very large on MUSM 2939, is separated from the labial end of the anteroloph and from the mesostyle on the less worn teeth, whereas these structures tend to be linked with wear. The protoloph is thick and strongly connected to the paracone. On M2s, the protolophe is oblique, whereas on M1, its labial part is more transverse. On M2s, a tiny lingual protoloph connects the protocone to the labial protoloph (i.e., non-taeniodont pattern), whereas it is very low on the MUSM 2937 M1 (i.e., pseudo-taeniodont pattern). The hypocone displays a long and strong anterior arm, mesiolabially directed. Distally, it connects to a long and curved posteroloph, extending labially and incorporating the metacone. The mesostyle is smaller than the paracone, but well defined compared to the metacone (crestiform), and it remains isolated on MUSM 2937 and 2939. With wear, the mesostyle is connected to the posteroloph-metacone crest (MUSM 2938). The third central crest is roughly transverse and continuous, composed of two crests: a long mesoloph stemming from the mesostyle, associated with a short mesolophular spur situated on the mesial extremity of the anterior arm of the hypocone. The mure is well marked, longitudinal, and it strongly connects the lingual extremity of the labial protoloph to the third transverse crest-anterior arm of the hypocone junction. There is no metaloph (or not well differentiated), but lingually, the posteroloph is mesiodistally enlarged on MUSM 2937 and 2939, a thickening which could indicate a residual connection of the metaloph with the posteroloph, or a fusion between these two crests. The flexi are deep. **Comparisons:** With its somewhat unique association of characters, these isolated teeth from TAR-21 can be attributed to a new genus and new species: Tarapotomys subandinus nov. gen. et sp. It is particularly difficult to attribute this new taxon to a caviomorph superfamily because if the teeth can be compared to those of some cavioid dasyproctids in some aspects, in other aspects they ressemble those of chinchilloids or even octodontoids. Tarapotomys teeth are somewhat highcrowned, notably for the upper molars, which is more common in cavioids, chinchilloids, but also occurs in some octodontoids. Besides, the reduction of the second transverse cristid characterises some dasyproctids

ond transverse cristid characterises some dasyproctids (e.g., *Australoprocta*), chinchilloids (e.g., *Incamys* and *Scleromys*), and octodontoids (e.g., *Galileomys* and Sallamys). Contrary to Tarapotomys, most Deseadan and early Miocene octodontoids are characterised by a metaconid that is particularly crestiform. In the latter taxa, the metaconid is often connected to an accessory cristid (i.e., metaconid cristid/spur), sometimes linked to the second transverse cristid. Moreover, there are neither neomesolophid, nor mesostylid, or posterior arm of the metaconid (or very poorly developed one) on the lower molars of these taxa. Tarapotomys has neither heterogeneous thickness of the enamel layer nor a dental pattern including laminated and almost isolated prisms, two features otherwise found in chinchilloids (although they lack in Branisamys, see Kramarz et al. 2013). Tarapotomys has no more well-defined metaloph on its upper molars, contrary to most of erethizontoid species.

Among Palaeogene caviomorphs, some of them (Eoincamys, Chambiramys sylvaticus, and Incamys) display lower molars with a strong posterior arm of the metaconid and a second transverse cristid limited to a neomesolophid, as in T. subandinus. Tarapotomys subandinus has tetralophodont upper molars as observed in *Eoincamys* and some specimens of *C. sylvaticus* and Incamys. Indeed, upper molars of C. sylvaticus and Incamys have a very variable distal area. This is particularly shown in the development, connection, and orientation of crests, with notably the variable presence of a well-defined or residual metaloph and cuspate metacone, all features lacking in *T. subandinus*. Crown height in T. subandinus is rather similar to that of C. sylvaticus molars. It exceeds that of Eoincamys and is lesser than in *Incamys*. *Tarapotomys* has smaller teeth than Eoincamys pascuali and Incamys. Dental size equals that of C. sylvaticus and Eoincamys amegh*inoi*. Like in *E. ameghinoi* and *Incamys*, upper molars of T. subandinus have transverse crests, contrary to Eoincamys pascuali in which they are markedly oblique. Tarapotomys has less transversely elongated upper molars than *Eoincamys* and *Incamys*. It differs from *Eoin*camys, C. sylvaticus and Incamys in having less clearly taeniodont teeth, notably for the upper molars. Like Eoespina/Eosachacui, Vallehermosomys, Galileomys, Leucokephalos VUCETICH et al., 2015, Llitun VUCE-TICH et al., 2015, Platypittamys, Deseadomys, Sallamys, and Xylechimys, Tarapotomys displays tetralophodont upper molars. Lower molars of *Tarapotomys* have a reduced second transverse cristid contrary to Eoespina/Eosachacui. Some other taxa (such as: Deseadomys, Galileomys, Leucokephalos, Llitun, Platypittamys, Sallamys, and Xylechimys) also show a reduced

second transverse cristid on lower molars, but they usually have a short posterior arm of the protoconid and/or have neither posterior arm of the metaconid nor neomesolophid, contrary to *Tarapotomys*. At last, *Tarapotomys* displays a labial protoloph and a third transverse crest shorter than *Vallehermosomys mazzonii* and *?Vallehermosomys merlinae*. *Tarapotomys* differs from *V. mazzonii* in having narrower and not clearly taeniodont upper molars, and from *?V. merlinae* in showing the mesostyle closer to the paracone, and accordingly a third transverse crest closer to the protoloph.

Tarapotomys mayoensis nov. sp. (Text-fig. 4T–H', Appendix S2)

Derivation of name: from the Mayo River, flowing beneath the type locality (TAR-01).

Holotype: MUSM 3496, left M2 (Text-fig. 4B'). Deposited in the MUSM, Lima, Peru.

Referred material: In addition to the holotype (MUSM 3496) - MUSM 3301, fragment of a right dp4, MUSM 3302, right dp4 (Text-fig. 4T), MUSM 3303, right p4 (Text-fig. 4U), MUSM 3304-3305, left m1s (Text-fig. 4V), MUSM 3306-3307, right mls (Text-fig. 4Z), MUSM 3308, fragmenta of a left m2, MUSM 3309, left m2 (Text-fig. 4W), MUSM 3310-3314, right m2s (Text-fig. 4Y), MUSM 3315, right m3 (Text-fig. 4X), MUSM 3316, fragment of a left dP4, MUSM 3366, fragment of a left dP4, MUSM 3317, left dP4 (Text-fig. 4D'), MUSM 3318, fragment of a left P4, MUSM 3319, left P4 (Text-fig. 4E'), MUSM 3320, fragment of a right P4, MUSM 3321, fragment of a left M1, MUSM 3322-3325, left M1s (Text-fig. 4A'), MUSM 3367, fragment of a right M1, MUSM 3326, right M1 (Text-fig. 4F'), MUSM 3494-3495, fragments of left M2s, MUSM 3497-3498, left M2s, MUSM 3499-3500, right M2s (Text-fig. 4G'), MUSM 3368, fragment of a left M3, MUSM 3501, left M3 (Text-fig. 4C'), MUSM 3502-3505, right M3s (Text-fig. 4H').

Type locality: TAR-01, Shapaja, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Diagnosis: Differs from *T. subandinus* in having slightly larger teeth, lower molars tending to be taeniodont, dP4s with a stronger metaloph, P4 lacking the third transverse crest, upper molars being more often fully taeniodont, and in showing upper molars having shorter protoloph and third transverse crest.

Description: The MUSM 3302 dp4 is slightly damaged at the level of the metaconid and the lingual part of the metalophulid I (Text-fig. 4T). MUSM 3301 is a distal fragment of a dp4 preserving only the distal margin of the mesial ectolophid, the distal ectolophid, the hypolophid, the entoconid, the hypoconid,

and the posterolophid. Both dp4s have cristids with thick enamel layers. The cuspids/stylids are slightly distinct and incorporated within the cristids, except the well-defined, cuspate, and isolated mesostylid on MUSM 3302. The metalophulid I and metalophulid II are curved, but the metalophulid I is mesially arcuate (convex), whereas the metalophulid II is distally concave. Being both labially and lingually linked to the protoconid and metaconid, respectively, they isolate an oval anterofossettid. The metaconid, lacking a posterior arm, remains well separated from the mesostylid. Labially, the mesial ectolophid is well marked, labiomesially oriented, and mesially disconnected to the protoconid, but it joints distally a short and longitudinal distal ectolophid. The anterior extremity of the mesial ectolophid is thickened forming a cuspid-like structure. There is neither mesolophid nor neomesolophid, thereby involving the confluence between the two mesoflexids (i.e., mesial and distal ones). The hypolophid extends from the poorly differentiated entoconid, which has no arm, to the distal extremity of the distal ectolophid. Like the mesial ectolophid, the hypolophid is labiomesially oriented, but it is more transverse than the mesial ectolophid. The hypoconid is slightly distally positioned with respect to the entoconid. It displays a weak and low anterior arm, a short anterior outgrowth, and a long and curved posterior arm, connected to a strong posterolophid. The latter is lingually well separated from the entoconid by a wide notch. On both dp4s, although it is low in its middle part, the anterior arm of the hypoconid connects the hypolophid-distal ectolophid junction and the hypoconid. Thus, the deep and broad metaflexid is partially confluent with a smaller hypoflexid (i.e., pseudo-taeniodont pattern), the latter having a wide opening.

The MUSM 3303 p4 is slightly damaged lingually (Text-fig. 4U). It is low-crowned and slightly longer than wide, with a talonid clearly wider than the trigonid. This tetralophodont lower premolar bears very massive cristids displaying thick enamel layers. By its rather high elevation and its isolation, the entoconid is the most distinct cuspid of the crown. It displays a strong but short anterior arm. The metaconid is moderately discernible, with a short posterior arm. Although damaged, the latter does not appear connected to a differentiated mesostylid. The posterior arm of the metaconid ends distally, close to the mesial extremity of the anterior arm of the entoconid and without joining it. The metalophulid I is short,

strongly connected to the metaconid, but separated from the large and labiolingually pinched protoconid by a very thin furrow. The second transverse cristid is short and discontinuous in its middle. It consists of two tiny cristulids: a lingual one stemming from the metaconid (probably a neocristulid), and a labial one, corresponding to a short posterior arm of the protoconid. The protoconid is distally connected to a very short cuspid-like ectolophid. There is no mesolophid. From the entoconid, a long hypolophid extends linguodistally (oblique) and links the ectolophid. Although the hypoconid is close to the hypolophid-ectolophid junction, there is no anterior arm of the hypoconid, which involves a narrow confluence between the furrow-like metaflexid and the retroverse hypoflexid (i.e., taeniodont pattern). The posterior arm of the hypoconid is merged with the thick and weakly curved posterolophid, the latter extending lingually and ending directly distal to the entoconid, without connecting it. The hypoconid displays a very short but massive anterior outgrowth, which generates a weak mesiodistal constriction of the hypoflexid.

The lower molars share similar dental features. Only one eroded specimen of m3 is available (MUSM 3315, Text-fig. 4X), whereas four m1s and five m2s are identified. The m3 and the teeth interpreted as m1 are smaller than those interpreted as m2. The m3s are slightly longer than m1s but with an equal width. The m1–2s have either a trigonid and a talonid similar in width or a narrower trigonid, whereas the m3 has a wider trigonid with respect to the trigonid. The lower molars, brachydont, tend to be trilophodont (i.e., reduction or even absence of the second transverse cristid) and taeniodont. The cuspids/stylids are somewhat undifferentiated from the well-marked cristids, which have thick enamel layers. The metaconid and entoconid are more mesially located than the protoconid and hypoconid, respectively. The protoconid, metaconid, and hypoconid are mesiolingually-distolabially pinched. The metalophulid I, straight and complete, shows a labial thinning, just before its connection with the protoconid. On MUSM 3306 (Text-fig. 4Z) and MUSM 3308, it is divided into two short parts (a lingual one and a labial one) separated by a very thin and shallow notch. The metaconid displays a strong posterior arm, usually merged with a small mesostylid, but it can be also separated from this stylid by a thin notch (MUSM 3312). The protoconid is in continuity and aligned with a strong ectolophid, thereby generating a long and oblique cristid. That cristid is connected to a rather large entoconid, displaying strong anterior and posterior arms, via a short hypolophid. The latter is transverse or more or less aligned with the protoconid-ectolophid complex. The second transverse cristid is usually reduced to a short neomesolophid, stemming from the mesostylid, which is generally labially free or connected to the metalophulid I, when it is longer. With wear, the neomesolophid is merged with the metalophulid I, generating a mesiolingual plateform. On MUSM 3304 and 3305, a very short posterior arm of the protoconid on the protoconid-ectolophid complex is oriented toward the neomesolophid but not joined to it. Besides, some lower molars (MUSM 3308 and 3310, Text-fig. 4Y) have no second transverse cristid (i.e., neither the neomesolophid nor the posterior arm of the protoconid). Owing to the reduction or even the absence of the second transverse cristid, the anteroflexid is confluent with the mesoflexid. The anterior and posterior arms of the entoconid are generally separated by thin furrows from the mesostylid and from the lingual extremity of the posterolophid, respectively. The posterolophid is long and curved. On MUSM 3310 (Text-fig. 4Y), the lingual extremity of the posterolophid is strongly connected to the entoconid, which involves a lingually closed metaflexid on this tooth (= metafossettid). The anterior arm of the hypoconid can be thin and low in its middle part (i.e., pseudo-taeniodont pattern, MUSM 3308, 3309, 3310, 3312) or absent (i.e., taeniodont pattern, MUSM 3306, Text-fig. 4Z). The anterior outgrowth of the hypoconid is labially directed, with a moderate or marked length. Given the orientation of the anterior outgrowth of the hypoconid, the labial aperture of the hypoflexid does not show any mesiodistal constriction.

MUSM 3316, 3317 and 3366 are identified as dP4s. MUSM 3317 is complete (Text-fig. 4D'), whereas MUSM 3316 and 3366 are labiodistally and distally broken, respectively. MUSM 3317 is pentalophodont. Given the fragmentary state of MUSM 3316 and 3366, the presence or absence of the metaloph cannot be evaluated for these teeth. Three dP4s are brachydont. MUSM 3316 and 3317 are subtrapezoidal, with a longer labial edge than the lingual one. The mesial and distal margins of these upper deciduous premolars are not parallel, the mesial one is mesiolabially directed whilst the distal one is almost transverse or slightly distolabially oblique. The oblique mesial margin of these premolars relies in the development of

an enlarged and mesially expensive anteroloph, bearing a well-marked, somewhat cuspate, median enamel swelling interpreted here as a mesially displaced anterocone-like cusp. On these teeth, the anteroloph is strongly constricted lingually before to reach a very large and oval protocone. The latter displays a short posterior arm, but it lacks a well-differentiated posterior outgrowth, probably short and merged within its distal aspect. The lingual protoloph (i.e., posterior arm of the protocone) corresponds to a thin enamel spur, which connects the protocone to the massive labial protoloph, stemming from an isolated but not well-defined (rather indistinct) paracone. On the less worn dP4 (MUSM 3366), this spur is very low causing the partial confluence of the paraflexus and hypoflexus (i.e., pseudo-taeniodont pattern). Like the paracone, the mesostyle is mesiodistally isolated on the labial margin of the teeth. It is only connected lingually to a short third transverse crest. The latter and labial protoloph are parallel, slightly oblique, and linked lingually by a short, thin and longitudinal mure. The hypoflexus is mesiodistally narrow but labiolingually expended due to a labial displacement of the mure. The protoloph and third transverse crest are therefore markedly short labiolingually. Linguodistally, the hypocone corresponds to a medium-sized dentine plate appearing with wear, strongly linked to its thick and oblique anterior arm, nearly aligned with the third transverse crest and to a transverse posteroloph. The latter extends labially and connects to a well-defined and mesiodistally elongated metacone. On MUSM 3317, a well-marked and curved metaloph extends lingually from the metacone, then turns distally to connect to the middle of the posteroloph, both isolating a small posterofossette. In contrast, all other flexi are labially or lingually open.

