PalZ (2022) 96:135–160
https://doi.org/10.1007/s12542-021-00551-0

RESEARCH PAPER

# Eocene caviomorph rodents from Balsayacu (Peruvian Amazonia)

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Received: 17 August 2020 / Accepted: 8 February 2021 / Published online: 3 June 2021

## Abstract

The Paleogene record of caviomorph rodents has substantially increased over the last decades, and their evolutionary history better understood by the discovery of their earliest representatives, so far recorded in several pre-Deseadan localities in Peruvian Amazonia. We report here the discovery of new caviomorph fossils from the Balsayacu area in Peru (TAR-55/TAR-55bis, TAR-76 and TAR-77 localities, San Martín Department). The study of this new material reveals the occurrence of four caviomorph taxa in these localities: *Balsayacuy huallagaensis* gen. et sp. nov., *Chachapoyamys kathetos* gen. et sp. nov. and Caviomorpha gen. et sp. indet. 1 and 2. It allows the revision and refinement of taxonomic assignments of previously described specimens. The first three taxa have a primitive dental pattern, as that characterizing stem Caviomorpha recorded in pre-Deseadan localities of Peru (Eocene localities of Contamana and ?late Eocene/early Oligocene Santa Rosa). We support here an Eocene age for the Balsayacu section due to the complete absence of morphologically derived taxa representing modern caviomorph superfamilies. By the presence of derived characters in *Balsayacuy* and *Chachapoyamys* compared to *Canaanimys maquiensis* and *Cachiyacuy contamanensis* from CTA-27 (Contamana, Peru; late middle Eocene), the Balsayacu section may document a time interval slightly younger than CTA-27 (which further yields *Chachapoyamys* cf. *kathetos*) and older than those of Santa Rosa and Tarapoto-Shapaja, likely documenting latest middle or early late Eocene times. These low-latitude stem caviomorph faunas provide new insights into the early evolutionary history and paleodiversity of that group immediately before the rise of modern superfamilies.

**Keywords** Rodentia · Systematics · Biostratigraphy · Peru · South America

## Introduction

Due to a complex ecological and geological history, Amazonia is one of the regions of the world with the maximum biodiversity of many groups of organisms (Jenkins et al. 2013). Understanding the emergence of such biodiversity raises many questions surrounding its evolution, dynamics, the geographic origin of taxonomic groups that compose it, and factors that could have constrained and molded it (Stebbins 1974; Hoorn et al. 2010). Paleontological studies are fundamental to understand the evolutionary dynamics of this biodiversity, yet the fossil record of this geographic area had long been elusive. Indeed, owing to the dense vegetation cover, extensive recent alluvial depositions, aggressive alteration and pedogenesis, frequent landslides and seasonal floodings, fossiliferous outcrops are rare and of difficult access most of the time. In addition, field conditions are particularly harsh in such moist and warm climate environment. Since the end of the last century, thanks to field efforts driven by several scientific teams, many mammal-bearing localities were discovered in this region including Santa Rosa (Peru; ?late Eocene/early Oligocene; e.g., Campbell 2004), Cerro Colorado (Peru; late Miocene–Late Pleistocene; Campbell et al. 2000, 2001, 2010), and Acre (Brazil; late Miocene; e.g., Frailey 1986; Campbell et al. 2006; Negri et al. 2010; Kerber et al. 2017). Since 2003, our paleontological surveys in several areas of Peruvian Amazonia (i.e., Bagua, Contamana, Fitzcarrald, Iquitos-Nueva Unión, Juanjui, Madre de Dios, and Tarapoto) led to the discovery of numerous fossils providing a better knowledge of the Cenozoic

Handling Editor: Thomas Mörs.

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record of many mammalian groups (e.g., Antoine et al. 2007, 2012, 2013, 2016, 2017, in revision; Goillot et al. 2011; Marivaux et al. 2012, 2016a,b, 2020; Bianucci et al. 2013; Pujos et al. 2013; Tejada-Lara et al. 2015; Boivin et al. 2017a, b, 2018a, b, 2019a). The fossil record of caviomorph rodents (Caviomorpha Wood, 1955) significantly increased after these discoveries, and the understanding of their evolutionary history improved, especially for its earliest stages. Indeed, Peruvian Amazonia has yielded the earliest representatives of the group, so far recorded in several pre-Deseadan localities: Contamana (late middle Eocene [~41 Ma]; Antoine et al. 2012; Boivin et al. 2017a, 2019a, b), Balsayacu (late middle Eocene; Assemat et al. 2019), Juanjui (late middle Eocene–early Oligocene; Assemat et al. 2019), Tarapoto-Shapaja (late Eocene–early Oligocene; Boivin et al. 2018a, 2019a, b; Assemat et al. 2019: 723, fig. 7; Antoine et al. in revision), and Santa Rosa (Frailey and Campbell 2004; Arnal et al. 2020). Based on the evolutionary stages of its rodent assemblage (Frailey and Campbell 2004; Arnal et al. 2020), its metatherian fauna (Goin and Candela 2004) and the presence of some primates (Bond et al. 2015), a ?late Eocene age was advocated for the mammal-bearing deposits of Santa Rosa. However, considering the entire mammalian fauna of that locality, and taking into account the fossil data assembled in recent years, notably from (bio)geographically close localities from Peruvian Amazonia, Santa Rosa is most likely earliest Oligocene in age (Shockey et al. 2004; Croft et al. 2008; Vucetich et al. 2010; Antoine et al. 2012, 2017; Kay 2015; De Vries and Seiffert 2017; Assemat et al. 2019; Seiffert et al. 2020).

During our 2018 and 2019 field seasons in Peruvian Amazonia, we returned to the Balsayacu area (San Martín Department, Peru), and collected larger amounts of sediments than previously found in TAR-55 and TAR-55bis fossil-bearing localities. Wet-screening of the sediments has allowed for the recovery of about thirty additional isolated rodent teeth. Additionally, in the same stratigraphic section, about a hundred meters below TAR-55, we discovered two new localities, TAR-76 and TAR-77, the samplings of which have yielded few dental remains of caviomorphs. The primary purpose of this contribution is to: (1) revise the caviomorph fauna from TAR-55 and TAR-55bis (Assemat et al. 2019) in light of the new material, and (2) describe the rodent material from the new localities TAR-76 and TAR-77. The systematic and biostratigraphical implications of these faunas are discussed. This work also includes the description of a new isolated tooth and the revision of two teeth from CTA-27 (Contamana area, Loreto Department, Peru). The study of these caviomorph assemblages, among the oldest known in South America, allows to further our understanding of the early evolutionary history and paleodiversity of the group.