The P4s (Text-fig. 4E') have a rounded occlusal outline, are shorter and structurally much simpler than the dP4s. They have deep flexi and they exhibit a nearly unilateral hypsodonty at early wear stages (HIg between 1.00 and 1.14 versus HIb between 0.45 and 0.48). The protocone and hypocone are crestiform and undifferentiated. They are merged together (hypoflexus closed lingually) and strongly connected to the massive anteroloph and posteroloph (mesially and distally, respectively), thereby generating a strong, long, and curved "mesiolinguodistal" enamel wall. The massive posteroloph extends labially and incorporates mediodistal tubercles that would have occurred in this part of the crown (i.e., undifferentiated metacone

and/or mesostyle). The long peripheral crest, associated with a large, isolated, and labial paracone plus its short anterior and posterior arms, form the entire occlusal outline of the tooth. The curved posteroloph running labially from the hypocone ends abruptly near the posterior arm of the paracone, without connecting it on MUSM 3318 and 3319 (Text-fig. 4E'). A minute but visible mesostyle is observed on MUSM 3320. On MUSM 3319 (Text-fig. 4E'), the posteroloph is sligthly grooved before its connection with the hypocone. On the MUSM 3320, a residual third transverse crest is still linked to the minute mesostyle (= mesoloph), whereas it is absent (as well as the mesostyle) on MUSM 3318 and 3319. Although MUSM 3320 is distally broken, the posteroloph seems to bear a very short crestule, forwardly oriented, which could be a relic of a metaloph. It is lacking on MUSM 3318 and 3319. A slightly oblique and strong labial protoloph extends from the paracone toward a short and longitudinal mure. The latter is aligned with the anterior arm of the hypocone, which is weakly connected to the hypocone. The lingual protoloph is absent (MUSM 3318 and 3319) or partially reduced to a short crestule stemming from the labial protoloph and disconnected to the protocone (MUSM 3320), thereby involving a taeniodont pattern.

Upper molars are brachydont/mesodont, with a lingually developed crown (HIg between 0.54 and 0.95, HIb between 0.22 and 0.46). M1s (Text-fig. 4A', F') and M2s (Text-fig. 4B', G') are subsquare except MUSM 3323, which is longer than wide. The M3s have usually a more rounded distal margin (Textfig. 4C', H'). From M1s to M3s, the hypocone occupies progressively a more labial position with respect to the protocone. The cusps/styles are incorporated within the crests, which have a massive base and thick enamel layers. The crestiform protocone, labiolingually pinched, forms with the anteroloph and its posterior outgrowth a long mesial crest, lingually curved and labially transverse. The posterior outgrowth of the protocone, long and massive notably on M2-3s, ends abruptly. The paracone is generally isolated from the labial extremity of the anteroloph, but both structures can be joined (MUSM 3326, 3497, 3501, 3504, and 3367). The paracone displays lingually a short labial protoloph, either transverse or slightly labiomesially directed. As a result, it tends to be aligned with a short mure. The latter can also be oblique and in continuity with the anterior arm of the hypocone or more longitudinal. The upper molars are usually fully

taeniodont, but some show a relictual lingual protoloph stemming from the protocone or from the mure (i.e., pseudo-taeniodont pattern, MUSM 3323, 3496, and 3498). Thus, the furrow-like paraflexus and hypoflexus are entirely or partially confluent. The hypostria does not reach the base of the crown. Because of its crestiform shape and its incorporation within the posteroloph, the metacone is faintly visible, except on three teeth (MUSM 3494, 3500 and 3367), where it is small, bulbous and well defined. More mesially, the mesostyle is well separated from the paracone, it is closer to the metacone-posteroloph complex, with which it can be disconnected, weakly linked, or even totally fused. The third transverse crestis either formed by one or two variably developed crests (i.e., mesoloph and/or mesolophule). On two specimens (MUSM 3496 and 3497, Text-fig. 4B'), the third transverse crest is markedly mesiodistally thin (strong mesiodistal pinch) before its connection with the anterior arm of the hypocone (or a very sort mesolophular spur), and thus, it essentially corresponds to a mesoloph. On MUSM 3322 (Text-fig. 4A'), 3501 (Text-fig. 4C'), 3502 (Text-fig. 4H') and 3368, the third transverse crest is divided into two linked or unlinked parts: a labial mesoloph connected to the mesostyle and a lingual mesolophule connected to the anterior arm of the hypocone. The third transverse crest is closely situated to the labial protoloph, transversely short like it, and it can be parallel with it but never oblique. Due to short and closely appressed labial protoloph and third transverse crest, the mesial mesoflexus is limited both mesiodistally and transversely. The metacone is usually connected to a residual metaloph, which is reduced to one or two tiny crest(s) lingually connecting or not to the posteroloph. On MUSM 3494, 3500 and 3368, the metaloph extends from the metacone or from its lingual flank toward the posteroloph (i.e., arcuate). Thus, the confluent distal mesoflexus and posteroflexus constitute the largest flexus on most upper molars.

Comparisons: The material from TAR-01 documents a new species of *Tarapotomys* (*T. mayoensis* nov. sp.), a genus represented by *T. subandinus* at TAR-21 (see above). *Tarapotomys mayoensis* has the closest affinities with *T. subandinus*. Both species share a similar size and height crown, a second transverse cristid reduced to a short neomesolophid on lower molars, a very weak connection between the anteroloph and the protocone on dP4s, a short protoloph and third transverse crest on dP4s, and they display a very similar

lar shape and morphology of their P4s. Besides, upper molars of *T. mayoensis* often show a metaloph very reduced, but some of them can be fully tetralophodont, like in T. subandinus. Nevertheless, Tarapotomys mayoensis differs from T. subandinus in having lower molars tending to be taeniodont, dP4s with a stronger metaloph, P4 lacking the third transverse crest, upper molars being more often fully taeniodont, and in showing upper molars with shorter protoloph and third transverse crest. Tarapotomys mayoensis shares also many characters with Pozomys found at CTA-29 (Contamana, late middle Eocene, BOIVIN et al. 2017b): a small size, pseudo-taeniodont/taeniodont pattern, a reduced metaloph associated to the posteroloph, and a tendency toward the alignment of the protoloph, mure and anterior arm of the hypocone (= diagonal central crest). However, Tarapotomys differs from Pozomys in having higher-crowned upper molars, and in showing M2s being mesiodistally longer and having shorter second transverse cristid, protoloph and third transverse crest. The reduction of the second transverse cristid and the tendency toward taeniodonty on lower molars are found in many Palaeogene and Miocene caviomorphs. For the Palaeogene genera, only Eoincamys, Chambiramys from CTA-32 (C. shipiborum) and from CTA-61 (C. sylvaticus), and Incamys document that type of lower molars. Contrary to Eoincamys pascuali, the lower molars of T. mayoensis have a metalophulid I, although labially thin, always connected to the protoconid, and also a less pronounced tendency toward taeniodonty. The upper molar patterns of *E. pascuali* and *Chambiramys* are markedly distinct from that of Tarapotomys, notably in developing strongly oblique loph(-id)s. Besides, in T. mayoensis, there is no link with the lingual extremity of the third transverse crest and the posteroloph, contrary to E. pascuali and C. sylvaticus. Tarapotomys mayoensis can be compared to Eoincamys ameghinoi, which has no connection between both latter structures. In E. ameghinoi, the third transverse crest is lingually free, like on some upper molars of Tarapotomys, but the latter is usually more isolated from the anterior arm of the hypocone. Moreover, the protoloph is longer in E. ameghinoi. Tarapotomys mayoensis differs from Incamys in having upper molars lower crowned and mesiodistally longer. The MUSM 3302 dp4 shows a particular pattern: a tendency toward the taeniodonty and the absence of mesolophid. This pattern is only found in *C. shipiborum*. However, MUSM 3302 is distinct from the dp4s of C. shipiborum in

showing a thinner and more curved metalophulid II, a mesial ectolophid disconnected to the protoconid, and in displaying mesiodistally longer metaflexid. The upper molars of *T. mayoensis* differ from those of C. shipiborum in exhibiting a strong and long third transverse crest. The Miocene genera showing a reduction of the second transverse cristid and the tendency toward the taeniodonty on lower molars are Scleromys, Garridomys, Neoreomys, Protadelphomys, Drytomomys and Microscleromys. The Palaeogene and Miocene genus *Eoviscaccia*, also displays these features. However, these aforementioned Miocene genera and *Eoviscaccia* share common characters not present in *T. mayoensis*: a pronounced degree of hypsodonty, and laminar and heavily thick loph(-id)s. Moreover, the upper molars of *T. mayoensis* and Miocene genera (plus *Eoviscaccia*) can be clearly distinguished. Indeed, in these Miocene taxa (except *Neoreomys*), the obliquity of lophs is more pronounced, with notably a third transverse crest, which is lingually connected to the posteroloph. Besides, in Drytomomys, there is no distal link between the hypocone and the posteroloph. In *Neoreomys*, the protoloph and third transverse crest are labiolingually longer, and the metaloph is usually more developed. Finally, T. mayoensis shares some characters with the Palaeogene genus Vallehermosomys, which is only known by two upper molars: a third transverse crest connected to the anterior arm of the hypocone, and a tendency toward the taeniodonty. However, on the upper molars of T. mayoensis, the protoloph and third transverse crest are topographically closer and labiolingually shorter.

aff. Tarapotomys sp.

(Text-fig. 5H, Appendix S2)

Referred material: MUSM 2940, fragment of a right upper molar (Text-fig. 5T).

Locality: TAR-21, Shapaja, San Martín Department, Peru. Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Description: MUSM 2940 (Text-fig. 5H) is a labial fragment of upper molar that lacks the labial part of the protocone, its posterior outgrowth and a part of the hypoflexus. The main preserved cusps and the mesostyle are faintly differentiated from the transverse crests. The paracone is the most cuspate and it displays short anterior and posterior arms. The paracone appears slighly more mesial than the protocone. The protocone displays a long and mesiolabially oriented anterior arm, which is markedly enlarged in its mesial-

most part, whereas the labial part of the anteroloph is shorter and more transverse. The latter is connected to the anterior arm of the large paracone. The labial protoloph is thick, markedly oblique, and strongly linked to the paracone (in continuity) but disconnected to the mure, the latter being oblique, and aligned (i.e., faintly distinct) with the anterior arm of the hypocone. The lingual protoloph is reduced to a low and very thin crestule, which connects a short spur of the mure, forwardly directed to the distal flank of the protocone (i.e., non-teaniodont/pseudo-taeniodont pattern). The anterior arm of the mesostyle is separated from the posterior arm of the paracone by a wide furrow, whereas the mesostyle is distally entirely merged within the metacone-posteroloph complex (the metaloph being undifferentiated). The third transverse crest consists of a very short mesoloph stemming from the mesostyle, and it remains lingually free (absence of mesolophule), thereby involving the confluence between both mesoflexi. There is no trace of metaloph. The posteroloph is lingually divided by a shallow notch into two parts: a very short lingual one stemming from the crestiform hypocone, and a long and curved labial one, which is connected to the mesostyle (via the crestiform metacone and its anterior arm).

Comparisons: Among all determined species from TAR-21, the morphology of MUSM 2940 is reminiscent to that of upper molars of Tarapotomys subandinus and some of T. mayoensis, especially by the absence of metaloph and cuspate metacone. MUSM 2940 shows similar size and occlusal outline with the upper molars of T. subandinus. However, MUSM 2940 differs from upper molars of *T. subandinus* in having a third transverse crest limited to a short mesoloph, a protoloph disconnected to the mure, the latter being oblique rather than longitudinal, and aligned with the anterior arm of the hypocone. As MUSM 2940, some upper molars of *T. mayoensis* display an alignment of the mure and the anterior arm of the hypocone, and a mesostyle fused with the posteroloph-metacone complexe. But, none upper molar of *T. mayoensis* has such a reduced third crest than MUSM 2940. So, MUSM 2940 is provisionally attributed to aff. *Tarapotomys* sp.

cf. Tarapotomys sp.

(Text-fig. 5I–T, Appendix S2)

Referred material: MUSM 2927 and 3327, left m1s (Text-fig. 5I, M, N), MUSM 3328, right m1 (Text-fig. 5L), MUSM 2926, 2928, 2967 and 3329, left m2s (Text-fig. 5J, O, P),

MUSM 3330, left m3 (Text-fig. 5K), MUSM 3331, fragment of a right dP4 (Text-fig. 5Q), MUSM 3332, fragment of a right M1 (Text-fig. 5R), MUSM 2910, fragment of a right M2, MUSM 3333, left M2 (Text-fig. 5S), MUSM 2911, left M3 (Text-fig. 5T).

Locality: TAR-20 (for MUSM 3327–3333), TAR-21 (for MUSM 2926–2928) and TAR-13 (only for MUSM 2967), Shapaja, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Description: These lower molars are brachydont and longer than wide. The m1s (Text-fig. 5I, L, M, N) are shorter than m2s (Text-fig. 5J, O, P) and are characterised by a trigonid narrower than the talonid. The trigonid and talonid of m2s are similar in width, and the trigonid is wider than the talonid on the MUSM 3330 (Text-fig. 5K). All lower molars are tetralophodont, non-taeniodont, with thick cristids. The lingual cupsids/stylids are well defined, notably on the pristine tooth MUSM 2926 (Text-fig. 5J), with respect to the labial ones, which are usually crestiform. However, on MUSM 3329 (Text-fig. 5P), the protoconid is well defined and more bulbous than on other lower molars. The protoconid is more distally located than the metaconid on MUSM 3329, whereas the latter is distally displaced and labiolingually opposed to the protoconid on MUSM 2926. The displacement of the metaconid on that tooth involves a mesiolabial obliquity of the metalophulid I, which is transverse on other lower molars. On all lower molars, the entoconid is more mesial than the hypoconid. On MUSM 2926 (Text-fig. 5J), the metalophulid I is strongly connected to the metaconid, but it only reaches the lingual base of the protoconid. MUSM 3330 (Textfig. 5K) also displays a weak connection between the metalophulid I and the protoconid. Both structures are well linked on other molars. The metaconid displays a short but strong posterior arm, which joins a weakly developed anterior arm of the mesostylid. On most lower molars, the second transverse cristid is labiolingually complete, linking the mesostylid to the protoconid. On MUSM 2967 (Text-fig. 5N), this cristid is complete, continuous and composed of a single cristid corresponding to the posterior arm of the protoconid (= metalophulid II). On MUSM 2928 (Textfig. 5O), the second transverse cristid consists of a long neomesolophid (the posterior arm of the protoconid is limited to a small spur), whereas on MUSM 2926 (Text-fig. 5J) and 3327 (Text-fig. 5M), it is formed by the fusion of a neomesolophid with a posterior arm of the protoconid, both equal in length. On MUSM

2927 (Text-fig. 5I) and 3330 (Text-fig. 5K), the second transverse cristid also consists of these two cristids, weakly linked on MUSM 2927 and disconnected but very close on MUSM 3330. On MUSM 2927, the neomesolophid is forewardly oriented and the posterior arm of the protoconid is lower, it reaches lingually the labial flank of the neomesolophid and labially the lingual flank of the protoconid. The ectolophid is mesiolabially directed on all lower molars, except on MUSM 2926, where it is sagittally oriented, thereby involving a shorter second transverse cristid on that tooth. The entoconid is larger than the mesostylid and isolated, except on MUSM 2928 and 3328, where it is connected (via its posterior arm on MUSM 3328) to the lingual end of the posterolophid. MUSM 3328 (Text-fig. 5L) differs from other lower molars in having a very strong and long posterior arm. On all teeth, the hypolophid is complete and transverse, or slightly linguodistally oblique as on MUSM 3328. On most lower molars, the anterior arm of the hypoconid is complete, long, and strong. In contrast, on the pristine m2 (MUSM 2926, Text-fig. 5J), it is very thin and lower (i.e., pseudo-taeniodont pattern). In addition to its anterior arm, the hypoconid displays a long and sloping anterior outgrowth, so that the hypoflexus is narrow (but not constricted) and buccolingually extensive. The posterolophid is arcuate and strongly connected to the hypoconid.

MUSM 3331 is a lingual fragment of dP4 (Textfig. 5Q). The protocone and hypocone, as well as the lingual parts of the anteroloph, protoloph, third transverse crest, metaloph, and posteroloph are preserved. The protocone and hypocone are both crestiform, mesiolingually-distolabially pinched, and they develop mesiolabially oblique anterior arms. The anterior arm of the protocone is shorter than that of the hypocone and connected to the anteroloph. The latter is parallel to the labial protoloph, and these crests, together to the thin mure, are also mesiolabially oriented, but with a different tilt with respect to the anterior arms of the protocone and of the hypocone. More distally, the protocone develops a short but complete posterior arm, as well as a very short posterior outgrowth. Accordingly, the narrow hypoflexus is not labially constricted but it displays instead a slight enlargement of its labial opening. The third transverse crest, more transverse comparatively to the anteroloph and labial protoloph, corresponds to a long mesoloph, reaching a short metalophular spur or directly the anterior arm of the hypocone-mure junction. The MUSM 3331dP4

shows a widely damaged metaloph, preserving only its anterior enamel margin. The latter is long, labially transverse, but its lingual end is lingually turned backwardly and connected to the posteroloph.