## Material and methods

All the caviomorph dental specimens described herein (except MUSM 2785, 2786, and 3943) originate from four localities in the vicinity of the small town of Balsayacu (San Martín Department, Peru; Fig. 1a): TAR-55, TAR-55bis, TAR-76, and TAR-77. These localities plus a fifth locality (TAR-56) belong to the same stratigraphic section along the Huallaga River (Assemat et al. 2019; Fig. 1b, c). This section is assigned to the lower member of the Pozo Formation ("Pozo Sands"; late middle Eocene) based on its fossil content, its stratigraphic position, and its lithological features (Assemat et al. 2019 and see below). TAR-55bis is located 1.5 m above TAR-55 and 121.5 m above TAR-56. TAR-76 and TAR-77 are situated between TAR-56 and TAR-55, TAR-76 is 165 m above TAR-56, and TAR-77 is 195 m above the latter. The fossil-bearing localities of this section consist of poorly-consolidated microconglomerates with limestone nodules, soft pebbles and oxidized plant remains, organized into lenticular channels of decimetric thickness and of fluvial to fluvio-deltaic origin (Fig. 1c).

TAR-55 and TAR-55bis yielded charophytes, fossilized wood, seeds, ostracods, crabs, chondrichthyans, actinopterygians, chelonians, caimanine alligatorids, and mammals (metatherians and placentals). The biostratigraphic age of the Balsayacu section is supported by its similarity with the top of the fossiliferous sequence of the lower member of the Pozo Formation at Contamana (CTA-27–CTA-29; late middle Eocene; Antoine et al. 2016), notably due to the occurrence at the TAR-55 of the freshwater ray *Potamotrygon ucayalensis* also found at the Contamana sequence, but absent from younger deposits, either at Contamana or at Shapaja (Chabain et al. 2017; Boivin et al. 2018a; Antoine et al. in revision). Moreover, the previous study of its caviomorph fauna revealed taxa close to those of the Eocene localities of Contamana (*Cachiyacuy* and *Canaanimys*; Assemat et al. 2019). Among the rodent taxa previously recorded in TAR-55 and TAR-55bis, none displayed an advanced evolutionary stage of their dental pattern (i.e., oblique loph(-id)s such as the chinchilloid *Eoincamys*) or incisive enamel microstructure (multiserial enamel subtype 2–3), contrary to younger deposits of the region from Juanjui (TAR-49 and TAR-50; Assemat et al. 2019) and Shapaja (Boivin et al. 2018a, 2019a) areas. The biostratigraphic implications of the caviomorph fauna from TAR-55 and TAR-55bis in the context of this present work are discussed in the section 'Age of TAR-55/TAR-55bis, TAR-76 and TAR-77' of the Discussion section. In addition to caviomorph teeth, crab and actinopterygian remains were found in TAR-76 and TAR-77. Finally, TAR-76 also yielded rests of wood, chelonians, metatherians and notungulates.

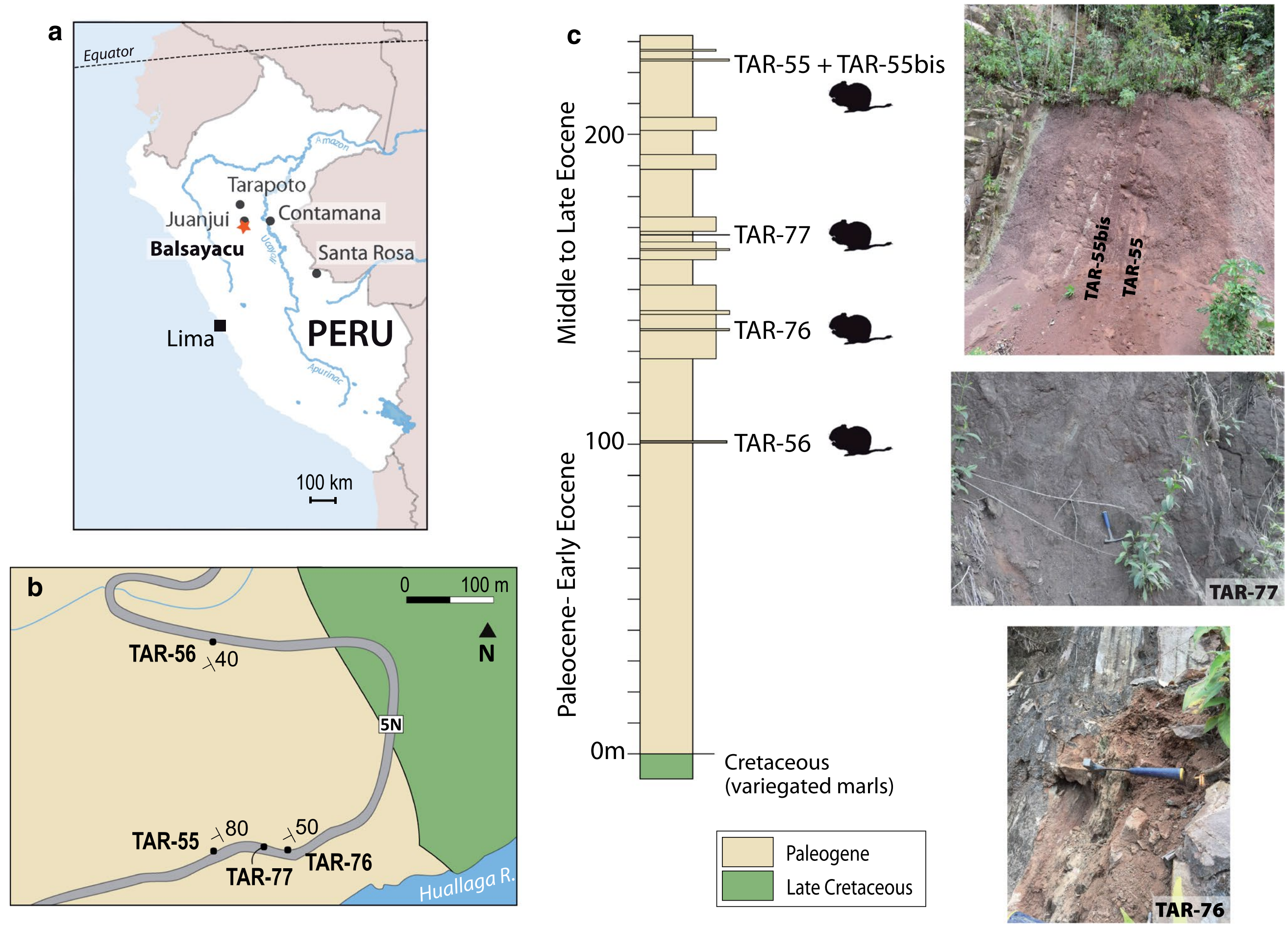


**Fig. 1** Geographic location and stratigraphy of TAR-76, TAR-77, TAR-55 and TAR-55bis localities (Balsayacu, Peru; late middle or early late Eocene). **a** General map of Peru with the Balsayacu area (San Martín Department; star symbol) and the other pre-Deseadan localities yielding caviomorphs in Amazonia (circle symbols): Contamana area (Loreto Department; late middle Eocene; Antoine et al. 2012; Boivin et al. 2017a, b), Juanjui area (late middle Eocene–early Oligocene; Assemat et al. 2019), Tarapoto area (Shapaja section; San Martín Department; late Eocene–early Oligocene; Boivin et al. 2018a, b) and Santa Rosa (Ucayali Department; ?late Eocene/early Oligocene; Frailey and Campbell 2004; Arnal et al. 2020). Scale bar: 100 km. **b** Simplified geological map of the Balsayacu area. Scale bar: 100 m. **c** synthetic stratigraphic section of Balsayacu with the position of the rodent-bearing localities TAR-56, TAR-76, TAR-77, TAR-55 and TAR-55bis, and photos of the last four localities. Modified from Assemat et al. (2019)

Since 2015, the material from TAR-55 and TAR-55bis was collected by excavating and screen-washing (1 mm mesh) a total of 610 kg of sediment. The caviomorph fossils from TAR-55 and TAR-55bis, collected in 2015 and 2016, as a result of the processing of 133 kg of sediments, corresponds to nine isolated teeth, which were previously studied and figured in Assemat et al. (2019). In 2018 and 2019, 465 kg of additional sediments were processed, allowing the discovery of 33 caviomorph teeth. As TAR-55 and TAR-55bis are levels with same geological characteristics, very close in position in the same outcrop, and yielding similar fossil contents, we chose to study the caviomorph material of these localities together. The localities TAR-76 and TAR-77 were discovered in 2019. In total, 75 kg of sediments for TAR-76 and 25 kg for TAR-77 were processed by screen-washing the same year.

The three isolated teeth from Contamana that we are describing/revisiting here (MUSM 2785, 2786, and 3943) come from the CTA-27 locality (late middle Eocene; Antoine et al. 2012, 2016). CTA-27 is located on the north-eastern flank of the Maquía Anticline and belongs to the lower member of the Pozo Formation (Antoine et al. 2016). It corresponds to inframetric channelized and unconsolidated sandstones, which include millimetric calcareous nodules of diagenetic origin locally encrusting fossil elements (Antoine et al. 2016). The fossil material from CTA-27 was collected by wet-screening (2 and 1 mm-mesh) during previous field seasons (2008–2010). MUSM 3943 was recently found in unprocessed sediments and thus was neither included in the original description of the fauna (Antoine et al. 2012) nor in its revision (Boivin et al. 2017a). MUSM 2785 and 2786 were attributed to *Cachiyacuy kummeli* by Boivin et al. (2017a: fig. 4.12, 4.13). We revised here these teeth in light of the new material from Balsayacu.

All teeth described in this contribution are permanently stored in the Vertebrate Paleontological collection of the "Museo de Historia Natural, Universidad Nacional Mayor de San Marcos" (MUSM), Lima, Peru. The terminology for rodent dentition follows Boivin and Marivaux (2020) and the literature cited therein. Uppercase letters are used for upper dentition (dP, for decidual premolar; P, for premolar; M, for molar) and lowercase letters are used for lower dentition (dp, for decidual premolar; p, for premolar; m, for molar). Working on isolated teeth requires the consideration of distinct levels of morphological variation: i. variation depending on the dental locus; ii. variation owing to the occlusal wear; iii. intraspecific or intrataxonomic variation; and iv. interspecific or intertaxonomic variation. In this study, several taxa are described. The association of the material attributed to these taxa is based on several points: i. a similar size; ii. a similar proportion of the maximum mesiodistal length and the maximum linguolabial width; iii. a similar occlusal outline; iv. a similar occlusal pattern (taeniodonty/non-taeniodonty; development, position of cusp[-id]s; presence/absence, continuity/discontinuity, length and height of loph[-id]s; absence/presence and intensity of connections between dental structures; and position of the opening of flexi[-ds]); and v. a compatible occlusal pattern between upper and lower teeth. For teeth at advanced stages of wear, we took into account the potential impact of occlusal wear on characters aforementioned. Based on a wide array of closely or distantly related rodent taxa, our comparisons led to preferentially used a size criterion for the recognition of m1s vs m2s and M1s vs M2s: we considered the m1/M1s to be smaller than the m2/M2s. The recognition of other loci is based on the occlusal shape of teeth (for more details, see descriptions in the Systematic Paleontology section) and on the presence of mesial/distal vertical contact facets due to next teeth. The M3s are characterized by a smaller and more labial hypocone with respect to the protocone than on M1–2 s, characters further constraining the occlusal shape. The argumentation for assigning the teeth to either *Balsayacuy huallagaensis* or *Chachapoyamys kathetos*, which are similar in size, is provided in Online Resource 1 (for upper teeth) and 2 (for lower teeth). From a taeniodont to a non-taeniodont condition, two patterns of pseudo-taeniodonty can be recognized on the studied material: i. pattern I: incomplete posterior arm of the protocone/cristulid from the hypolophid-ectolophid junction and/or crestule from the labial protoloph-mure junction/anterior arm of the hypoconid (if both are present, they are disconnected); and ii. pattern II: posterior arm of the protocone/cristulid from the hypolophid-ectolophid junction and crestule from the labial protoloph-mure junction/anterior arm of the hypoconid linked at their base but not at their top. We restricted our diagnoses and comparisons to the taxa showing a closer morphology. The caviomorph taxa cited in the text and used for comparisons in this study are listed in Table 1. The list of the studied specimens from TAR-55/TAR-55bis, TAR-76 and TAR-77 is available in Table 2, which also includes the measurements made on this material (i.e., maximum mesiodistal length and maximum linguolabial width). For the material from TAR-55/TAR-55bis collected in 2015–2016, we used the measurements made by A. Assemat with a measuroscope Nikon 10 (Assemat et al. 2019). The rest of material was measured by M. Boivin from photos (SEM and optical) using Adobe Photoshop CS4 (2008 Adobe Systems Incorporated). We used Adobe Illustrator CS4 (2008 Adobe Systems Incorporated) and Inkscape 0.92.4 (2020) to design the figures.