MUSM 2910 is broken in its labial part and MUSM 3332 (Text-fig. 5R) is broken in its lingual part. Other upper molars (MUSM 2911 and 3333, Text-fig. 5S, T) are complete and less worn. MUSM 2910 and 2911 are also slightly corroded (digested). All upper molars are non-taeniodont, submesodont (HIg between 0.77 and 0.83), and subsquare. MUSM 2911 displays a more rounded occlusal outline with a more reduced hypocone than other molars, which suggests that this tooth is a M3 (Text-fig. 5T). The MUSM 3332 (Text-fig. 5R) is smaller than M2-3s. On the pristine molar MUSM 3333 (Text-fig. 5S), the cusps/styles are very crestiform, the paracone being the more distinct one. On MUSM 2911, heavily worn, the hypocone and mesostyle are more recognisable and well defined because of their particular wear. The metacone is very close to the mesostyle, almost twinned, especially on MUSM 3333. With wear, it is entirely merged with a long and strong posteroloph. The protocone is massive but strongly labiolingually pinched, and in continuity with its anterior arm. It also bears a long posterior outgrowth, especially on MUSM 2911 (Text-fig. 5T), nearly closing the hypoflexus lingually (mesiodistal constriction of the hypoflexus). The long anteroloph extends labially from the protocone, and remains separated from the latter on MUSM 3333, whereas it reaches the anterior arm of a large and high paracone on MUSM 2911. On all molars, the posterior arm of the paracone is short and separated from a well-developed mesostyle. From the paracone, a massive labial protoloph extends lingually, either transverse (MUSM 2911, Text-fig. 5T), more mesiolabially directed (MUSM 3333, Textfig. 5S), or labially transverse and lingually oblique (MUSM 3332, Text-fig. 5R). On MUSM 2910, 2911 and 3332, it connects to the protocone via its strong and slightly labiodistally oblique lingual branch (i.e., non-taeniodont pattern). On MUSM 3333 (Textfig. 5S), a short crestule runs from the distal end of the posterior outgrowth of the protocone toward the labial prototoloph it does not reach. By its very distal location, that crestule is probably a part of the posterior outgrowth of protocone or a neostructure, instead of being a posterior arm of the protocone. MUSM 2911 (Text-fig. 5T) has an additional longitudinal crestule (absent on other molars), stemming

from the middle part of the protoloph, and that links a short longitudinal spur of the anteroloph, thereby dividing the parafossette into two subfossettes. On all molars, the hypocone, strongly connected to the posteroloph, displays a moderately long and oblique anterior arm reaching the mure. On MUSM 2911, this arm is only weakly connected to the strong and well-defined hypocone (labiolingual pinch), contrary to what it is observed on other molars. On all teeth, the mure is complete, linking the mesial extremity of the anterior arm of the hypocone to the protoloph. The mure is longitudinal on MUSM 2910, 3332 and 3333, whereas its distal part is mesiolabially directed and aligned with the anterior arm of the hypocone on MUSM 2911. Labially, on MUSM 2911 and 3333, the mesostyle and metacone are virtually twinned and equally sized, they are almost indistinct on MUSM 3333, whereas the mesostyle is more distinct than the metacone on MUSM 2911. The connection between the mesostyle and the metacone is weaker on MUSM 3332 than on MUSM 2911 and 3333. On MUSM 2911, the third transverse crest is composed of two parts: a long and slightly curved mesoloph stemming from the mesostyle, which joins a small mesolophule originating from the mesial extremity of the anterior arm of the hypocone. On MUSM 3333 (Text-fig. 5S), the third crest is not transverse but sinuous, which might also be the result of a fusion of a mesolophule with a mesoloph. Due to strong wear and bad preservation, the configuration of the third crest cannot be observed on MUSM 2910. On MUSM 2911, the mesolophule bears a very short spur, backwardly oriented. On MUSM 2910, 2911 and 3333, the metaloph is long, strongly connected to the metacone, and it lingually turns backwardly to join the posteroloph in its middle part. Thus, the metaloph and posteroloph isolate a small and oval posterofossette. On MUSM 3332 (Text-fig. 5R), a very short expansion of the posteroloph probably corresponds to a relictual metaloph or to its connection with the posteroloph. The posteroloph, transverse, becomes labially curved before its connection with the metacone. The flexi are deep on the least worn molars (MUSM 2911 and 3333, Textfig. 5S, T), notably the mesial mesoflexus and hypoflexus. Both are further narrow.

Remark: The MUSM 2967 m1 is larger than other lower molars assigned to cf. *Tarapotomys* sp. but is has closest morphological affinities with them. Accordingly, we consider this size discrepancy as documenting interspecific variation.

Comparisons: By their size and morphology, these teeth, especially the upper molars, recall those of Tarapotomys, a genus documented at TAR-01 (T. mayoensis), TAR-21 and TAR-22 (*T. subandinus*, see above). Indeed, the upper molars from TAR-20 are subsquare and tend to have a submesodont crown and short transverse crests, notably the labial protoloph and third crest, like in Tarapotomys. The material from TAR-20 is closer to *T. mayoensis* in its size (*T. suband*inus is smaller) and variably developed metaloph (absent on all upper molars of *T. subandinus*). However, the labial protoloph and third crest of upper molars from TAR-20 are longer than in T. mayoensis, and much longer than in *T. subandinus*. Besides, the upper molars from TAR-20 are usually non-taeniodont, a condition which is more frequently observed in T. subandinus than in T. mayoensis. As the second transverse cristid is long and mostly complete on lower molars, whereas it is reduced or absent in the referred species of Tarapotomys, we prefer to keep the dental material from TAR-20 in open nomenclature, as cf. Tarapoto*mys* sp. By their brachydonty, non-taeniodonty, transverse loph(-id)s, the teeth of cf. *Tarapotomys* sp. could document either an erethizontoid or an octodontoid. The pentalophodonty of upper molars with a well-developed metaloph would point to erethizontoids. In addition, some erethizontoids, such as Neosteiromys bombifrons CANDELA, 2004 (Andalhuala Fm., Argentina, late Miocene) and ?Neosteiromys tordillense (Collón Cura Fm., Argentina, middle Miocene, VU-CETICH et al. 1993b), can show a strong reduction or even the absence of the metaloph on some of upper molars, like in cf. Tarapotomys sp. However, Neostei*romys* is clearly larger, with thicker loph(-id)s and taeniodont upper molars. The size of these lower molars would be compatible with MUSM 2925 referred to the erethizontoid Kichkasteiromys raimondii from TAR-21. Nevertheless, although no lower molars are available for Kichkasteiromys, these lower molars described here do not display extended flexids as it is observed in Palaeogene erethizontoids (e.g., Protosteiromys and Shapajamys (see p.8)). Moreover, these lower molars do not show any neolophid in the anteroflexid, which characterises some erethizontoid species (e.g., Palaeosteiromys, Branisamyopsis australis CANDELA, 2003, Branisamyopsis praesigmoides KRA-MARZ, 2004, Steiromys duplicatus, and Neosteiromys pattoni CANDELA, 2004). The subsquare occlusal outline of upper molars of cf. *Tarapotomys* sp. does not match with MUSM 2925, which is more transversely

elongated. This material from TAR-20 does not show some characteristics found in *Kichkasteiromys* and in erethizontoids in general: i.e., a mure rather lingually positioned implying a long lenght of the labial protoloph and third transverse crest and a hypoflexus labiolingually shorter. By its pentalophodont-tetralophodont upper molars and variably developed second transverse cristid (continuous or discontinuous), cf. Tarapotomys sp. also recalls early stem caviomorphs or octodontoids, and especially some species found in CTA-27 (i.e., Cachiyacuy ANTOINE et al., 2012 and Canaanimys ANTOINE et al., 2012) and in Santa Rosa (i.e., Eoespina/Eosachacui and Eosallamys). Otherwise, cf. *Tarapotomys* sp. is characterised by upper molars with twinned mesostyle and metacone, a feature lacking in Cachiyacuy, Canaanimys, Eoespina/Eosachacui and Eosallamys. cf. Tarapotomys sp. differs from Cachiyacuy and Canaanimys in having slighly higher crowns, more crestiform cusp(-id)s, thicker cristids on lower molars and more subsquare upper molars. The upper molars of cf. Tarapotomys sp. have a size and thick crests, which recall the upper molar characteristics of *Eosallamys simpsoni* Frailey & Campbell, 2004, whereas Eosallamys paulacoutoi FRAILEY & CAMPBELL, 2004 is larger and displays thicker crests. Moreover, the upper molars of cf. *Tarapotomys* sp. are subsquare like those of *Eosallamys simpsoni*, but the latters are more angular in outline, and bear a shorter posterior outgrowth of the protocone and a more developed mesostylid. Lastly, cf. Tarapotomys sp. differs from *Eoespina/Eosachacui* in having a more frequent and stronger development of the metaloph on M1–2s.

Caviomorpha gen. et sp. indet. 1

(Text-fig. 5U–X, Appendix S2)

Referred material: MUSM 2909 and 2913–2917, fragmentary left dp4s (Text-fig. 5U, X), MUSM 2918–2920, fragments of right dp4s, MUSM 2921, fragment of a left dP4, MUSM 2922, left dP4, MUSM 2923, right dP4 (Textfig. 5W), MUSM 2924, left P4 (Text-fig. 5V).

Locality: TAR-21 and TAR-20 (only for MUSM 2909), Shapaja, San Martín Department, Peru.

Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Description: All dp4s attributed to this new taxon are fragmentary, MUSM 2913 being the most complete (Text-fig. 5X). These dp4s are longer than wide, and characterised by a trigonid only slighly narrower than the talonid (on the specimens where this feature is discernable). These deciduous premolars are brachydont, pentalophodont, non-taeniodont, and

with well-defined cuspids and mesostylid, except the crestiform hypoconid. The metaconid, mesostylid, and entoconid are roughly equal in size except on MUSM 2909 (Text-fig. 5U), which shows a distally inflated mesostylid. The protoconid is large and much more mesially canted with respect to the metaconid. Both mesial cuspids are linked by an oblique and slightly arcuate metalophulid I, which forms the mesial margin of the tooth. On MUSM 2914 and 2919, the second transverse cristid corresponds to a short posterior arm of the protoconid, which reaches the labial flank of the metaconid. On MUSM 2913 (Textfig. 5X) and MUSM 2909 (Text-fig. 5U), in addition to a dominant and oblique posterior arm of the protoconid, a very short and transverse lingual cristulid stems from the metaconid. The mesostylid is mesially and distally separated from the metaconid and entoconid, respectively. A roughly transverse mesolophid extends from the ectolophids (i.e., mesial and distal) to the mesostylid. On MUSM 2913, at mid-width, a very short spur, forwardly directed, stems from the mesolophid. The mesial ectolophid is slightly labiomesially oriented. The labial end of the mesial ectolophid shows a well-marked cuspid-like enamel swelling, either connected or not to the protoconid. This swelling is more labially positioned with respect to the protoconid (occurring on the labial margin of the crown). The longitudinal distal ectolophid links the mesolophid-mesial ectolophid junction to a massive and long hypolophid, strongly connected to the entoconid. Like the mesostylid, the entoconid is often mesially and distally isolated, although on MUSM 2913, the lingual end of the posterolophid contacts the base of the entoconid. On MUSM 2915, these two structures are entirely fused, due to wear. The hypolophid and posterolophid are arcuate, mesially concave, and with thick enamel layers. The hypoconid is somewhat indistinct, as it is entirely subsumed within the posterolophid. It bears a strong anterior outgrowth, forming a long distal cristid. It also develops a strong anterior arm, which joins the hypolophid-distal ectolophid junction (i.e. non-taeniodont pattern). The flexids are shallow.

The three dP4s are worn, longer than wide, and with a subquadrangular crown outline. The mesial margin is slightly oblique (mesiolabially directed) and parallel to the distal one. The labial cusps and styles are undifferentiated, being included in the transverse crests. In contrast, the lingual cusps (protocone and hypocone) are particularly well defined and some-

what bulbous. On three heavily worn dP4s, they appear as two broad platforms of dentine, separated by a narrow and deep hypoflexus. The hypoflexus is either labiolingually oriented (transverse, MUSM 2923, Text-fig. 5W) or slightly proverse (MUSM 2921 and 2922). The anteroloph is well separated labially from the small paracone and it faintly connects to the protocone lingually. An important mesiodistal thickening (cusp-like enamel swelling) of the lingual part of the anteroloph is only observed on MUSM 2923 (Textfig. 5W). The protoloph and third transverse crest extend lingually from the paracone and mesostyle, respectively, to connect to each extremity of the mure, the latter occupying a central position on the crown. The protoloph and third transverse crest are strong, parallel, and slightly oblique on MUSM 2921 and 2922, whereas they are more transverse on MUSM 2923. The posterior arm of the protocone is strong and connected to the protoloph-mure junction (i.e., non-taeniodont pattern). The mure is longitudinal, whereas the anterior arm of the hypocone is oblique (mesiolabially oriented). The posteroloph is well recognisable, transverse and connected to the hypocone on MUSM 2923, less distinct on MUSM 2922 (as it is partly eroded), and non observable on MUSM 2921 (tooth distally broken). Due to wear, the posteroloph appears enlarged mesiodistally on MUSM 2922 and 2923, a thickening likely indicating the presence of a metaloph, short, backwardly directed in its lingual part, and merged with the posteroloph. The metacone is indistinct, entirely subsumed labially within the metaloph-posteroloph complex. On MUSM 2922 and 2923, the metacone displays a long anterior arm reaching the mesostyle. All flexids are narrow, roughly transverse and parallel.

The MUSM 2924 P4 (Text-fig. 5V) is much eroded and damaged, notably in its labial part. MUSM 2924 is wider than long, with a suboval occlusal outline. The anteroloph is slightly curved. The labial part of the anteroloph is damaged, but it appears to be lower than the lingual one, and very thick in its labialmost part. Lingually, the anteroloph shows a narrowing at its junction with the labial flank of the anterior arm of the protocone. Labially, it connects to the large paracone. Although the protocone is well defined and somewhat bulbous, it displays a strong anterior arm, a short and lingually directed posterior outgrowth, and a strong but short posterior arm, linked to the protoloph (i.e., non taeniodont pattern). The latter is transverse, straight, thick and long, and extending

from a large paracone to the mure-posterior arm of the protocone junction. The mure is oblique and aligned with the crestiform hypocone via its very short anterior arm (when present), forming a long and oblique crest. That crest displays a tiny labial mesolophular spur, which appears connected to a longer mesoloph stemming from the heavily damaged mesostyle. The third transverse crest, the hypocone, its anterior arm and the posteroloph, isolate a small and oval fossette (= confluence of the distal mesoflexus with posteroflexus?), which suggests that the mesoloph might be partly fused with the posteroloph labially. As the tooth is fragmentary, the presence of a metaloph and of the labial connections of the mesoloph with a potential metaloph are not identifiable. The mesial mesoflexus and hypoflexus are very narrow, whereas the paraflexus is more mesiodistally extended.

Comparisons: The association of these three teeth is based on the fact that they have a similar size and share several dental features: brachyodonty, non-taeniodonty, thick crests and large cusp(-id)s. The MUSM 2924 P4 from TAR-21 is oval in occlusal outline, like the MUSM 1974 P4 of cf. Microsteiromys sp. from Madre de Dios (MD-67, ANTOINE et al. 2013). Moroever, it shows a similar pattern (without lingual connection between the protocone and the hypocone, a third crest lingually connected to the anterior arm of the hypocone) with the P4 identified at MD-67. Nevertheless, the dp4s from TAR-21 are very different from that attributed to Microsteiromys jacobsi (FMNH PM 54 672, WALTON 1997), in being longer and in having a pentalophodont pattern. Finally, these teeth from TAR-21 are too large and they develop far too thick loph(-id)s to be associated to the MUSM 2925 M1 or M2 also found at TAR-21 and attributed to Kichkasteiromys raimondii (see above). As MUSM 2924, P4s of some octodontoids (Galileomys and Acaremys) are molariform, tetralofodont and oval in occlusal outline. However, the lophs are thicker and the labial protoloph and the third crest appear more proximal on MUSM 2924 than on P4s of Galileomys and Acaremys. MUSM 2924 also differs from P4s of Acraemys in having a lower crown.

Caviomorpha gen. et sp. indet. 2

(Text-fig. 2F, Appendix S2)

Referred material: MUSM 3438, fragment of tooth (Text-fig. 2F).

Locality: TAR-22, Shapaja, San Martín Department, Peru. Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene. **Description and comparisons:** MUSM 3438 (Textfig. 2F) is a large fragment of tooth (upper of lower tooth ?) where three loph(-id)s are distinct. These loph(-id)s are transverse and separated by narrow flexi(-ds). MUSM 3438 is larger than MUSM 2970 from TAR-13, assigned to ?*Eoincamys* sp. Moreover, MUSM 3438 does not show any oblique loph(-id)s contrary to the latter. By its very large size, MUSM 3438 documents a taxon clearly distinct from all other taxa described in this work.

Caviomorpha gen. et sp. indet. 3

(Text-fig. 2C, Appendix S2)

Referred material: MUSM 3439, right p4 or m1? (Text-fig. 2C).