*Institutional abbreviations*. LACM, Los Angeles County Museum, Los Angeles, USA; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima, Peru.

*Other abbreviations*. max length, maximum mesiodistal length; max width, maximum labiolingual width; SALMA, South American Land Mammal Age.

## Systematic paleontology

*Nomenclatural remark*. The new species and genus described below shall be referred to Boivin, 2021, following the article 50.1 and the "recommendation 50A concerning multiple authors" of the International Code of Zoological Nomenclature (ICZN 1999: 182).

Order **Rodentia** Bowdich, 1821
Suborder **Ctenohystrica** Huchon, Catzeflis and Douzery, 2000
Infraorder **Hystricognathi** Tullberg, 1899
Parvorder **Caviomorpha** Wood, 1955

Genus ***Balsayacuy*** gen. nov.

*Etymology*. From "Balsayacu", the Sub-Andean Peruvian village in the vicinity of which the type locality was discovered, and "cuy", which means guinea pig in Quechua language. The name Balsayacu refers to the balsa wood, *Ochroma*, with which the rafts are built and used to navigate the Huallaga River and other Amazonian rivers. As

**Table 1** Paleogene caviomorph taxa used for comparisons in this study and cited in the text

| Genus | Species | Locality and/or formation (Fm.) | Age | Observed material (original or cast) | Primary references |
|---|---|---|---|---|---|
| *Cachiyacuy* | *Cc. contamanensis* | Contamana CTA-27 (lower Mb., Pozo Fm.), Peru | Late middle Eocene | MUSM and UM (original and cast) | Antoine et al. (2012); Boivin et al. (2017a) |
| | *Cc.* cf. *contamanensis* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | | Arnal et al. (2020) |
| | *Cc. kummeli* | Contamana CTA-27 (lower Mb., Pozo Fm.) and Santa Rosa ("Yahuarango Fm."), Peru | Late middle Eocene–early Oligocene | MUSM and UM (original and cast) | Antoine et al. (2012); Boivin et al. (2017a) |
| *Canaanimys* | *Cn. maquiensis* | Contamana CTA-27 (lower Mb., Pozo Fm.), Peru | Late middle Eocene | MUSM and UM (original and cast) | Antoine et al. (2012); Boivin et al. (2017a) |
| | *Cn.* cf. *maquiensis* | Santa Rosa ("Yahuarango Fm."), Peru | Late middle Eocene | | Arnal et al. (2020) |
| *Eobranisamys* | *Eb. javierpradoi* | Contamana CTA-27 (lower Mb., Pozo Fm.), Peru | Late middle Eocene | MUSM and UM (original and cast) | Antoine et al. (2012); Boivin et al. (2017a) |
| | *Eb. romeropittmanae* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004) |
| | *Eb. riverai* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004) |
| *Pozomys* | *P. ucayaliensis* | Contamana CTA-29 (lower Mb., Pozo Fm.) and Santa Rosa ("Yahuarango Fm."), Peru | Late middle Eocene–early Oligocene | MUSM and UM (original and cast) | Boivin et al. (2017a, b); Arnal et al. (2020) |
| *Eosallamys* | *Es. paulacoutoi* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004); Arnal et al. (2020) |
| *'Eosallamys'* | *'Es.' simpsoni* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004); Arnal et al. (2020) |
| *Eoespina* | *Ep. woodi* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004); Arnal et al. (2020) |
| *Eosachacui* | *E. lavocati* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004) |
| Chinchilloidea | | | | | |
| *Eoincamys* | *E. ameghinoi* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004) |
| | *E. pascuali* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004) |
| | *E.* aff. *pascuali* | Juanjui TAR-50, Peru | Early Oligocene | MUSM and UM (original and cast) | Assemat et al. (2019) |
| | *E.* cf. *pascuali* | Tarapoto-Shapaja TAR-01 (upper Mb., Pozo Fm.), Peru | Early Oligocene | MUSM and UM (original and cast) | Boivin et al. (2018a) |
| | *E. valverdei* | Tarapoto-Shapaja TAR-20, 21, 13, 22 (upper Mb., Pozo Fm.), Peru | Late Eocene–early Oligocene | MUSM and UM (original and cast) | Boivin et al. (2018a) |
| | *E. parvus* | Tarapoto-Shapaja TAR-20, 21, 22 (upper Mb., Pozo Fm.), Peru | Late Eocene–early Oligocene | MUSM and UM (original and cast) | Boivin et al. (2018a) |
| | *Eoincamys* sp. | Juanjui TAR-49, Peru | Early Oligocene | MUSM and UM (original and cast) | Assemat et al. (2019) |

**Table 1** (continued)

| Genus | Species | Locality and/or formation (Fm.) | Age | Observed material (original or cast) | Primary references |
|---|---|---|---|---|---|
| Octodontoidea | | | | | |
| *Eodelphomys* | *E. almeidacomposi* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004) |
| Erethizontoidea | | | | | |
| *Eopululo* | *E. wigmorei* | Santa Rosa ("Yahuarango Fm."), Peru | ?Late Eocene/early Oligocene | INGEMMET (holotype) | Frailey and Campbell (2004) |

The suprageneric assignment of the taxa follows the phylogenetic results of Boivin et al. (2019b). Fm., Formation; INGEMMET, Instituto Geológico Minero y Metalúrgico Lima; Mb, Member; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos Lima; UM, Université de Montpellier

the new rodent *Balsayacuy* being probably one of the early stem Caviomorpha, its name is also in reference to the "raft" hypothesis to explain the trans-Atlantic dispersal and arrival of hystricognathous rodents in South America from Africa.

*Type species*. *Balsayacuy huallagaensis* sp. nov.

*Species content*. Only the type species.

*Geographic and stratigraphic distribution*. Balsayacu (TAR-55/TAR-55bis and TAR-77 localities), San Martín Department, Pozo Formation, lower member (late middle or early late Eocene), Peru.

*Generic diagnosis*. As for the type and only known species.

***Balsayacuy huallagaensis*** sp. nov.
Figures 2a–v, Table 2

2019 *Cachiyacuy* cf. *kummeli*—Assemat et al.: 707, fig. 3C–E.
2019 *Canaanimys* aff. *maquiensis*—Assemat et al.: 711, fig. 4O, P.

*Etymology*. From the Peruvian Huallaga River, which flows near the type locality.

*Holotype*. MUSM 3935, left M2 (Fig. 2p).

*Referred material*. MUSM 3373 (Assemat et al. 2019: 707, fig. 3E; Fig. 2g), 3908 (Fig. 2i), 3921 (Fig. 2d), left m1s; MUSM 3922 (Fig. 2a), 3923 (Fig. 2e), right m1s; MUSM 3924 (Fig. 2j), 3925, left m2s; MUSM 3910 (Fig. 2h), 3926 (Fig. 2b), 3927 (Fig. 2f), right m2s; MUSM 3928 (Fig. 2c), left m3; MUSM 3929 (Fig. 2n), right fragmentary P4; MUSM 3930 (Fig. 2m), right fragmentary upper molar; MUSM 3934, left fragmentary M1; MUSM 3931–3933 (Fig. 2o, s, t), left M1s; MUSM 3377 (Assemat et al. 2019: 707, fig. 3C; Fig. 2r), right fragmentary M1; MUSM 3378 (Assemat et al. 2019: 707, fig. 3D; Fig. 2k), 3936 (Fig. 2l), left M2s; MUSM 3379 (Assemat et al. 2019: 711, fig. 4P; Fig. 2v), left fragmentary M3; MUSM 3371 (Assemat et al. 2019: 711, fig. 4O; Fig. 2q), left M3; MUSM 3938 (Fig. 2u), right M3.

*Type locality*. TAR-55/TAR-55bis, Balsayacu, San Martín Department, Western Amazonia, Peru.

*Other locality*. TAR-77 (only for MUSM 3921), Balsayacu, San Martín Department, Western Amazonia, Peru.

*Formation and age*. Pozo Formation, lower member, late middle Eocene to early late Eocene (i.e., Barrancan or Mustersan SALMAs).

*Diagnosis*. Small-sized rodent characterized by brachydont and bunolophodont teeth. Lower molars with a pseudo-taeniodont pattern at early stages of wear. Upper teeth with a variable morphology of the lingual protoloph, which can be either complete, reduced to one or two connected or disconnected crestules (i.e., posterior arm of the protocone or crestule from the labial protoloph-mure junction), or absent, but the pseudo-taeniodont pattern is more frequently present. Round P4s with a transverse lingual protoloph, and with a connection of its labial structures (i.e., anteroloph, paracone, mesostyle, and posteroloph) at a moderate stage of wear. P4s and upper molars with a frequently incomplete third transverse crest. P4s and M1–2s without metaloph. If it is present, the metaloph is strongly reduced and lingually free on M3s at early stage of wear. M1–2s frequently with a long mesoloph faintly linked to the mesolophular spur or lingually free (the mesophular spur being absent). Accessory, thin and short enamel structures (posteroloph spur included) may be present between the third crest and the posteroloph, and connected to either or both transverse crests on upper molars. Differs from *Cachiyacuy contamanensis*, *Eobranisamys*, *Eosallamys paulacoutoi*, and '*Eosallamys*' *simpsoni* in having a smaller size. Differs from *Canaanimys*

**Table 2** Dental measurements (in millimeters) of rodent material from TAR-55/TAR-55bis, TAR-76 and TAR-77 (Peru; late middle or early late Eocene) and from CTA-27 (Peru; late Middle Eocene)

| Inventory number | Taxon | Specimen | State | Localitiy | References and figuration | Previous identification | Max lenght | Max width |
|---|---|---|---|---|---|---|---|---|
| MUSM 3908 | *Balsayacuy huallagaensis* | Left m1 | Strongly worn, slightly anteriorly broken | TAR-55/TAR-55bis | This work: Fig. 2i | | 1.43 | 1.45 |
| MUSM 3373 | *Balsayacuy huallagaensis* | Left m1 | | TAR-55/TAR-55bis | Assemat et al. (2019): fig. 3E; this work: Fig. 2g | Cachiyacuy cf. *kummeli* | 1.62 | 1.68 |
| MUSM 3921 | *Balsayacuy huallagaensis* | Left m1 | | TAR-77 | This work: Fig. 2d | | 1.51 | 1.41 |
| MUSM 3922 | *Balsayacuy huallagaensis* | Right m1 | | TAR-55/TAR-55bis | This work: Fig. 2a | | 1.58 | 1.60 |
| MUSM 3923 | *Balsayacuy huallagaensis* | Right m1 | | TAR-55/TAR-55bis | This work: Fig. 2e | | 1.54 | 1.45 |
| MUSM 3924 | *Balsayacuy huallagaensis* | Left m2 | Strongly worn | TAR-55/TAR-55bis | This work: Fig. 2j | | 1.71 | 1.63 |
| MUSM 3925 | *Balsayacuy huallagaensis* | Left m2 | Slightly anterolingually broken | TAR-55/TAR-55bis | This work | | 1.76 | 1.72 |
| MUSM 3910 | *Balsayacuy huallagaensis* | Right m2 | Almost a pristine tooth | TAR-55/TAR-55bis | This work: Fig. 2h | | 1.81 | 1.81 |
| MUSM 3926 | *Balsayacuy huallagaensis* | Right m2 | | TAR-55/TAR-55bis | This work: Fig. 2b | | 1.67 | 1.72 |
| MUSM 3927 | *Balsayacuy huallagaensis* | Right m2 | Pristine, slightly posterolingually broken eroded | TAR-55/TAR-55bis | This work: Fig. 2f | | 1.72 | 1.67 |
| MUSM 3928 | *Balsayacuy huallagaensis* | Left m3 | | TAR-55/TAR-55bis | This work: Fig. 2c | | 1.89 | 1.57 |
| MUSM 3929 | *Balsayacuy huallagaensis* | Right P4 | Anterolabially broken | TAR-55/TAR-55bis | This work: Fig. 2n | | 1.21 | 1.30 |
| MUSM 3930 | *Balsayacuy huallagaensis* | Right M | Lingual fragment, slightly anterolabially broken | TAR-55/TAR-55bis | This work: Fig. 2m | | – | – |
| MUSM 3931 | *Balsayacuy huallagaensis* | Left M1 | | TAR-55/TAR-55bis | This work: Fig. 2o | | 1.46 | 1.59 |
| MUSM 3932 | *Balsayacuy huallagaensis* | Left M1 | | TAR-55/TAR-55bis | This work: Fig. 2t | | 1.54 | 1.76 |
| MUSM 3933 | *Balsayacuy huallagaensis* | Left M1 | | TAR-55/TAR-55bis | This work: Fig. 2s | | 1.43 | 1.55 |
| MUSM 3934 | *Balsayacuy huallagaensis* | Left M1 | Labially broken | TAR-55/TAR-55bis | This work | | 1.55 | 1.64 |
| MUSM 3377 | *Balsayacuy huallagaensis* | Right M1 | Sligthly posterolabially and anterolabially broken | TAR-55/TAR-55bis | Assemat et al. (2019): fig. 3C; this work: Fig. 2r | Cachiyacuy cf. *kummeli* | 1.28 | 1.53 |
| MUSM 3378 | *Balsayacuy huallagaensis* | Left M2 | Sligthly posteriorly broken | TAR-55/TAR-55bis | Assemat et al. (2019): fig. 3D; this work: Fig. 2k | Cachiyacuy cf. *kummeli* | 1.69 | 1.78 |
| MUSM 3935* | *Balsayacuy huallagaensis* | Left M2 | | TAR-55/TAR-55bis | This work: Fig. 2p | | 1.68 | 1.82 |