Locality: TAR-22, Shapaja, San Martín Department, Peru. Formation and age: Pozo Fm., Upper Shale Mb., most probably early Oligocene.

Description: MUSM 3439 (Text-fig. 2C) is a damaged lower tooth with digestion marks, especially on the labial crown. The trigonid is clearly narrower than the talonid, thereby suggesting that this tooth could be a p4 or an m1. MUSM 3439 is tetralophodont, with roughly transverse and parallel metalophulid I, second transverse cristid, and hypolophid, whereas the posterolophid is concave. Although the metaconid is broken here, it was probably connected to the linguomesially-labiodistally pinched crestiform protoconid, via the metalophulid I. The metaconid or its posterior arm also appears to be posteriorly linked to a small mesostylid. The complete second transverse cristid connects the protoconid to the mesostylid. Thus, with their configuration, the metaconid, metalophulid I, protoconid, second transverse cristid, and mesostylid delimit the anterofossettid. The latter is divided in its middle into two subfossettids, by a labiomesially oblique cristid joining the metalophulid I and the second transverse cristid. The ectolophid is strongly oblique (i.e., labiomesially directed) and aligned with the crestiform protoconid, but not with the transverse and long hypolophid. The massive entoconid develops strong arms: the anterior one is separated from the mesostylid, whereas the posterior one is connected to the lingual end of the posterolophid. The hypoconid displays a very short anterior arm reaching a longer cristulid from the ectolophid-hypolophid junction. As a result of this connection, the metaflexid and hypoflexid remain separated (i.e., non-taeniodont pattern). That cuspid also develops a short anterior outgrowth slightly labiomesially oblique, thus involving a wide labial opening of the "U-shaped" hypoflexid.

Comparisons: MUSM 3439 slightly exceeds in size teeth of *Eoincamys valverdei*, also found in TAR-22. Moreover, MUSM 3439 is tetralophodont, non-taeniodont and it does not show strongly oblique cristids contrary to *E. valverdei*. With its tetralophodont and non-taeniodont pattern, straight transverse cristids and oblique ectolophid, MUSM 3439 is reminiscent of the p4 of *Migraveramus latus* (PATTERSON & WOOD 1982). However, the second transverse cristid on MUSM 3439 appears more complete than in *M. latus*. By its size (second largest tooth of TAR-22, after the huge MUSM 3438) and morphology, this tooth probably documents a distinct taxon at TAR-22, provisionally identified as Caviomorpha gen. et sp. indet. 3.

4 Discussion

4.1 Shapaja localities: a cluster of highly similar faunal assemblages

In addition to be stratigraphically close (within a single 80 m-thick section), with similar conditions regarding depositional environment (low-energy fluvial stream, KLAUS et al. 2017, see Material and methods), the localities of Shapaja, Tarapoto area (TAR), have several rodent taxa in common, either at the species (TAR-21, -13, -22 and -20) or at the genus level (TAR-01 vs. other localities) or at a superior level (TAR-20 and -21). Indeed, *Eoincamys valverdei* occurs at TAR-21, -13, -22 and -20, Eoincamys parvus at TAR-21, -22 and -20, cf. Tarapotomys sp. at TAR-21, -13 and -20, Tarapotomys subandinus at TAR-21 and -22, and Caviomorpha gen. et sp. indet. 1 at TAR-20 and -21 (Table 1). This would attest to a short time interval between all the localities from the lower part of the stratigraphic section (Text-fig. 1B), and under homogeneous ecological conditions. In contrast, Eoincamys and Tarapotomys are also documented at the uppermost locality of the section, i.e. TAR-01 (Text-fig. 1B), but they are referred to species distinct from those of older Shapaja localities: Eoincamys cf. pascuali and Tarapotomys mayoensis (Table 1). Accordingly, the existence of a more significant stratigraphic gap may be suspected between TAR-01 and other Shapaja localities. The hypothesis of an ecological discrepancy is not strongly favoured, as the depositional environment is similar and other faunal elements (such as chondrichthyes, osteichthyes, crocodyliforms, and marsupials) also support a close ecological similarity between all these Shapaja assemblages.

In terms of taxonomic richness, the most diversified rodent assemblage from Shapaja is recorded at TAR-21 (seven taxa), followed by TAR-22 (six taxa), TAR-01 (five taxa), and lastly TAR-20 and TAR-13 (four taxa) (Table 1). Compared with other pre-Deseadan caviomorph assemblages, TAR-21 ranks second, well-below that of Santa Rosa (Peru, 17 taxa, FRAILEY & CAMPBELL 2004). TAR-22 and TAR-01 are equal to those of La Cantera (Argentina, VUCE-TICH et al. 2010b) and Contamana CTA-27 (Peru, BOIVIN et al. 2017b), respectively. Four taxa were found at Contamana CTA-29, like in TAR-20 and TAR-13, and less than four taxa are documented in other pre-Deseadan localities (other Eocene localities of Contamana (BOIVIN et al. 2017b) and Termas del Flaco (Chile, BERTRAND et al. 2012)). A total of 17 distinct caviomorph taxa (14 identified at the superfamilial and/or genus and/or species level) are recognised from the localities of Shapaja, with the co-occurrence of at least three extant superfamilies: Erethizontoidea, Octodontoidea and Chinchilloidea. Cavioidea are possibly represented by *Eoincamys* although here, we consider this taxon as ?Chinchilloidea (see the remark in the 'Systematic Palaeontology' section, p. 22). In addition, the superfamilial attribution of Tarapotomys (occurring at TAR-21, TAR-22, and TAR-01) is also debattable. Like *Chambiramys* from Contamana (CTA-32 and CTA-61, late Oligocene, BOIVIN et al. 2017a), but to a lesser extent, Tarapotomys displays a suite of characters recalling chinchilloids (such as: the reduction or absence of the second transverse cristid on lower molars, a tendency toward taeniodonty and tetralophodonty, and an increase in crown height), convergently acquired in octodontoids (e.g., Protadelphomys), alleged dasyproctid cavioids (*Microscleromys*), and potential chinchilloids (*Eoincamys*). The Shapaja assemblages and the Santa Rosa fauna (FRAILEY & CAMPBELL 2004) show a similar number of erethizontoids (two at Shapaja versus one at Santa Rosa) and then they constitute the only pre-Deseadan faunas recording members of this superfamily (Text-fig. 6). The Shapaja localities have also a similar number of species of *Eoincamys* (three versus two, Text-fig. 6). However, regarding octodontoids, the Shapaja localities record much less representatives of this superfamily than the Santa Rosa (three versus seven, see BOIVIN et al. 2017b regarding a possible synonymy between *Eoespina/Eosachacui*) and La Cantera localities (Text-fig. 6). Finally, at Santa Rosa, no undisputable chinchilloids have been so far **Table 1.** List of described taxa depending the studied localities of Shapaja and the comparison with the main Eocene localities of Contamana (CTA-27 and CTA-29, Peru, ANTOINE et al. 2012, BOIVIN et al. 2017b), Santa Rosa (Peru, FRAILEY & CAMPBELL 2004), and late Oligocene localities of Contamana (CTA-61 and CTA-32, Peru, BOIVIN et al. 2017a).

	TAR-20	TAR-21	TAR-13	TAR-22	TAR-01	Santa Rosa
Erethizontoidea						
Kichkasteiromys raimondii nov. gen. et sp.		Х				
Shapajamys labocensis nov. gen. et sp.					Х	
Octodontoidea						
Mayomys confluens nov. gen. et sp.					Х	
Selvamys paulus nov. gen. et sp.				Х		
Octodontoidea gen. et sp. indet.	Х					
Echimyidae						
Adelphomiynae						
Adelphomyinae gen. et sp. indet.			Х			
<i>Eobranisamys javierpradoi</i> sp. nov.						
Chinchilloidea						
Chinchilloidea gen. et sp. indet.					Х	
?Chinchilloidea						
<i>Eoincamys valverdei</i> nov. sp.	Х	Х	Х	Х		
<i>Eoincamys parvus</i> nov. sp.	Х	Х		Х		
Eoincamys cf. pascuali					Х	
?Eoincamys sp.			Х			
Eoincamys ameghinoi						Х
Eoincamys pascuali						Х
Superfamily Indeterminate						
Tarapotomys subandinus nov. gen. et sp.		Х		Х		
Tarapotomys mayoensis nov. gen. et sp.					Х	
aff. <i>Tarapotomys</i> sp.		Х				
cf. Tarapotomys sp.	Х	Х	Х			
Caviomorpha indet. 1		Х				
Caviomorpha indet. 2				Х		
Caviomorpha indet. 3				Х		

reported, whereas one clear representative (chinchilloid indet.) is documented at Shapaja (Text-figs. 2 and 6). Compared with the other pre-Deseadan localities, the only other undisputable chinchilloid is *Eoviscaccia frassinettii* from Termas del Flaco (BERTRAND et al. 2012) (Text-fig. 6). Caviomorphs from the Shapaja localities also display a well-marked disparity regarding crown height, including brachydont, mesodont, and subprotohypsodont/protohypsodont (but not euhypsodont) morphs. However, it is worth noting that the size of the specimens (only isolated teeth) is quite uniform, documenting primarily small-bodied species. Indeed, the majority of rodent teeth recovered in the Shapaja localities are small, close to the size of the sediment grains, and the largest specimens are rare and always broken (only small fragments of medium-sized teeth: MUSM 2970 and 3351 with estimated ML and MW probably between 3 and 4.5 mm), which likely results from a taphonomic bias due to size sorting. The same is true for co-occurring elements of large mammals (native ungulates), for which only fragmentary teeth are preserved. As a consequence, it may be expected that the rodent diversity as documented in localities of Shapaja is widely underestimated.



Text-fig. 6. Superfamilial richness of caviomorph rodents for the pre-Deseadan localities: Eocene localities of Contamana (Peru, ANTOINE et al. 2012, BOIVIN et al. 2017b), Santa Rosa (Peru, ?late Eocene/early Oligocene, FRAILEY & CAMPBELL 2004), Shapaja localities (Peru, early Oligocene, this work), Termas del Flaco (Chile, early Oligocene – late Oligocene, BER-TRAND et al. 2012) and La Cantera (Argentina, late early Oligocene, VUCETICH et al. 2010b). *Eoincamys* species from Santa Rosa and Shapaja localities are considered as '?Chinchilloidea' (see the remark in the 'Systematic Palaeontology' section, p. 22). 'Superfamily indet.' corresponds to taxa usually determinate at a generic and/or specific level(s), but for which, the superfamilial assignation is not clear or indeterminate. 'Caviomorpha indet.' corresponds to the taxa assigned as Caviomorpha gen. et sp. indet. Scale bar: 1000 km.

4.2 Age of the Shapaja localities: biostratigraphic implications

The localities of Shapaja are considered as being early Oligocene in age (Upper Pozo Mb.), based on their non-rodent fossil content (especially marsupials and native ungulates, see Material and methods, p. 4 and on their sedimentologic signature. The caviomorph faunas also provide some clues consistent with this age estimate for the Shapaja assemblages:

Firstly, in sharing conspicuously Eoincamys, the Shapaja caviomorph faunas strongly recall that of Santa Rosa (?late Eocene/early Oligocene, FRAILEY & CAMPBELL 2004, see ANTOINE et al. 2017), the only locality in which Eoincamys was so far reported (type-locality of *E. pascuali* and *E. ameghinoi*).

Secondly, the Shapaja localities yield species-rich and rather diversified (at higher ranks) rodent assemblages, showing neither morphological nor taxonomic affinities with the Eocene caviomorph faunas from Contamana (Lower Pozo Fm., ANTOINE et al. 2012, 2016, 2017, BOIVIN et al. 2017b). Indeed, there is no genus or species in common between the Shapaja localities and the Eocene CTA localities. Moreover, contrary to the Eocene CTA localities where only brachydont forms are recorded, the Shapaja localities yield several mesodont and subprotohypsodont/protohypsodont rodents. Additionally, no taxon from Shapaja displays a dental pattern reminiscent to that of Cachiyacuy or Canaanimys, both recorded in Eocene CTA localities (e.g., CTA-27). These two basal caviomorphs are characterised by a suite of plesiomorphic dental features (e.g., small size, brachydonty, bunolophodonty, loph(-id)s thin and transverse, tetralophodont lower molars, and pentalophodont M1-2s with a lingual connection between the third transverse crest and the metaloph), which are otherwise primarily found in the earliest Afro-Asian hystricognaths ("phiomyids" and "baluchimyines", ANTOINE et al. 2012, BARBIÈRE & MARIVAUX 2015, BOIVIN et al. 2017b). Although the teeth of Eosallamys are larger than those of Cachiyacuy and Canaanimys, and display thicker loph(-id)s, this taxon from Santa Rosa is the only taxon showing pentalophodont M1-2s with some specimens having a lingual connection between the third transverse crest and the metaloph (FRAILEY & CAMPBELL 2004). The total absence of Cachiyacuy-, Canaanimys- or Eosallamys-like dental morphotypes in Shapaja localities indicates that they widely postdate the Eocene CTA localities and, to a lesser extent, that of Santa Rosa.

Thirdly, the Shapaja localities have no taxon in common with other Oligocene caviomorph faunas (i.e.,

Termas del Flaco, La Cantera, and Deseadan assemblages). They also include species to some extent more primitive, at least with respect to Deseadan faunas, as exemplified by the octodontoid Mayomys found at TAR-01. The latter taxon displays characters typical of octodontoids but somewhat less advanced over Deseadan octodontoid representatives, such as Platypittamys, Galileomys, or Deseadomys (see comparisons in the Systematic Palaeontology section, pp. 18–20). At last, compared with Deseadan and Miocene faunas from Amazonia, the new localities of Shapaja yield rodents primarily mesodont or subprotohypsodont/ protohypsodont. Caviomorph teeth comparable in crown height are found at the Deseadan localities CTA-61 and CTA-32 (BOIVIN et al. 2017a). Yet, higher-crowned teeth (attributed to Scleromys praecursor) also occur at CTA-61. Some Miocene taxa (e.g., Drytomomys or Potamarchus BURMEISTER, 1885, CAN-DELA & NASIF 2006, ANTOINE et al. 2013, 2016a, TEJADA-LARA et al. 2015, KERBER et al. 2016) have a higher crown than S. praecursor. The first euhypsodont taxa in Amazonia are documented much later, i.e., during the middle Miocene (e.g., Neoepiblema AMEGHINO, 1889 and caviids, ANTOINE et al. 2013, 2016a, TEJADA-LARA et al. 2015, KERBER et al. 2017).

To sum up, the Shapaja localities are close in age to Santa Rosa but they seem to postdate the latter locality. Pending chemostratigraphic and/or radioisotopic datings and based on vertebrate biostratigraphy, the Shapaja assemblages are considered as early Oligocene in age. The range of *Eoincamys* is therefore expanded, with a FAD recorded at Santa Rosa and a LAD at Shapaja (TAR-01). Accordingly, the unidentified chinchilloid from TAR-01 likely represents one of the undisputable oldest members of that superfamily, in addition of *E. frassinettii* from Termas del Flaco (Chile, Tinguirirican, early Oligocene, Wyss et al. 1993, FLYNN et al. 2003, BERTRAND et al. 2012) and a potential chinchilloid, ?Chinchilloidea gen. et sp. indet. 2, from La Cantera (Argentina, early Oligocene, VUCETICH et al. 2010b). Moreover, this discovery from Shapaja considerably broadens northward the geographical range of that superfamily for the early Oligocene epoch (Text-fig. 6).

5 Conclusions

The rodent assemblages of the Shapaja localities represent an important addition to the knowledge of the early Oligocene caviomorph record in northern South America, so far only potentially documented by Santa

Rosa regarding rodents. These new caviomorph assemblages are characterised by 17 taxa documenting at least three caviomorph superfamilies. Among them, eight new taxa are described: the erethizontoids Kichkasteiromys raimondii nov. gen. et sp. and Shapajamys labocensis nov. gen. et sp., the octodontoids Selvamys *paulus* nov. gen. et sp. and *Mayomys confluens* nov. gen. et sp., the ?chinchilloids Eoincamys valverdei nov. sp. and *E. parvus* nov. sp., and caviomorphs of uncertain affinities, such as Tarapotomys subandinus nov. gen. et sp. and T. mayoensis nov. gen. et sp. The different rodent assemblages of Shapaja have very similar taxonomic contents. They constitute a diversified set in terms of taxonomic richness and secondary morphological disparity. With the conspicuous occurrence of several species of *Eoincamys* (E. valverdei and E. par*vus*), the caviomorph faunas from Shapaja are strongly comparable to that of Santa Rosa (Peru, ?late Eocene/ early Oligocene). Conversely, they have no genus or species in common with the Contamana Eocene localities or other Oligocene assemblages at the South American scale (Termas del Flaco, La Cantera, and Deseadan faunas). Such biostratigraphic clues suggest that the Shapaja and Santa Rosa localities are close in age, which is further supported by other faunal elements (marsupials and native ungulates) consistently pointing to an early Oligocene age, at least for the former. According to the evolutive degree of Shapaja caviomorphs, the Shapaja localities are younger than Santa Rosa. *Eoincamys* then extends from Santa Rosa to Shapaja (TAR-01). The undisputable chinchilloid recorded at TAR-01 represents one of the oldest members of that superfamily.

A cladistic assessment of the dental evidence available is in progress in order to formalise the phylogenetic position of these early taxa within a high level caviomorph phylogenetic framework. Additionally, it would further our understanding of the emergence of the four extant superfamilies, the timing of their appearance, their morphological evolution, and their historical biogeography in South America.

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Appendix S1

Palaeogene and Miocene caviomorph taxa used for comparisons in this study

Primary references	Antoine et al., 2012; Boivin et al., 2017a	Antoine et al., 2012; Boivin et al., 2017a	Antoine et al., 2012; Boivin et al., 2017a	Boivin et al., 2017a	Boivin et al., 2017a	Vucetich et al., 2015	Vucetich et al., 2015	Boivin et al., 2017b	Boivin et al., 2017b		Frailey & Campbell, 2004	Vucetich et al., 2010a	Vucetich et al., 2010a	Vucetich et al., 2010a	Patterson & Wood, 1982	Hoffstetter & Lavocat, 1970; Lavocat, 1976; Patterson & Wood, 1982	Shockey et al., 2009	Vucetich et al., 1993a	Patterson & Pascual, 1968	Wood, 1949; Wood & Patterson, 1959				
Observed material (original or cast)	MUSM (original)	MUSM (original)	MUSM (original)	MUSM (original)	MUSM (original)	UM (cast)	UM (cast)	MUSM (original)	MUSM (original)		INGEMMET (holotype)	UM (cast)	UM (cast)	UM (cast)		MNHN-Bol, MNHN & HNHN & UM (original)	MUSM (original)	MLP (cast)	MLP (original)	UM (cast)				
Age	late middle Eocene	late middle Eocene	late middle Eocene	late middle Eocene	late middle Eocene	late early Oligocene – late Oligocene	late early Oligocene – late Oligocene	late Oligocene	late Oligocene		?late Eocene / early Oligocene	Plate Eocene / early Oligocene	?late Eocene / early Oligocene	Plate Eocene / early Oligocene	?late Eocene / early Oligocene	late early Oligocene	late early Oligocene	late early Oligocene	late early Oligocene – late Oligocene	late early Oligocene – late Oligocene	late Oligocene	late early Oligocene – late Oligocene	late early Oligocene – late Oligocene	late Oligocene
Locality and/or Formation (Fm.)	Contamana CTA-27 (Pozo Fm.), Peru	Contamana CTA-27 (Pozo Fm.), Peru	Contamana CTA-27 (Pozo Fm.), Peru	Contamana CTA-47 (Pozo Fm.), Peru	Contamana CTA-29 (Pozo Fm.), Peru	Cabeza Blanca (Sarmiento Fm.), Argentina	Cabeza Blanca (Sarmiento Fm.), Argentina	Contamana CTA-32 (Chambira Fm.), Peru	Contamana CTA-61 (Chambira Fm.), Peru		Santa Rosa (Yahuarango Fm.), Peru	La Cantera (Sarmiento Fm.), Argentina	La Cantera (Sarmiento Fm.), Argentina	La Cantera (Sarmiento Fm.), Argentina	Salla (Salla Beds), Bolivia	Salla (Salla Beds), Bolivia	Cerro Pan de Azúcar (Moquega Fm.), Peru	Fazenda Santa Fé (Tremembé Fm.), Brazil	Laguna de los Machos (Sarmiento Fm.), Argentina	Scaritt Pocket (Sarmiento Fm.), Argentina				
Species	C. contamanensis	C. kummeli	C. maquiensis	Canaanimys sp.	P. ucayaliensis	L. notuca	L. zeffiae	C. shipiborum	C. sylvaticus		E. paulacoutoi	$E.\ simpsoni$	E. woodi	E. lavocati	E. almeidacomposi	D.verai	V. mazzionii	?Vallehermosomys merlinae	M. beatus	S. pascuali	S. quispea	P. paulista	X. obliquus	P. brachyodon
Genre	Cachiyacuy		Canaanimys		Pozomys	Llitun	Leucokephalos	Chambiramys		Octodontoidea	Eosallamys		Eoespina	Eosachacui	Eodelphomys	Draconomys	Vallehermosomys	?Vallehermosomys	Migraveramus	Sallamys		Paulacoutomys	Xylechimys	Platypittamys

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Wood & Patterson, 1959	Wood & Patterson, 1959; Vucetich et al., 2015	Boivin et al., 2017b	Vucetich et al., 2015; Arnal et al. 2017	Ameghino, 1902; Vucetich et al., 2010b; Arnal et al. 2017	Ameghino, 1887; Kramarz, 2004; Arnal et al. 2017	Ameghino, 1887; Kramarz, 2004; Arnal et al. 2017	Ameghino, 1887; Arnal et al. 2017	Vucetich et al., 2015	Vucetich & Kramarz, 2003; Vucetich et al., 2010b	Kramarz, 2004	Vucetich et al., 2015	Ameghino, 1902; Vucetich et al., 2010b	Ameghino, 1902; Vucetich et al., 2010b	Vucetich et al., 1993b	Arnal et al., 2014	Vucetich & Verzi, 1996; Vucetich et al., 2010b	Ameghino, 1887; Arnal & Vucetich, 2015	Vucetich & Verzi, 1991; Vucetich et al., 2010b	Ameghino, 1902; Vucetich et al., 2010b	Arnal & Kramarz, 2011	Vucetich et al., 2010b	Bordas, 1939; Arnal & Vucetich, 2015	Arnal & Vucetich, 2015
MHNH (original)	UM (cast)	MUSM (original)	UM (cast)		MLP (original)	MACN & MLP (original)	MLP (original)	UM (cast)	MACN & MLP (original)	MACN (original)	UM (cast)	MACN (original)		MLP (original)	MACN (original)	MACN (original)	MACN & MLP (original)	MLP (original & cast)	MACN (original)	MACN (original)		MACN (original)	MACN (original)
late early Oligocene – late Oligocene	late early Oligocene – late Oligocene	late Oligocene	late early Oligocene – late Oligocene	early Miocene – late early Miocene	early Miocene – middle Miocene	late early Miocene – late middle Miocene	late early Miocene	late early Oligocene – late Oligocene	early Miocene	late early Miocene	late early Oligocene – late Oligocene	early Miocene	early Miocene	middle Miocene	early Miocene	early Miocene	early Miocene	early Miocene	early Miocene	early Miocene	early Miocene	early Miocene	early Miocene
Cabeza Blanca (Sarmiento Fm.) and La Flecha, Argentina	Cabeza Blanca (Sarmiento Fm.), Argentina	Contamana CTA-32 (Chambira Fm.), Peru	Cabeza Blanca (Sarmiento Fm.), Argentina	Gran Barranca (also collected by Ameghino; Sarmiento Fm.) and Santa Cruz Fm., Argentina	Pinturas Fm. (for the list of localities, see Kramarz, 2004), Santa Cruz Fm., and Collon Cura Fm., Argentina; La Venta (Villavieja Fm.), Colombia	Santa Cruz Fm. and Collon Cura Fm., Argentina; Quebrada Honda (unnamed Fm., Chile	Santa Cruz Fm., Argentina	Cabeza Blanca (Sarmiento Fm.), Argentina	Bryn Gwyn, Gran Barranca (Sarmiento Fm.), Argentina	Pinturas Fm. (for the list of localities, see Kramarz, 2004), Argentina	Cabeza Blanca (Sarmiento Fm.), Argentina	Gran Barranca (also collected by Ameghino; Sarmiento Fm.), Argentina	Gran Barranca (also collected by Ameghino; Sarmiento Fm.), Argentina	Localities 1 and 5 of the Cañadon del Tordillo (Collón Cura Fm.), Argentina	Bryn Gwyn (Sarmiento Fm.), Argentina	Bryn Gwyn and Gran Barranca (Sarmiento Fm.), Paso Córdoba (Chinchinales Fm.) and Cerro Bandera (Cerro Bandera Fm.), Argentina	Sarmiento Fm., Pinturas Fm. and Santa Cruz Fm. (for the list of localities, see Arnal and Vucetich, 2015), Argentina	Paso Córdoba (Chinchinales Fm.) and Bryn Gwyn (Sarmiento Fm.), Argentina	Gran Barranca, Bryn Gwyn?, Sacanana (also collected by Ameghino; Sarmiento Fm.), Argentina	Pampa de Gran Gan (Sarmiento Fm.), Argentina	Gran Barranca (Sarmiento Fm.), Argentina	Bryn Gwyn (Sarmiento Fm.), Argentina	Santa Cruz, River Cliffs, La Cueva, Killik Aik (Santa Cruz Fm.), Argentina
D. arambourgi	E. loomisi	L. minutus	A. leucothea	A. gracilis	A. minutissimus	A. minutus	A. constans	G. baios	G. antelucanus	G. eurygnathus	?Protacaremys adilos	P. prior	P. avunculus	P. denisae	D. ruigomezi	C. lucasi	A. murinus	W. esteparius	P. priscus	P. cf. priscus	P. sp. 1	A. preminutus	P. kramarzi
Deseadomys	Ethelomys	Loretomys	Acarechimys					Galileomys			?Protacaremys	Protacaremys			Dudumus	Caviocricetus	Acaremys	Willidewu	Prospaniomys			'Acaremys'	Pseudoacaremys

Kramarz, 2001a, 2004; Kramarz et al., 2010	Ameghino, 1887; Kramarz, 2004	Patterson & Pascual, 1968; Vucetich et al., 2010b	Ameghino, 1902; Vucetich & Bond, 1984; Vucetich et al., 1992, 2010b; Vucetich & Verzi, 1994	Vucetich & Vieytes, 2006	Ameghino, 1887; Kramarz, 2004; Kay et al., 2012	Ameghino, 1887, 1894; Flynn et al., 2002	Ameghino, 1887	Ameghino, 1887; Arnal & Vucetich, 2011; Arnal & Pérez, 2013; Flynn et al., 2002	Arnal & Pérez 2013	Walton, 1990, 1997	Croft et al., 2011		Frailey & Campbell, 2004	Ameghino, 1903; Wood & Patterson, 1959	Wood & Patterson, 1959	Candela, 2000	Boivin et al., 2017b	Boivin et al., 2017b	Ameghino, 1902; Candela, 2000; Candela & Vucetich, 2002; Vucetich et al., 2010b	Ameghino, 1902; Candela, 2000; Candela & Vucetich, 2002; Vucetich et al., 2010b	Ameghino, 1887; Candela, 2000; Candela et al., 2012; Kay et al., 2012	Ameghino, 1887; Candela, 2000; Flynn et al., 2002; Candela et al., 2012; Kay et al., 2012
MACN (original)	MACN & MLP (original)	MLP (original)	MLP (original)	MLP (original)	MACN & MLP (original)	MACN & MLP (original)	MACN (original)	MACN & MLP (original)					INGEMMET (holotype)	MACN & MHNH (original)	MHNH (original)	UM (original)	MUSM (original)	MUSM (original)	MACN (original)	MACN & MLP (original)	MACN & MLP (original)	MACN & MLP (original)
early Miocene	early Miocene	early Miocene	early Miocene	middle Miocene	late early Miocene	late early Miocene	late early Miocene	late early Miocene	middle Miocene	late middle Miocene	late middle Miocene		Plate Eocene / early Oligocene	late early Oligocene – late Oligocene	late early Oligocene – late Oligocene	late early Oligocene – late Oligocene	late Oligocene	late Oligocene	early Miocene	early Miocene	early Miocene	early Miocene
Gran Barranca (Sarmiento Fm.) and Pinturas Fm. (for the list of localities, see Kramarz, 2001, 2004), Argentina	Lago Cardiel and Gobernador Gregores (Pinturas Fm.) and Santa Cruz Fm., Argentina	Gran Brranca (Sarmiento Fm.), Argentina	Gran Brranca, Bryn Gwyn, Sacanana (Sarmiento Fm.), Argentina	Estancia Cerro San Antonio (Collón Cura Fm.), Argentina	Pinturas Fm. (for the list of localities, see Kramarz, 2004) and Santa Cruz Fm., Argentina	Santa Cruz Fm., Argentina; Pampa Castillo (unnamed Fm.), Chile	Santa Cruz Fm., Argentina	Santa Cruz Fm., Argentina; Pampa Castillo (unnamed Fm.), Chile	El Petiso, Argentina	La Venta (Villavieja Fm.), Colombia	Quebrada Honda (unnamed Fm.), Bolivia		Santa Rosa (Yahuarango Fm.), Peru	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	La Flecha (Sarmiento Fm.), Argentina	Salla (Salla Beds), Bolivia	Contamana CTA-32 (Chambira Fm.), Peru	Contamana CTA-61 (Chambira Fm.), Peru	Bryn Gwyn and Grand Barranca (also collected by Ameghino, Sarmiento Fm.), Argentina	Gran Barranca (also collected by Ameghino, Sarmiento Fm.), Argentina	Santa Cruz Fm., Argentina	Santa Cruz Fm., Argentina; Pampa Castillo (unnamed Fm.), Chile
P. bowni	A. candidus	P. fissus	P. latus	P. koenigswaldi	S. modestus	S. riparius	S. regularis	S. principalis	S. petisensis	R. longidens	Q. potosiensis		E. wigmorei	P. medianus	P. asmodeophilus	?Protosteiromys sp.	P. amazonensis	P. newelli	H. axiculus	H. nectus	S. detentus	S. duplicatus
Prostichomys	Adelphomys	Paradelphomys	Protadelphomys	Plesiacarechimys	Spaniomys		Stichomys	Sciamys		Ricardomys	Quebradahondomys	Erethizontoidea	Eopululo	Protosteiromys		? Protosteiromys	Palaeosteiromys	Plesiosteiromys	Hypsosteiromys		Steiromys	

Drytomomys	D. aequatorialis	near the hacienda of Señor Carrasco (near Nabon), Equador; La Venta (Villavieja Fm.), Colombia	late middle Miocene		Anthony, 1922; Fields, 1957; Walton, 1997; Candela & Nasif, 2006
	D. typicus	Ituzaingo Fm., Argentina	late Miocene		Ameghino, 1889; Candela & Nasif, 2006
?Chinchilloidea					
Eoincamys	E. ameghinoi	Santa Rosa (Yahuarango Fm.), Peru	Plate Eocene / early Oligocene	INGEMMET (holotype)	Frailey & Campbell, 2004
	E. pascuali	Santa Rosa (Yahuarango Fm.), Peru	?late Eocene / early Oligocene	INGEMMET (holotype)	Frailey & Campbell, 2004
Cavioidea					
Eobranisamys	E. javierpradoi	Contamana CTA-27 (Pozo Fm.), Peru	late middle Eocene	MUSM (original)	Antoine et al., 2012; Boivin et al., 2017a
	E. romeropittmanae	Santa Rosa (Yahuarango Fm.), Peru	Plate Eocene / early Oligocene	INGEMMET (holotype)	Frailey & Campbell, 2004
	E. riverai	Santa Rosa (Yahuarango Fm.), Peru	Plate Eocene / early Oligocene	INGEMMET (holotype)	Frailey & Campbell, 2004
Australoprocta	A. fleagei	Bryn Gwyn, Sacanana (Sarmineto Fm.) and Paso Córdoba (Chinchinales Fm.), Argentina	early Miocene		Kramarz, 1998; Vucetich et al., 2010b
Neoreomys	N. pinturensis	Gran Barranca (Sarmiento Fm.) and Carmen Lower and Potezuelo Sumich Norte (Pinturas Fm.), Argentina	early Miocene		Kramarz, 2006; Kramarz et al., 2010
	N. australis	Santa Cruz Fm. and Pinturas Fm. (for the list of localities, see Kramarz 2006), Argentina: Pampa Castillo (unnamed Fm.), Chile	late early Miocene	MACN & MLP (original)	Ameghino, 1887; Kramarz, 2006; Flynn et al., 2002; Candela et al., 2012; Kay et al., 2012
Microscleromys	M. paradoxalis	La Venta (Villavieja Fm.), Colombia	late middle Miocene		Walton, 1990, 1997
	M. cribriphilus	La Venta (Villavieja Fm.), Colombia	late middle Miocene		Walton, 1990, 1997
Incertae sedis extin-	ct superfamily				
Cephalomys	C. arcidens	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	late early Oligocene – late Oligocene	MNHN (original)	Ameghino, 1897; Wood & Patterson, 1959
	C. plexus	Cabeza Blanca and La Flecha (Sarmiento Fm.), Argentina	late early Oligocene – late Oligocene		Ameghino, 1897; Wood & Patterson, 1959
	C. ceciae	Cabeza Blanca (Sarmiento Fm.), Argentina	late early Oligocene – late Oligocene	UM (cast)	Vucetich et al., 2015
	C. bolivianus	Salla (Salla Beds), Bolivia	late early Oligocene – late Oligocene	MNHN-Bol, MNHN & UM (original)	Lavocat, 1976; Patterson & Wood, 1982
Soriamys	S. gaimanensis	Bryn Gwyn (Sarmiento Fm.), Argentina	early Miocene		Kramarz, 2001 <i>c</i> ; Vucetich et al., 2010b
	S. ganganensis	Pampa de Gan Gan/Sacanana (Sarmiento Fm.), Argentina	early Miocene		Kramarz, 2001c; Vucetich et al., 2010b
Fm., Formation; INC	GEMMET , Instituto G	ieológico Minero y Metalúrgico, Lima; MACN, Mu	seo Argentino de Ciencias Naturales, B	uenos Aires; MLP, Museo de	: Ciencias Naturales de La Plata;

MUSM, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima; MNHN-Bol, Museo Nacional de Historia Natural, La Paz, Bolivia; MNHN, Musée National d'Histoire Naturelle, Paris, UM, Université de Montpellier.