**Table 2** (continued)

| Inventory number | Taxon | Specimen | State | Localitiy | References and figuration | Previous identification | Max lenght | Max width |
|---|---|---|---|---|---|---|---|---|
| MUSM 3936 | *Balsayacuy huallagaensis* | Left M2 | Strongly worn | TAR-55/TAR-55bis | This work: Fig. 2l | | 1.67 | 1.82 |
| MUSM 3371 | *Balsayacuy huallagaensis* | Left M3 | Pristine tooth | TAR-55/TAR-55bis | Assemat et al. (2019): fig. 4O; this work: Fig. 2q | Canaanimys aff. *maquiensis* | 1.68 | 1.81 |
| MUSM 3379 | *Balsayacuy huallagaensis* | Left M3 | Anteriorly broken | TAR-55/TAR-55bis | Assemat et al. (2019): fig. 4P; this work: Fig. 2v | Canaanimys aff. *maquiensis* | 1.35 | 1.74 |
| MUSM 3938 | *Balsayacuy huallagaensis* | Right M3 | | TAR-55/TAR-55bis | This work: Fig. 2u | | 1.6 | 1.82 |
| MUSM 3907 | *Chachapoyamys kathetos* | Right p4 | Strongly worn | TAR-55/TAR-55bis | This work: Fig. 3n | | 1.51 | 1.53 |
| MUSM 3909 | *Chachapoyamys kathetos* | Left m1 | Eroded | TAR-55/TAR-55bis | This work | | 1.59 | 1.72 |
| MUSM 3374 | *Chachapoyamys kathetos* | Right m1 | Pristine tooth | TAR-55/TAR-55bis | Assemat et al. (2019): fig. 3G; this work: Fig. 3m | Cachiyacuy cf. *kummeli* | 1.73 | 1.85 |
| MUSM 3375 | *Chachapoyamys kathetos* | Right m1 | Anterolingually broken | TAR-55/TAR-55bis | Assemat et al. (2019): fig. 3F; this work: Fig. 3l | Cachiyacuy cf. *kummeli* | 1.37 | 1.58 |
| MUSM 3911 | *Chachapoyamys kathetos* | Left dP4 | Anterolabially broken | TAR-55/TAR-55bis | This work: Fig. 3e | | 1.41 | 1.32 |
| MUSM 3372 | *Chachapoyamys kathetos* | Left P4 | pristine tooth, broken in its middle | TAR-55/TAR-55bis | Assemat et al. (2019): fig. 3A; this work: Fig. 3j | *Cachiyacuy* cf. *kummeli* | 1.31 | 1.81 |
| MUSM 3912 | *Chachapoyamys kathetos* | Right P4 | Pristine tooth, lingually and labially broken | TAR-55/TAR-55bis | This work | | – | – |
| MUSM 3913 | *Chachapoyamys kathetos* | Right P4 | Slightly labially broken | TAR-55/TAR-55bis | This work: Fig. 3d | | 1.44 | 1.58 |
| MUSM 3376 | *Chachapoyamys kathetos* | Left M1 | Eroded, slightly distolabially broken | TAR-55/TAR-55bis | Assemat et al. (2019): fig. 3b; this work: Fig. 3k | Cachiyacuy cf. *kummeli* | 1.17 | 1.62 |
| MUSM 3915 | *Chachapoyamys kathetos* | Right M1 | Strongly worn, slightly labially and posterolingually broken | TAR-55/TAR-55bis | This work: Fig. 3f | | 1.69 | 1.90 |
| MUSM 3937 | *Chachapoyamys kathetos* | Right M1 | | TAR-55/TAR-55bis | This work: Fig. 3i | | 1.72 | 2.01 |
| MUSM 3916 | *Chachapoyamys kathetos* | Left M2 | Nearly a pristine tooth | TAR-55/TAR-55bis | This work: Fig. 3c | | 1.63 | 1.98 |
| MUSM 3917 | *Chachapoyamys kathetos* | Right M2 | | TAR-55/TAR-55bis | This work: Fig. 3b | | 1.89 | 2.32 |
| MUSM 3918* | *Chachapoyamys kathetos* | Right M2 | | TAR-55/TAR-55bis | This work: Fig. 3h | | 1.82 | 2.13 |
| MUSM 3919 | *Chachapoyamys kathetos* | Right M3 | | TAR-55/TAR-55bis | This work: Fig. 3a | | 1.71 | 2.00 |