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Appendix S2 Dental measurements (in millimetres) of rodent material from TAR-21, TAR-13, TAR-22, TAR-01 and TAR-20 (early Oligocene, Peruvian Amazonia)

Collection number	Locality	Taxon	Locus	ML	MW	Hg	нь	HIg	HIP
MUSM 2909	TAR 20	Caviomorpha indet. 1	left dp4						
MUSM 3327	TAR 20	cf. Tarapotomys sp.	left m1	1.81	1.85	1.06	1.03	0.58	0.57
MUSM 3328	TAR 20	cf. Tarapotomys sp.	right m1	1.89	1.81	0.90	0.82	0.48	0.43
MUSM 3329	TAR 20	cf. Tarapotomys sp.	left m2	1.90	1.76		1.42		0.75
MUSM 3330	TAR 20	cf. Tarapotomys sp.	left m3	1.80					
MUSM 3331	TAR 20	cf. Tarapotomys sp.	right dP4	1.80	1.44				
MUSM 3332	TAR 20	cf. Tarapotomys sp.	right M1	1.58			0.75		
MUSM 2910	TAR 20	cf. Tarapotomys sp.	right M2			1.33			
MUSM 3333	TAR 20	cf. Tarapotomys sp.	right M2	1.98	2.01	1.66		0.84	
MUSM 2911	TAR 20	cf. Tarapotomys sp.	left M3	1.84	2.15	1.42	0.73	0.77	0.39
MUSM 3334	TAR 20	Eoincamys valverdei sp. nov.	right P4	1.66	1.93	1.38	0.54	0.83	0.32
MUSM 3335	TAR 20	<i>Eoincamys valverdei</i> sp. nov.	left upper molar						
MUSM 3336	TAR 20	<i>Eoincamys valverdei</i> sp. nov.	left M1	2.16	2.52	1.86	1.23	0.86	0.57
MUSM 3337	TAR 20	Eoincamys parvus sp. nov.	right P4			1.01			
MUSM 2913	TAR 21	Caviomorpha indet. 1	left dp4	2.57		0.63		0.25	
MUSM 2914	TAR 21	Caviomorpha indet. 1	left dp4						
MUSM 2915	TAR 21	Caviomorpha indet. 1	left dp4		1.37	0.72	0.88		
MUSM 2916	TAR 21	Caviomorpha indet. 1	left dp4		1.58		0.65		
MUSM 2917	TAR 21	Caviomorpha indet. 1	left dp4						
MUSM 2918	TAR 21	Caviomorpha indet. 1	right dp4						
MUSM 2919	TAR 21	Caviomorpha indet. 1	right dp4						
MUSM 2920	TAR 21	Caviomorpha indet. 1	right dp4		1.55				
MUSM 2921	TAR 21	Caviomorpha indet. 1	left dP4						
MUSM 2922	TAR 21	Caviomorpha indet. 1	left dP4	1.83	1.70				
MUSM 2923	TAR 21	Caviomorpha indet. 1	right dP4	2.00	1.88	0.64	0.97	0.32	0.48
MUSM 2924	TAR 21	Caviomorpha indet. 1	left P4	1.74	2.11		1.38		0.79
MUSM 2925	TAR 21	<i>Kichkasteiromys raimondii</i> gen. et sp. nov.	right M1 or M2	1.75	2.12	0.94		0.53	
MUSM 2927	TAR 21	cf. Tarapotomys sp.	left m1	1.85	1.82	1.01	1.31	0.55	0.71
MUSM 2926	TAR 21	cf. Tarapotomys sp.	left m2	1.84	1.78	0.97	1.15	0.53	0.62
MUSM 2928	TAR 21	cf. Tarapotomys sp.	left m2	1.84	1.75	0.69	0.88	0.38	0.48
MUSM 2929	TAR 21	Tarapotomys subandinus gen. et sp. nov.	right lower molar	1.42	1.11				
MUSM 2930	TAR 21	Tarapotomys subandinus gen. et sp. nov.	right m2	1.79	1.59		0.79		0.44
MUSM 2931	TAR 21	Tarapotomys subandinus gen. et sp. nov.	right m3	1.60	1.51	0.89	0.89	0.55	0.55
MUSM 2932	TAR 21	Tarapotomys subandinus gen. et sp. nov.	left dP4			0.93			
MUSM 2933	TAR 21	Tarapotomys subandinus gen. et sp. nov.	left dP4	1.46	1.30	0.56	0.29	0.38	0.20
MUSM 2934	TAR 21	Tarapotomys subandinus gen. et sp. nov.	right ?P4						
MUSM 2935	TAR 21	Tarapotomys subandinus gen. et sp. nov.	right P4	1.29	1.49	1.24	0.79	0.96	0.61
MUSM 2936	TAR 21	Tarapotomys subandinus gen. et sp. nov.	right P4	1.32	1.64	1.17	0.41	0.88	0.31
MUSM 3339	TAR 21	Tarapotomys subandinus gen. et sp. nov.	left upper molar						
MUSM 2937	TAR 21	Tarapotomys subandinus gen. et sp. nov.	right M1	1.37	1.58	1.44	0.61	1.05	0.45
MUSM 2938	TAR 21	Tarapotomys subandinus gen. et sp. nov.	left M2				0.57		
MUSM 2939	TAR 21	Tarapotomys subandinus gen. et sp. nov.	right M2	1.64	1.72	1.37	0.75	0.84	0.45
MUSM 2940	TAR 21	aff. <i>Tarapotomys</i> sp.	right upper molar	1.55			0.56		0.36
MUSM 2952	TAR 21	Eoincamys valverdei sp. nov.	right p4 or m1	2.24	1.97	0.99	0.99	0.44	0.44
MUSM 2941	TAR 21	<i>Eoincamys valverdei</i> sp. nov.	left lower molar						
MUSM 2942	TAR 21	<i>Eoincamys valverdei</i> sp. nov.	right lower molar						
MUSM 2944	TAR 21	<i>Eoincamys valverdei</i> sp. nov.	left upper molar				1.21		
MUSM 2945	TAR 21	<i>Eoincamys valverdei</i> sp. nov.	right upper molar	2.18		0.93		0.43	
MUSM 2946	TAR 21	<i>Eoincamys valverdei</i> sp. nov.	right upper molar	2.01					

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MUSM 2947	TAR 21	<i>Eoincamys valverdei</i> sp. nov.	right M1	2.07	2.47	2.15	1.04	1.04	0.50
MUSM 2948	TAR 21	Eoincamys valverdei sp. nov.	right M1	2.09	2.3/	1.82	0.92	0.8/	0.44
MUSM 2943	TAR 21	<i>Eoincamys valverdei</i> sp. nov.	lett ?M2	1.95		1.80		0.92	
MUSN 2949	TAR 21	<i>Eoincamys parvus</i> sp. nov.	left upper molar	1 5 1	1.46	1.10		0.07	
MUSM 2950	TAR 21	<i>Eoincamys parvus</i> sp. nov.		1.51	1.46	1.4/	0.46	0.97	0.20
MUSM 2951	TAR 21	<i>Eoincamys parvus</i> sp. nov.	right M1	1.55	1.61	1.34	0.46	0.8/	0.30
MUSM 2960	TAR 22	Selvamys paulus gen. et sp. nov.	right M2	1.22	1.44				
MUSM 3340	TAR 22	Selvamys paulus gen. et sp. nov.	right MT or Z	1.18	1.29	1 7 1	0.94	1.20	0.50
MUSM 2961	TAR 22	<i>Tarapotomys subanainus</i> gen. et sp. nov.	right P4	1.43	1.6/	1./1	0.84	1.20	0.59
MUSM 3341	TAR 22	Eoincamys valveraei sp. nov.	left upper molar	1.59	1.93	0.98	0.80	0.62	0.51
MUSM 3342	TAR 22	<i>Eoincamys valverdei</i> sp. nov.	left M3	1.9/	2.16	2.40	1.11	1.22	0.56
MUSM 2966	TAR 22	<i>Eoincamys parvus</i> sp. nov.	right dp4	2.00	1.21		0.57		0.20
MUSM 3343	TAR 22	<i>Eoincamys parvus</i> sp. nov.	left dp4	2.08	1.31		0.57		0.28
MUSM 3344	TAR 22	<i>Eoincamys parvus</i> sp. nov.	right lower molar			0.0/	1.21		
MUSM 3345	TAR 22	<i>Eoincamys parvus</i> sp. nov.	left ml	1.0.(1.(2	0.94	1.31		
MUSM 3346	TAR 22	<i>Eoincamys parvus</i> sp. nov.	left ?m3	1.86	1.63	1.05	1.00	0.7/	0.50
MUSM 2962	TAR 22	<i>Eoincamys parvus</i> sp. nov.	right m3	1.69	1.42	1.25	1.00	0.74	0.59
MUSM 2963	TAR 22	<i>Eoincamys parvus</i> sp. nov.	right P4	1.53	1.86		0.72		0.47
MUSM 334/	TAR 22	<i>Eoincamys parvus</i> sp. nov.	right P4				1.07		2.67
MUSM 2964	TAR 22	<i>Eoincamys parvus</i> sp. nov.	left upper molar	1.64	1.13		1.07		0.65
MUSM 3348	TAR 22	<i>Eoincamys parvus</i> sp. nov.	right upper molar	1.72	1.74		0.72		0.42
MUSM 3349	TAR 22	<i>Eoincamys parvus</i> sp. nov.	left M2	1.74	1.85	1.10	0.5.(0.77	0.00
MUSM 3350	TAR 22	<i>Eoincamys parvus</i> sp. nov.	left M3	1.42	1.61	1.10	0.54	0.77	0.38
MUSM 2965	TAR 22	Eoincamys parvus sp. nov.	left M3	1.56	1.77	1.44	0.81	0.93	0.52
MUSM 3351	TAR 22	Caviomorpha indet. 2	right m1 or 2 ?	3.73	3.77	2.61	1.50	0.70	
MUSM 3352	TAR 22	Caviomorpha indet. 3	right p4 or m1?	2.24	2.14	1.02	1.50	0.46	0.67
MUSM 2967	TAR 13	ct. Tarapotomys sp.	left m1	1.91	2.31	0.78	0.89	0.41	0.47
MUSM 2968	TAR 13	Adelphomyinae indet.	right lower molar	1.78	2.18	1.49		0.50	2 (2
MUSM 2969	TAR 13	<i>Eoincamys valverdei</i> sp. nov.	right M3	1.93	1.97	1.95	0.95	1.01	0.49
MUSM 29/0	TAR 13	<i>Eoincamys</i> sp.	left upper molar	2.56			0.70		
MUSM 3341	TAR 01	Shapajamys labocensis gen. et sp. nov.	left lower molar	2.56	2.58	0.81	0.72	0.32	0.28
MUSM 29/1	TAR 01	Shapajamys labocensis gen. et sp. nov.	left dp4	2.83	1.82	1.11	1.23	0.39	0.44
MUSM 29/2	TAR 01	Shapajamys labocensis gen. et sp. nov.	right ?p4	2.15	2.15	1.28	1.66	0.59	0.77
MUSM 2973	TAR 01	Shapajamys labocensis gen. et sp. nov.	left m1	2.33	2.21	1.16	1.24	0.50	0.53
MUSM 2974	TAR 01	Shapajamys labocensis gen. et sp. nov.	right m l			1.05			
MUSM 2975	TAR 01	<i>Shapajamys labocensis</i> gen. et sp. nov.	right m1		2.19	0.86	1.05		
MUSM 2981	TAR 01	Shapajamys labocensis gen. et sp. nov.	left m2	2.53	2.47	1.22	1.31	0.48	0.52
MUSM 2976	TAR 01	Shapajamys labocensis gen. et sp. nov.	left m2	2.72	2.40	1.00	0.83	0.37	0.30
MUSM 2977	TAR 01	Shapajamys labocensis gen. et sp. nov.	right m3	2.73	2.48	1.28	1.61	0.47	0.59
MUSM 2978	TAR 01	Shapajamys labocensis gen. et sp. nov.	right m2						
MUSM 2979	TAR 01	Shapajamys labocensis gen. et sp. nov.	right m2	- /-					
MUSM 2980	TAR 01	Shapajamys labocensis gen. et sp. nov.	right m2	2.47	1.50	1.12		0.46	0.0-
MUSM 2982	TAR 01	Shapajamys labocensis gen. et sp. nov.	lett dP4	1.10	2.22	1.35	0.94	1.23	0.85
MUSM 2983	TAR 01	Shapajamys labocensis gen. et sp. nov.	left dP4	2.46	2.02	1.14	0.79	0.47	0.32
MUSM 2984	TAR 01	Shapajamys labocensis gen. et sp. nov.	right P4	2.05	2.33	1.42		0.69	
MUSM 2985	TAR 01	Shapajamys labocensis gen. et sp. nov.	left upper molar	1.73	1.53				
MUSM 2986	TAR 01	Shapajamys labocensis gen. et sp. nov.	left upper molar	1.37	2.27	1.54		1.12	
MUSM 2987	TAR 01	Shapajamys labocensis gen. et sp. nov.	right upper molar	2.22	1.88	1.46		0.66	
MUSM 2988	TAR 01	Shapajamys labocensis gen. et sp. nov.	right upper molar	2.15	2.29				
MUSM 2989	TAR 01	Shapajamys labocensis gen. et sp. nov.	right upper molar	1.82	1.95	1.40	1.09	0.77	0.60
MUSM 2990	TAR 01	Shapajamys labocensis gen. et sp. nov.	right upper molar	1.09					
MUSM 2991	TAR 01	Shapajamys labocensis gen. et sp. nov.	right upper molar			1.88			
MUSM 2992	TAR 01	Shapajamys labocensis gen. et sp. nov.	right upper molar	2.18	2.58	0.95		0.44	
MUSM 2993	TAR 01	Shapajamys labocensis gen. et sp. nov.	left M1	2.29				ļļ	
			1 6	- / -					
MUSM 2994	TAR 01	Shapajamys labocensis gen. et sp. nov.	left M1	2.48					