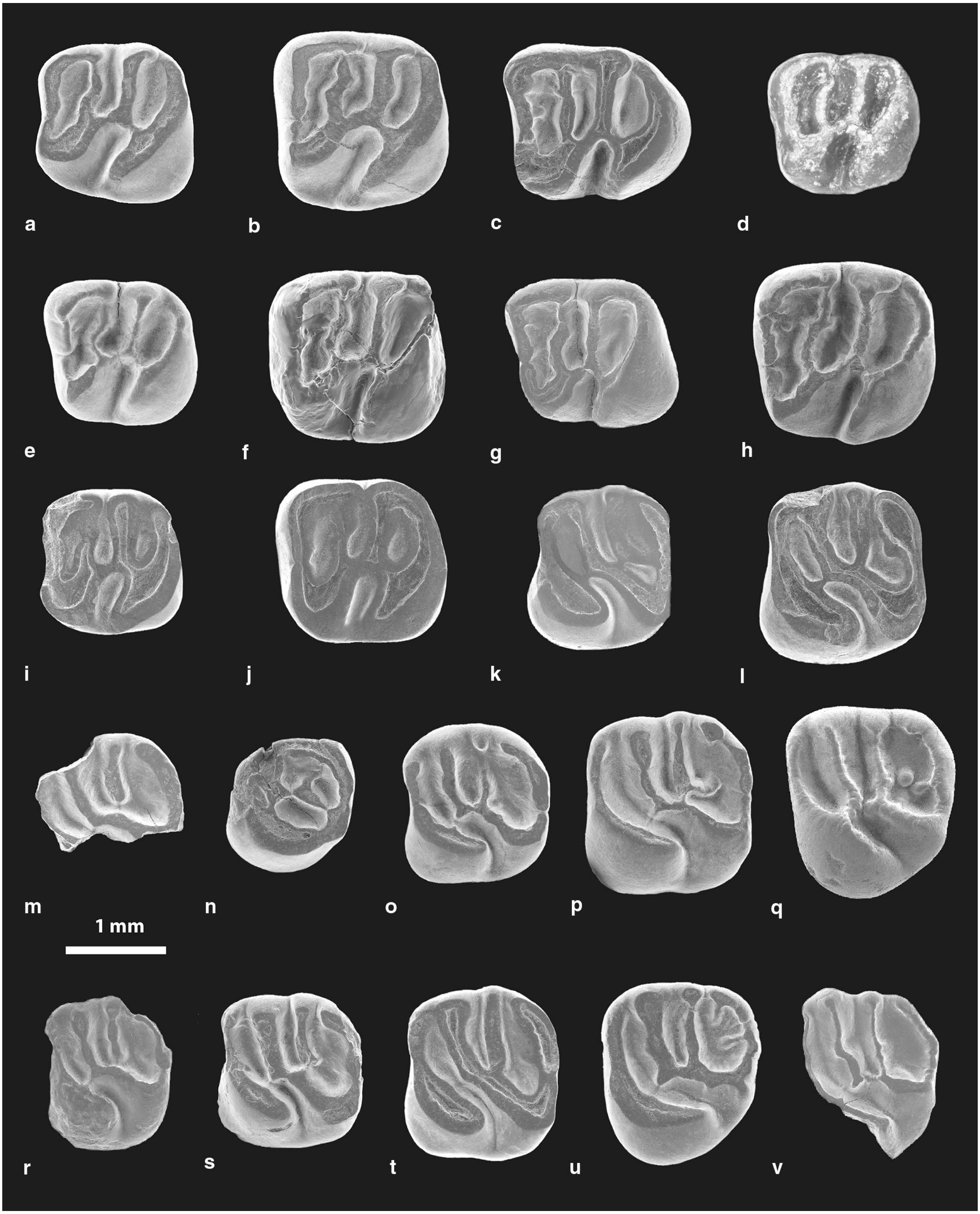
**Table 2** (continued)

| Inventory number | Taxon | Specimen | State | Localitiy | References and figuration | Previous identification | Max lenght | Max width |
|---|---|---|---|---|---|---|---|---|
| MUSM 3920 | *Chachapoyamys kathetos* | Right M3 | Strongly worn | TAR-55/TAR-55bis | This work: Fig. 3g | | 1.71 | 1.98 |
| MUSM 2786 | *Chachapoyamys* cf. *kathetos* | Left M1 or M2 | | CTA-27 | Boivin et al. (2017a): fig. 4.13; this work: Fig. 3o | *Cachiyacuy kummeli* | 1.52 | 1.80 |
| MUSM 3943 | *Chachapoyamys* cf. *kathetos* | Left M1 or M2 | | CTA-27 | This work: Fig. 3p | | 1.47 | 1.90 |
| MUSM 2785 | *Cachiyacuy kummeli* | Left M2 | Pristine, slightly labially broken | CTA-27 | Boivin et al. (2017a): fig. 4.12; this work: Fig. 3q | *Cachiyacuy kummeli* | 1.52 | 1.80 |
| MUSM 3939 | Caviomorpha gen. et sp. indet. 1 | Right m or left M | Labial or lingual fragment | TAR-55/TAR-55bis | This work: Fig. 3s | | 2.11 | 0.91 |
| MUSM 3940 | Caviomorpha gen. et sp. indet. 1 | Left P4 | Eroded, labially broken | TAR-55/TAR-55bis | This work: Fig. 3r | | 1.80 | 2.31 |
| MUSM 3941 | Caviomorpha gen. et sp. indet. 2 | Left dp4 or p4 | Poorly worn, posterior fragment | TAR-76 | This work: Fig. 3t | | 1.35 | 1.79 |

The holotypes of *Balsayacuy huallagaensis* gen. et sp. nov. and *Chachapoyamys kathetos* gen. et sp. nov. are marked with an asterisk. Max lenght, maximum mesiodistal length; Max width, maximum linguolabial width

*maquiensis* in having more square-shaped M1–2s and from *Eobranisamys*, *Es. paulacoutoi*, '*Es.*' *simpsoni*, *Eoespina*, and *Pozomys* in having more transverse M1–2s. Differs from *Cc. contamanensis*, *Cachiyacuy kummeli*, *Es. paulacoutoi*, '*Es.*' *simpsoni*, *Eoespina*, and *Eosachacui* in having a higher tendency toward the taeniodonty; and from *Eobranisamys* and *Pozomys* in having a lower tendency toward the taeniodonty. The metaloph is absent on M1–2s of *Balsayacuy*, differing from the most frequent morphology of this crest in *Cc. contamanensis*, *Canaanimys*, *Eobranisamys*, and *Es. paulacoutoi*, in which the metaloph is present. Differs from *Cc. contamanensis*, *Cc. kummeli*, *Cn. maquiensis*, *Eobranisamys*, *Es. paulacoutoi*, '*Es.*' *simpsoni*, *Eoespina*, and *Eosachacui* in having a mesoloph more frequently faintly linked to the mesolophular spur or lingually free on M1–2s. It further differs from *Cc. kummeli*, *Eobranisamys*, *Eoespina*, and *Pozomys* in having more important developed accessory structures between the third crest and the posteroloph on some upper molars; from *Cc. contamanensis*, *Eobranisamys*, *Eoespina*, and *Es. paulacoutoi* in having more rounded P4s; from *Cc. contamanensis* in having a connection of the labial structures (i.e., anteroloph, paracone, mesostyle, and posteroloph) on P4s at an earlier stage of wear; from *Eoespina* and '*Es.*' *simpsoni* in having a transverse lingual protoloph on P4s; from *Eoespina* in having a stronger connection of the labial structures on P4s at moderate stage of wear; from *Eobranisamys* and *Eosachacui* in having a complete mure on P4s; from *Eosachacui*, *Es. paulacoutoi*, and '*Es.*' *simpsoni* in having a reduced third crest; and from *Pozomys* in having a third crest on P4s.