MUSM 2996	TAR 01	Shapajamys labocensis gen, et sp. nov.	left M3	2.45	2.85	1.99	1.26	0.81	0.51
MUSM 2997	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4	1.46	1.07	1.,,,	1120	0.01	0.91
MUSM 2998	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4	1110	1.07				
MUSM 2999	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4						
MUSM 3000	TAR 01	Mayomys confluens gen et sp. nov	left dp4	1.66	1 16				
MUSM 3001	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4	1.78	1.25	0.76	1.01	0.43	0.57
MUSM 3002	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4	1.80	1.33	0.77	0.66	0.43	0.37
MUSM 3003	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4	1.27	1.18	0.97	0.00	0.76	0.07
MUSM 3004	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4	1.29	1.14	0.79	0.94	0.61	0.73
MUSM 3005	TAR 01	Mayomys confluens gen. et sp. nov.	left dp4	1.72	1.20	,			
MUSM 3006	TAR 01	Mayomys confluens gen. et sp. nov.	left dp4	1.72	1.19	0.74	0.95	0.43	0.55
MUSM 3007	TAR 01	Mayomys confluens gen. et sp. nov.	left dp4	1.63	1.19	0.71		0.43	
MUSM 3008	TAR 01	Mayomys confluens gen. et sp. nov.	left dp4	1.71		0.59		0.34	
MUSM 3009	TAR 01	Mayomys confluens gen. et sp. nov.	left dp4	1.22					
MUSM 3010	TAR 01	Mayomys confluens gen. et sp. nov.	left dp4	1.77					
MUSM 3011	TAR 01	Mayomys confluens gen. et sp. nov.	left dp4	1.81			0.46		0.25
MUSM 3012	TAR 01	Mayomys confluens gen. et sp. nov.	left dp4	1.67	1.20	0.87	0.87	0.52	0.52
MUSM 3013	TAR 01	Mavomvs confluens gen. et sp. nov.	left dp4	1.46	1.11				
MUSM 3014	TAR 01	Mavomvs confluens gen. et sp. nov.	left dp4	1.41	1.20				
MUSM 3015	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4	1.62	1.15	0.67	0.57	0.41	0.35
MUSM 3353	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4	1.35	1.08	0.93	0.78	0.69	0.58
MUSM 3354	TAR 01	Mayomys confluens gen, et sp. nov.	left dp4	1.48	1.30	0.73	0.78	0.49	0.53
MUSM 3016	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.87	1.29	017.0	01, 0	0.1)	0.95
MUSM 3017	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.67	1.16	0.86	1.01	0.52	0.60
MUSM 3018	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.89	1 31	0.83	0.89	0.92	0.00
MUSM 3019	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.05	1.91	0.72	0.07	0.11	0.1/
MUSM 3020	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.81	1.20	0.72	0.95	0.11	0.52
MUSM 3021	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.01	1.55		0.86		0.92
MUSM 3022	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.86	1.29		0.69		0.37
MUSM 3023	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.46	1.18	0.79	1.05	0.54	0.72
MUSM 3024	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.77	1.24	,	0.79		0.44
MUSM 3025	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.68	1.22		0.89		0.53
MUSM 3026	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.75	1.29		0.87		0.50
MUSM 3027	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.75	,	0.70	,	0.40	
MUSM 3028	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.69	1.13	0.62	0.92	0.37	0.54
MUSM 3029	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.39	1.12	0.54	0.40	0.39	0.29
MUSM 3030	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.67	1.2.9	0.76	0.56	0.46	0.34
MUSM 3031	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1107	112)	0.69	0.90	0.10	0.01
MUSM 3032	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4			0.07			
MUSM 3033	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.76	1.25				
MUSM 3034	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.84	1.27				
MUSM 3035	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.58	1.23	0.84	0.81	0.56	0.56
MUSM 3036	TAR 01	Mavomvs confluens gen. et sp. nov.	right dp4	1.29	1.01	0.84		0.65	
MUSM 3037	TAR 01	Mayomys confluens gen, et sp. nov.	right dp4	1.65	1.20			,	
MUSM 3038	TAR 01	Mayomys confluens gen, et sp. nov.	right p4	1.69	1.37				
MUSM 3039	TAR 01	Mayomys confluens gen, et sp. nov.	left m1						
MUSM 3040	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.61	1.42	0.83	1.01	0.52	0.63
MUSM 3041	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.70		0.05	1101	0.92	
MUSM 3042	TAR 01	Mayomys confluens gen, et sp. nov	left m1	1.54	1.55	0.89	0.88	0.58	0.57
MUSM 3043	TAR 01	Mayomys confluens gen, et sp. nov	left m1	1.62	1.56	,	0.00	0.90	,
MUSM 3044	TAR 01	Mayomys confluens gen et sp. nov.	left m1	1.66	1.56	0.82	0.84	0.49	0.51
MUSM 3045	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.65	1.55	0.97	0.01	0.59	0.71
MUSM 3046	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.05	1.55	0.88	0.73	0.57	0.47
MUSM 3047	TAR 01	Mayomys confluens gen et sp. nov.	left m1	1.55	1 46	0.75	0.89	0.46	0.55
MUSM 3048	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.61	1.46	0.74	0.71	0.46	0.44
MUSM 3049	TAR 01	Mayomys confluens gen et sp. nov.	left m1	1.74	1.36	I	~•/ 1		~
		2.2. jonrys conjunctus gen. et sp. 1104.	1010 1111	1.1/1	1.50				

MUSM 3050	TAR 01	Mayomys confluens gen et sp. nov	left m1				0.72		
MUSM 3051	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.63	1.34		0.56		0.35
MUSM 3052	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.63	1.51		0.56		0.41
MUSM 3053	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.62	1.11	0.60	0.55	0.37	0.34
MUSM 3054	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.01	1.10	0.66	0.55	0.26	0.38
MUSM 3055	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.56	1.41	0.48	0.57	0.31	0.37
MUSM 3056	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.59	1.65	0.56	0.58	0.35	0.36
MUSM 3057	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.68	1.68	0.34	0.46	0.20	0.27
MUSM 3058	TAR 01	Mayomys confluens gen, et sp. nov.	left m1	1.59	1.48				
MUSM 3059	TAR 01	Mavomys confluens gen. et sp. nov.	left m1	1.65	1.65	0.79		0.48	
MUSM 3355	TAR 01	Mavomys confluens gen. et sp. nov.	left m1	1.37	1.43	,			
MUSM 3060	TAR 01	Mayomys confluens gen. et sp. nov.	right m1	1.60	1.43				
MUSM 3061	TAR 01	Mayomys confluens gen. et sp. nov.	right m1						
MUSM 3062	TAR 01	Mayomys confluens gen. et sp. nov.	right m1	1.56	1.38	0.95	0.94	0.61	0.60
MUSM 3063	TAR 01	Mayomys confluens gen. et sp. nov.	right m1	1.77	1.51	0.96	1.09	0.54	0.62
MUSM 3064	TAR 01	Mayomys confluens gen. et sp. nov.	right m1						
MUSM 3065	TAR 01	Mayomys confluens gen. et sp. nov.	right m1	1.58	1.35				
MUSM 3066	TAR 01	Mayomys confluens gen. et sp. nov.	right m1	1.61	1.40	0.80	0.80	0.50	0.50
MUSM 3067	TAR 01	Mayomys confluens gen. et sp. nov.	right m1	1.83	1.63	0.84		0.46	
MUSM 3068	TAR 01	Mayomys confluens gen. et sp. nov.	right m1		1.52	0.87			
MUSM 3069	TAR 01	Mayomys confluens gen. et sp. nov.	right m1	1.72	1.28	0.95	0.96	0.55	0.55
MUSM 3070	TAR 01	Mayomys confluens gen. et sp. nov.	right m1	1.63	1.37				
MUSM 3071	TAR 01	Mayomys confluens gen, et sp. nov.	right m1		1.47				
MUSM 3072	TAR 01	Mayomys confluens gen, et sp. nov.	right m1	1.67	1.57	0.86	1.02	0.52	0.61
MUSM 3356	TAR 01	Mayomys confluens gen, et sp. nov.	right m1			0.88			
MUSM 3073	TAR 01	Mayomys confluens gen, et sp. nov.	left m2	1.78	1.67	0.94	1.11	0.53	0.62
MUSM 3074	TAR 01	Mayomys confluens gen, et sp. nov.	left m2	1.70	1107	0171		0.95	0.02
MUSM 3075	TAR 01	Mayomys confluens gen, et sp. nov.	left m2			0.65	0.90		
MUSM 3076	TAR 01	Mayomys confluens gen, et sp. nov.	left m2			0.97	1.22		
MUSM 3077	TAR 01	Mayomys confluens gen, et sp. nov.	left m2			0.83	0.82		
MUSM 3078	TAR 01	Mayomys confluens gen, et sp. nov.	left m2	1.71	1.63	0.88	0.88	0.52	0.51
MUSM 3079	TAR 01	Mayomys confluens gen, et sp. nov.	left m2	1.80	1.63	0.91	1.11	0.51	0.62
MUSM 3080	TAR 01	Mayomys confluens gen, et sp. nov.	left m2	1.75	1.77	0.86	0.92	0.49	0.53
MUSM 3081	TAR 01	Mayomys confluens gen, et sp. nov.	left m2	1.78	1.81	0.70	0.76	0.39	0.43
MUSM 3082	TAR 01	Mayomys confluens gen. et sp. nov.	left m2		1.63	0.98	1.11		
MUSM 3083	TAR 01	Mayomys confluens gen, et sp. nov.	left m2			0.77	0.96		
MUSM 3084	TAR 01	Mayomys confluens gen, et sp. nov.	left m2	1.83	1.90	0.76	0.74	0.42	0.41
MUSM 3085	TAR 01	Mayomys confluens gen, et sp. nov.	left m2	1.85	1.86	0.76	0.80	0.41	0.43
MUSM 3086	TAR 01	Mayomys confluens gen. et sp. nov.	left m2	1.77	1.71	1.02		0.58	
MUSM 3087	TAR 01	Mayomys confluens gen. et sp. nov.	left m2	1.71	1.66				
MUSM 3088	TAR 01	Mayomys confluens gen. et sp. nov.	left m2	1.70	1.62		0.87		0.51
MUSM 3089	TAR 01	Mayomys confluens gen. et sp. nov.	right m2	1.97	1.89	0.88	1.12	0.45	0.57
MUSM 3090	TAR 01	Mayomys confluens gen. et sp. nov.	right m2	1.89	1.74				
MUSM 3091	TAR 01	Mayomys confluens gen. et sp. nov.	right m2	1.90	1.71				
MUSM 3092	TAR 01	Mayomys confluens gen. et sp. nov.	right m2	1.67	1.56	0.93	0.94	0.56	0.56
MUSM 3093	TAR 01	Mayomys confluens gen. et sp. nov.	right m2	1.95	1.76				
MUSM 3094	TAR 01	Mavomvs confluens gen. et sp. nov.	right m2	1.86	1.65	0.86	0.91	0.46	0.49
MUSM 3095	TAR 01	Mavomvs confluens gen. et sp. nov.	right m2	1.93		0.73	0.66	0.38	0.34
MUSM 3096	TAR 01	Mayomys confluens gen. et sp. nov.	right m2				0.77		
MUSM 3097	TAR 01	Mayomys confluens gen. et sp. nov.	right m2	1.94	1.70		0.86		0.44
MUSM 3357	TAR 01	Mayomys confluens gen. et sp. nov.	right m2	2.03	1.46	0.94	-	0.46	
MUSM 3098	TAR 01	Mayomys confluens gen. et sp. nov.	left m3	1.76	1.51	1.04	1.02	0.59	0.58
MUSM 3099	TAR 01	Mayomys confluens gen. et sp. nov.	left m3	1.83	1.57	0.92	1.11	0.50	0.61
MUSM 3100	TAR 01	Mayomys confluens gen. et sp. nov.	left m3	1.81	1.56	0.97	1.19	0.54	0.66
MUSM 3101	TAR 01	Mayomys confluens gen. et sp. nov.	left m3	1.73	1.58	0.86	0.83	0.50	0.48
MUSM 3102	TAR 01	Mayomys confluens gen. et sp. nov.	left m3	1.76	1.47	0.66	0.72	0.38	0.41
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MUSM 3103	TAR 01	Mayomys confluens gen. et sp. nov.	left m3	1.99	1.66	0.66	0.78	0.33	0.39
MUSM 3104	TAR 01	Mayomys confluens gen. et sp. nov.	left m3	1.76	1.59	0.78		0.44	
MUSM 3105	TAR 01	Mayomys confluens gen. et sp. nov.	left m3	1.83	1.56	0.78	1.01	0.42	0.55
MUSM 3106	TAR 01	Mayomys confluens gen. et sp. nov.	left m3	1.96	1.63	0.92	0.85	0.47	0.43
MUSM 3107	TAR 01	Mayomys confluens gen, et sp. nov.	left m3	1.94	1.71	0.60	0.59	0.31	0.31
MUSM 3108	TAR 01	Mayomys confluens gen et sp. nov	left m3	1.72	1.63	0.69	0.57	0.40	0.01
MUSM 3109	TAR 01	Mayomys confluens gen, et sp. nov.	right m3	2.12	1.65	0.07		0.10	
MUSM 3110	TAR 01	Mayomys confluens gen, et sp. nov.	right m3	1.68	1.09	0.76	0.78	0.45	0.46
MUSM 3111	TAR 01	Mayomys confluens gen. et sp. nov.	right m3	1.00	1.51	0.70	0.70	0.45	0.46
MUSM 3112	TAR 01	Mayomys confluens gen. et sp. nov.	right m3	1.01	1.00	0.57	0.04	0.39	0.46
MUSM 2112	TAP 01	Mayomys confluens gen. et sp. nov.	right m ²	1.75	1.52	0.00	0.30	0.38	0.40
MUSM 3113	TAD 01	Mayomys confluens gen. et sp. nov.	right m2	1.07	1.52	0.71	0.72	0.38	0.39
MUSM 3114	TADOL	Mayomys confluens gen. et sp. nov.	right m3	1.70	1.37	0./1	0.76		
MUSM 3113	TADOL	Mayomys confluens gen. et sp. nov.	right m3	1./9	1.67	0.79	0.02	0 / 1	0.40
MUSM 3116	TARUI	Mayomys confluens gen. et sp. nov.	right m3	1.90	1.55	0.78	0.93	0.41	0.49
MUSM 3117	TARUI	Mayomys confluens gen. et sp. nov.	right m3	1./6	1.49	0.81	0.76	0.46	0.43
MUSM 3358	TAR 01	Mayomys confluens gen. et sp. nov.	right m3			0.3/	0.63		
MUSM 3359	TAR 01	Mayomys confluens gen. et sp. nov.	right m3			0.60			
MUSM 3118	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.57	1.39				
MUSM 3119	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.34	1.25				
MUSM 3120	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.39	1.32	0.96	0.75	0.69	0.54
MUSM 3121	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.45	1.34	0.75	0.55	0.52	0.38
MUSM 3122	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.44	1.35	0.45		0.31	
MUSM 3123	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.32	1.33	0.94		0.71	
MUSM 3124	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.44	1.39	0.80	0.65	0.56	0.45
MUSM 3125	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.27	1.19	0.83	0.48	0.65	0.37
MUSM 3126	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.32	1.19		0.54		0.41
MUSM 3127	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	11.29	1.17	0.96		0.08	
MUSM 3128	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.55	1.43	0.87	0.62	0.56	0.40
MUSM 3129	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.46	1.41	0.91	0.72	0.62	0.49
MUSM 3130	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.37	1.38	0.84	0.54	0.62	0.39
MUSM 3131	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.40	1.40	0.89	0.59	0.63	0.42
MUSM 3132	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.39	1.35	0.69	0.55	0.50	0.39
MUSM 3133	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4		1.25	0.54	0.52		
MUSM 3134	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4			0.53			
MUSM 3135	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.44	1.47	0.58	0.69	0.40	0.48
MUSM 3136	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.50	1.44	0.50		0.33	
MUSM 3137	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4	1.30	1.32				
MUSM 3138	TAR 01	Mayomys confluens gen. et sp. nov.	left dP4						
MUSM 3139	TAR 01	Mayomys confluens gen. et sp. nov.	right dP4	1.53	1.36				
MUSM 3140	TAR 01	Mayomys confluens gen. et sp. nov.	right dP4	1.41	1.35	1.08	0.63	0.77	0.45
MUSM 3141	TAR 01	Mayomys confluens gen. et sp. nov.	right dP4	1.50	1.43	0.90	0.53	0.60	0.35
MUSM 3142	TAR 01	Mayomys confluens gen. et sp. nov.	right dP4	1.49	1.45	0.98	0.86	0.65	0.58
MUSM 3143	TAR 01	Mayomys confluens gen. et sp. nov.	right dP4	1.35	1.20	0.80	0.56	0.60	0.42
MUSM 3144	TAR 01	Mayomys confluens gen. et sp. nov.	right dP4	1.36	1.37	1.03	0.64	0.76	0.47
MUSM 3145	TAR 01	Mayomys confluens gen. et sp. nov.	right dP4	1.34	1.15	0.55		0.41	
MUSM 3146	TAR 01	Mayomys confluens gen, et sp. nov.	right dP4	1.51	1.39	0.79	0.36	0.53	0.24
MUSM 3147	TAR 01	Mayomys confluens gen, et sp. nov.	right dP4	1.91	1.57	0.91	0.66	0.62	0.45
MUSM 3148	TAR 01	Mayomys confluens gen. et sp. nov.	right dP4	1.1/	1 43	1.05	0.00	0.02	0.19
MUSM 3149	TAR 01	Mayomys confluens gen, et sp. nov.	right dP4		1 38	1.05	0.59		
MUSM 3150	TAR 01	Mayomys confluens gen, et sp. nov.	right dP4	1 36	1.36	0.87	0.63	0.64	0.46
MUSM 2151	TAR 01	Mayomys confluence gen et sp. nov.	right dD/	1.50	1 40	0.89	0.65	0.01	0.10
MUSM 2152	TAP 01	Mayomys confluence gen, et sp. nov.	right dD/	1 37	1.10	0.00	0.00	0.60	0.37
MUSM 2152	TAP 01	Manamus confluence gon at an new	right JD/	1.57	1.34	1.04	0.90	0.00	0.37
MUSM 2154	TAP 01	Manamas confluence con at an new	right JD/	1.50	1.33	1.00		0.70	
MUCM 2155	TADOI	Manamais confluence gon at an anot	right dD4	1.40	1.23				
MUSM 2150	TADOL	Management and futures gen. et sp. nov.	right JD/	1.(0	1 / 1	1 17		0.72	
MUSM 3156	1 AK 01	wayomys confluens gen. et sp. nov.	right aP4	1.60	1.41	1.1/		0./3	

MUSM 3157	TAR 01	Mayomys confluens gen et sp. poy	left >P4						
MUSM 3158	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.73	1.53	1.93		1.11	
MUSM 3159	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.53	1.59	0.98		0.64	
MUSM 3160	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.66	1.68	1.19	0.73	0.71	0.44
MUSM 3161	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.59	1.56	1.14		0.72	
MUSM 3162	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.51	1.49	0.92	0.53	0.61	0.35
MUSM 3163	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.58	1.70	1.13	0.78	0.71	0.49
MUSM 3164	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.57	1.60	1.04	0.66	0.67	0.42
MUSM 3165	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.61	1.70	0.89	0.50	0.55	0.31
MUSM 3166	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.60	1.57	1.02	0.69	0.64	0.43
MUSM 3167	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1100	1.97	1.11	0.70	0101	0.15
MUSM 3168	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.60	1.58				
MUSM 3169	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.46	1.63	1.07	0.67	0.73	0.46
MUSM 3170	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.58	1.54	0.90	0.63	0.57	0.39
MUSM 3171	TAR 01	Mayomys confluens gen. et sp. nov.	left M1	1.64	1.72	0.79	0.56	0.48	0.34
MUSM 3360	TAR 01	Mayomys confluens gen, et sp. nov.	left M1	1.70	1.82	1.18	0.75	0.69	0.44
MUSM 3361	TAR 01	Mayomys confluens gen, et sp. nov.	left M1					,	
MUSM 3172	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.64	1.59				
MUSM 3173	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.57	1.65	1.05	1.78	0.67	1.13
MUSM 3174	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.64	1.56	0.87	0.59	0.53	0.36
MUSM 3175	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.61	1.56	1.10	0.81	0.68	0.50
MUSM 3176	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.76	1.57	0.97	0.78	0.55	0.44
MUSM 3177	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.65	1.74	1.01	0.74	0.61	0.45
MUSM 3178	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.57	1.54	1.00	017 1	0.63	0.15
MUSM 3179	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.97	1.51	1.00	0.73	0.05	
MUSM 3180	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.48	1.49	0.92	0.63	0.62	0.43
MUSM 3181	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.10	1.17	1.22	0.67	0.02	0.15
MUSM 3182	TAR 01	Mayomys confluens gen, et sp. nov.	right M1	1.51	1.66	1.12	0.74	0.75	0.49
MUSM 3183	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.76	1.67	1.03	0.7 1	0.59	0.17
MUSM 3184	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.59	1.76	1.13	0.79	0.71	0.50
MUSM 3185	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.74	1.92	1.06	0.72	0.61	0.41
MUSM 3186	TAR 01	Mayomys confluens gen. et sp. nov.	left M2	1.69	1.83	1.42	0.93	0.84	0.55
MUSM 3187	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.67	1.05	1.12	0.89	0.73	0.53
MUSM 3188	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.07	1.82	0.77	0.61	0.45	0.36
MUSM 3244	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.62	1.85	0.99	0.61	0.15	0.38
MUSM 3245	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.62	1.0 9	0.93	0.67	0.55	0.40
MUSM 3246	TAR 01	Mayomys confluens gen. et sp. nov.	left M2	1.60	1.65	0.95	0.63	0.55	0.10
MUSM 3247	TAR 01	Mayomys confluens gen. et sp. nov.	left M2	1.00	1.05	0.90	0.051	0.50	0.29
MUSM 3248	TAR 01	Mayomys confluens gen. et sp. nov.	left M2	1.75	1.00	0.88	0.51	0.54	0.42
MUSM 3249	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.03	1.82	0.00	0.67	0.91	0.12
MUSM 3250	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.60	1.02	0.85	0.50	0.53	0.21
MUSM 3251	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.54	1.83	0.65	0.57	0.55	0.37
MUSM 3362	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.91	1.05	0.63	0.34	0.12	0.57
MUSM 3252	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.68	1 72	1.05	0.77	0.62	0.46
MUSM 3363	TAR 01	Mayomys confluens gen, et sp. nov.	left M2	1.00	1.72	1.09	0.68	0.02	0.10
MUSM 3253	TAR 01	Mayomys confluens gen, et sp. nov.	right M2	1.7 2	1.00	1 1 4	0.00	0.62	0.50
MUSM 3254	TAR 01	Mayomys confluens gen, et sp. nov.	right M2	1.02	1.90	1.11	0.89	0.02	0.49
MUSM 3255	TAR 01	Mayomys confluens gen, et sp. nov.	right M2	1.67	1.66	1.20	0.87	0.67	0.17
MUSM 3256	TAR 01	Mayomys confluens gen, et sp. nov.	right M2	1.07	1.00	1 15	0.84	0.65	0.17
MUSM 3257	TAR 01	Mayomys confluens gen, et sp. nov.	right M2	1.70	1.67	1.19	0.68	0.60	0.40
MUSM 2258	TAR 01	Mayomys confluens gen et sp. nov.	right M2	1.70	1.02	1.02	0.76	0.71	0.44
MUSM 3250	TAR 01	Mayomys confluence gen et en poy	right M2	1.71	1.00	0.86	0.70	0.50	0.38
MUSM 3260	TAR 01	Mayomys confluence gen et en poy	right M2	1./1	1.77	0.30	0.57	0.50	0.35
MUSM 3261	TAR 01	Mayomys confluens gen, et sp. nov.	right M2	1.01	1.70	0.74	0.57	0.40	0.55
MUSM 2262	TAR 01	Mayomys confluence gen et en nov	right M2	151	1.69	0.70	0.03	0 4/1	0.15
MUSM 2262	TAR 01	Mayomys confluences gen. et sp. 1104.	right M2	1.51	1.90	1.01	0.23	0.59	0.19
110 311 3203	17101	wiayomys conjuens gen. et sp. nov.		1./)	1.00	1.01		0.30	

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MUSM 3264	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.62	1.79	1.01	0.81	0.62	0.50
MUSM 3265	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.65	1.95	1.02	0.86	0.62	0.52
MUSM 3266	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.65	1.89	0.87	0.71	0.53	0.43
MUSM 3267	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.53	1.57	0.80	0.65	0.52	0.42
MUSM 3268	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.39	1.58	0.72	0.65	0.52	0.47
MUSM 3269	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.32	1.49	0.73	0.63	0.56	0.48
MUSM 3270	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.53	1.77	1.14	0.63	0.75	0.41
MUSM 3271	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.58	1.81	1.20	0.78	0.76	0.49
MUSM 3272	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.58	1.83	1.02	0.77	0.65	0.48
MUSM 3273	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.63	1.74	1.05	0.69	0.65	0.42
MUSM 3274	TAR 01	Mayomys confluens gen. et sp. nov.	left M3	1.43	1.53	0.97	0.69	0.68	0.48
MUSM 3275	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.78	1.79				
MUSM 3276	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.58	1.82	1.20		0.76	
MUSM 3277	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.51	1.70	0.97	0.78	0.64	0.52
MUSM 3278	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.70		0.96	0.86	0.57	0.51
MUSM 3279	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.76		1.20		0.68	
MUSM 3280	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.34	1.49	0.96	0.65	0.72	0.49
MUSM 3281	TAR 01	Mayomys confluens gen. et sp. nov.	right M3			0.98	0.75		
MUSM 3282	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.44	1.61	1.09		0.76	
MUSM 3283	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.47		0.83	0.73	0.56	0.50
MUSM 3284	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.50	1.68	0.93	0.90	0.62	0.60
MUSM 3285	TAR 01	Mayomys confluens gen. et sp. nov.	right M3			0.88			
MUSM 3286	TAR 01	Mayomys confluens gen. et sp. nov.	right M3			0.76			
MUSM 3287	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.39	1.67		0.75		0.54
MUSM 3288	TAR 01	Mayomys confluens gen. et sp. nov.	right M3	1.46	1.60	0.55	0.53	0.38	0.36
MUSM 3289	TAR 01	Eoincamys cf. pascuali	left dp4	2.49		0.58	0.78	0.23	0.31
MUSM 3364	TAR 01	Eoincamys cf. pascuali	left dp4			0.83			
MUSM 3290	TAR 01	Eoincamys cf. pascuali	right dp4	2.59	1.65	0.72	0.77	0.28	0.30
MUSM 3291	TAR 01	Eoincamys cf. pascuali	left m1 or 2						
MUSM 3365	TAR 01	Eoincamys cf. pascuali	left m1 or 2						
MUSM 3292	TAR 01	Eoincamys cf. pascuali	right m1	2.18	2.22		0.71		0.33
MUSM 3293	TAR 01	Eoincamys cf. pascuali	left m2						
MUSM 3294	TAR 01	Eoincamys cf. pascuali	left m2	2.39	2.34	0.89	1.28	0.37	0.54
MUSM 3295	TAR 01	Eoincamys cf. pascuali	left m2	2.36	2.09				
MUSM 3296	TAR 01	Eoincamys cf. pascuali	right m2	2.21					
MUSM 3297	TAR 01	Eoincamys cf. pascuali	right m3	2.16	1.92				
MUSM 3298	TAR 01	Eoincamys cf. pascuali	left M1	2.21		0.96		0.43	
MUSM 3299	TAR 01	Eoincamys cf. pascuali	left M1				0.52		
MUSM 3300	TAR 01	Eoincamys cf. pascuali	right M2	2.25		1.39		0.62	
MUSM 3301	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right dp4		1.21	0.53	0.59		
MUSM 3302	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right dp4	2.09	1.25	0.56	0.78	0.27	0.38
MUSM 3303	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right p4	1.73	1.54	0.92	1.08	0.53	0.62
MUSM 3304	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left m1	1.64	1.62	0.76	0.98	0.46	0.60
MUSM 3305	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left m1	1.59	1.43	0.48	0.65	0.30	0.41
MUSM 3306	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right m1	1.67	1.47		0.95		0.57
MUSM 3307	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right m1	1.65	1.54		0.97		0.59
MUSM 3308	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left m2			0.97			
MUSM 3309	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left m2	1.87	1.74	0.86	1.18	0.46	0.63
MUSM 3310	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right m2	1.83	1.62	0.83	1.04	0.45	0.57
MUSM 3311	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right m2	1.82	1.69	0.93	0.91	0.51	0.50
MUSM 3312	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right m2	1.82	1.58	0.70	0.84	0.39	0.46
MUSM 3313	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right m2	1.78	1.59	0.67	0.69	0.38	0.38
MUSM 3314	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right m2	1.85	1.84	0.92		0.49	
				1					
MUSM 3315	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right m3						
MUSM 3315 MUSM 3316	TAR 01 TAR 01	Tarapotomys mayoensis gen. et sp. nov. Tarapotomys mayoensis gen. et sp. nov.	right m3 left dP4	1.86		0.78		0.42	

MUSM 3366	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left dP4						
MUSM 3318	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left P4	1.43					
MUSM 3319	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left P4	1.43	1.67		0.69		0.48
MUSM 3320	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right P4		1.97				
MUSM 3321	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M1	1.55	1.37	1.12		0.72	
MUSM 3322	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M1	1.34	1.64	1.06	0.53	0.79	0.39
MUSM 3323	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M1	1.85	1.78	0.99	0.79	0.54	0.43
MUSM 3324	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M1	1.74	1.79				
MUSM 3325	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M1						
MUSM 3326	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right M1	1.72	1.97	1.28	0.69	0.75	0.40
MUSM 3367	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right M1						
MUSM 3327	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M2	1.74					
MUSM 3328	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M2	1.88					
MUSM 3329	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M2	1.77	1.83	1.43	0.61	0.81	0.35
MUSM 3330	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M2	2.00	2.00	1.19	0.73	0.60	0.36
MUSM 3331	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M2	1.57	1.99	1.10	0.58	0.70	0.37
MUSM 3332	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right M2	1.77	2.06	1.27	0.69	0.72	0.39
MUSM 3333	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right M2	1.88	2.01	1.79		0.95	
MUSM 3334	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M3	1.55	1.67	1.15	0.56	0.75	0.36
MUSM 3368	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	left M3						
MUSM 3335	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right M3	1.70	1.83	1.37	0.58	0.80	0.34
MUSM 3336	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right M3	1.62	1.77	1.45	0.45	0.89	0.28
MUSM 3337	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right M3	1.67	1.58	1.24	0.39	0.74	0.23
MUSM 3338	TAR 01	Tarapotomys mayoensis gen. et sp. nov.	right M3	1.55	1.67	1.40	0.65	0.90	0.42
MUSM 3339	TAR 01	Chinchilloidea indet.	dentary fragment						
MUSM 3340	TAR 01	Chinchilloidea indet.	dentary fragment						

Hb, maximum labial crown height; Hg, maximum lingual crown; HIb, hypsodont index (calculated from Hb); HIg, hypsodont index (calculated from Hg); ML, maximum anteroposterior length; MW, maximum linguolabial width.

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Size comparison of Eoincamys species from Santa Rosa (*E. pascuali* and *E. amegbinoi*, FRAILEY & CAMPBELL 2004) and from Shapaja (in bold, *E. advendations* of *E. passuali* and *E. of passual*: the model of the second of the

Species		I	P4				Мx			4	41				M2		L		M3					
LENGTH	ц	'n.	min.	max.	ц	'n.	min.	max.	ц	n.	min.	max.	ц	'n.	min.	max.	u	m.	min.	max.				
E. pascuali	б	1.62	1.49	1.73	10	1.91	1.53	2.31									-	1.53						
E. ameghinoi	б	1.12	1.01	1.26	12	1.57	1.23	1.73	-	1.23			-	1.66			7	1.52	1.43	1.61				
valverdei nov. sp.	-	1.66			~	2.04	1.93	2.18	ŝ	2.11	2.07	2.16	-	1.95			5	1.95	1.93	1.97				
parvus nov. sp.	7	1.52	1.52	1.53	4	1.59	1.51	1.74	5	1.53	1.51	1.55	-	1.74			-	1.56						
E. cf. pascuali					7	2.23	2.21	2.25	-	2.21			П	2.25										
WIDTH	ц	ш.	min.	max.	ц	m.	min.	max.	ц	ü.	min.	max.	п	m.	min.	max.	ц	'n.	min.	max.				
E. pascuali	б	1.83	1.79	1.92	10	2.16	1.7	2.49									-	1.7						
E. ameghinoi	2	1.54	1.45	1.63	11	1.58	1.26	1.8	-	1.31			-	1.5			2	1.62	1.48	1.76				
valverdei nov. sp.	1	1.93			Ś	2.3	1.97	2.52	З	2.45	2.37	2.52					2	2.07	1.97	2.16				
. parvus nov. sp.	7	1.95	1.86	2.05	4	1.67	1.46	1.85	2	1.53	1.46	1.61	Г	1.85			-	1.77						
E. cf. pascuali																								
		q	p4				p4				nx		1		nl				m2				13	
LENGTH	u	m.	min.	max.	u	m.	min.	max.	u	m.	min.	max.	n	m.	min.	max.	u	m.	min.	max.	u	m.	min.	max
E. pascuali	1	1.85			4	1.76	1.72	1.84	17	1.99	1.61	2.16	Г	1.9							2	2.08	2.03	2.12
E. ameghinoi					2	1.44	1.32	1.55	9	1.6	1.33	1.98												
valverdei nov. sp.																								
parvus nov. sp.	1	2.08							3	1.8	1.69	1.86	1	1.85			1	1.86			1	1.69		
E. cf. pascuali	2	2.54	2.49	2.59					5	2.26	2.16	2.39	1	2.18			3	2.32	2.21	2.39	1	2.16		
WIDTH	u	m.	min.	max.	ц	m.	min.	max.	ц	m.	min.	max.	u	m.	min.	max.	ц	m.	min.	max.	u	m.	min.	max
E. pascuali	4	1.61	1.57	1.68	4	1.59	1.41	1.7	17	1.71	1.5	1.89	-	1.5							2	1.74	1.65	1.82
E. ameghinoi					2	1.42	1.38	1.45	9	1.38	1.23	1.56												
valverdei nov. sp.																								
. parvus nov. sp.	1	1.31							3	1.57	1.42	1.67	1	1.67			1	1.63			1	1.42		
E. cf. pascuali	Г	1.65							4	2.14	1.92	2.34	Г	2.22			2	2.21	2.09	2.34	1	1.92		

value; min., minimum value; n, specimen number. Σ