*Description*. The lower molars (m1–3s) share the same dental structure (Fig. 2a–j). They are rectangular- or square-shaped. The m1s are clearly smaller than m2s. The unique identified m3 (MUSM 3928; Fig. 2c) has a similar width to that of m1s, but it is longer than m1s and m2s. MUSM 3928 is distinguished by a lingual margin of the entoconid that is more labial in position to the mesiolingual corner of the tooth, and by showing a distal expansion and a labiolingual shortness of the posterolophid (Fig. 2c). The m2s have a trigonid and talonid with an equal width, as well as the m1s, but the latter can also show a shorter labiolingual trigonid (MUSM 3922; Fig. 2a). Mesially, there is no trace of anterocingulid at the base of the crown. The protoconid is distally located with respect to the metaconid, and both are linked by a straight metalophulid I. The latter is high and continuous on MUSM 3921 (Fig. 2d). The other lower molars at early stages of wear (MUSM 3910, 3923, 3926, and 3927; Fig. 2b, e, f, h) show a discontinuous metalophulid I, with an anterior arm of the metaconid separate from the anterior arm of the protoconid by a tiny notch, much thinner and shallower on MUSM 3927. On MUSM 3910, 3923, and 3926 (Fig. 2b, e, h), the anterior arm of the protoconid is lower and shorter than the anterior arm of the metaconid,



whereas both are rather similar in size and height on MUSM 3927 (Fig. 2f). On MUSM 3373 (Fig. 2g), the anterior arm of the protoconid is slightly linked to the anterior arm of the metaconid. On MUSM 3922 (Fig. 2a) and the lower molars at more advanced stages of wear (MUSM 3924 and 3928; Fig. 2c, j), the metalophulid I is continuous, but is thinner

◀**Fig. 2** Scanning electron microscope images (in occlusal view) of *Balsayacuy huallagaensis* gen. et sp. nov. from TAR-55/TAR-55bis and TAR-77 (Balsayacu, San Martín Department, Peru; late middle or early late Eocene). **a–c**, **e–p** from TAR-55/TAR-55bis and **d** from TAR-77. **a** MUSM 3922, right m1 (reversed); **b** MUSM 3926, right m2 (reversed); **c** MUSM 3928, left m3; **d** MUSM 3921, left m1; **e** MUSM 3923, right m1 (reversed); **f** MUSM 3927, right m2 (reversed); **g** MUSM 3373, left m1; **h** MUSM 3910, right m2; **i** MUSM 3908, left m1; **j** MUSM 3924, left m2; **k** MUSM 3378, left M2; **l** MUSM 3936, left M2; **m** MUSM 3930, labial fragment of right M (reversed); **n** MUSM 3929, right P4 (reversed); **o** MUSM 3931, left M1; **p** MUSM 3935, left M2; **q** MUSM 3371, left M3; **r** MUSM 3377, right M1 (reversed); **s** MUSM 3933, left M1; **t** MUSM 3932, left M1; **u** MUSM 3938, right M3 (reversed); **v** MUSM 3379, left M3

in its middle part. They had probably a discontinuity of this lophid at an earlier stage of wear. On MUSM 3373, the metaconid bears a very tiny cristulid, distally free on the anteroflexid (i.e., metaconid cristid; Fig. 2g). MUSM 3910 (Fig. 2h) has a cuspid-shaped structure on the anteroflexid and a cristilid on the distal part of the second cristid. The lower molars show a strong and long posterior arm of the metaconid, which is well connected to a mesostylid or to its anterior arm. In contrast, a deep and narrow furrow separates the mesostylid from the entoconid on m1–2s. On the MUSM 3928 m3 (Fig. 2c), the mesostylid has a short, but strong posterior arm, which reaches the anterior arm of the entoconid, thus closing the mesoflexid lingually. The second transverse cristid can be straigth or sinuous (S-shaped). It is somewhat difficult to describe it in some cases inasmuch as it appears continuous and without interruption or irregularities. However, on some teeth (MUSM 3373, 3908, 3910, 3921, and 3928; Fig. 2c, d, g, h, i), this cristid is formed by a long posterior arm of the protoconid, which is connected to a shorter neomesolophid. On MUSM 3923 (Fig. 2e), the neomesolophid is dominant and the posterior arm of the protoconid is short and thin. The ectolophid is continuous and strongly mesiolabially directed, except on some specimens (MUSM 3924, 3925, and 3927, in which it is more longitudinal (i.e., parallel to the mesiodistal axis of the tooth; Fig. 2f, j). The hypoconid and entoconid are labiolingually opposed on MUSM 3910, 3921 and 3927 (Fig. 2d, f, h), whereas the entoconid is more mesially situated than the hypoconid on other lower molars. These two cuspids are linked by a long and straight or slightly oblique hypolophid, which usually connects labially to a short anterior arm of the hypoconid (i.e., absence of taeniodont pattern). On MUSM 3923, 3910, 3921 and 3927 (Fig. 2d–f, h), there are two very short cristulids, one on the distolabial margin of the hypolophid and the other stemming from the hypoconid (its anterior arm), both are clearly spaced, but are joined by the base. Due to the non-connection of these cristulids at their top, the hypoflexid is partly confluent with the metaflexid on this tooth (i.e., pattern II of pseudo-taeniodont). Two lower molars at moderate stages of wear (MUSM 3922 and 3926; Fig. 2a, b) are non-taeniodont, but have a cristulid from the hypolophid + anterior arm of the hypoconid that is thin in its middle or showing difference of height of its anterior and posterior parts. Hence, they were probably pseudo-taeniodont at an earlier stage of wear. The entoconid can display anterior and posterior arms. When it is present, the anterior arm of the entoconid is thin and faintly visible (except on MUSM 3910 and 3921; Fig. 2d, h), contrary to the posterior arm, which is usually stronger. It connects to the posteroloph (MUSM 3373, 3921, and 3926; Fig. 2b, d, g) or remains separated from the latter by a thin and shallow furrow (MUSM 3908, 3910, 3922, 3925, and 3927; Fig. 2a, f, h, i) or by a larger and deeper one (MUSM 3923 and 3928; Fig. 2c, e). The hypoconid is mesiolingually-distolabially compressed and develops a strong and curved posterolophid. There is no hypoconulid. The anteroflexid and metaflexid are mesiodistally wide.

The MUSM 3929 P4 is moderately worn and mesiolabially broken (Fig. 2n). In occlusal view, its crown outline is round with a continuous surrounding crest, which forms the complete margin of the tooth. This surrounding crest is composed of a crestiform protocone, its posterior outgrowth, a minute hypocone, the anteroloph, and the posteroloph. It could also include a mesiolingual crestule stemming from the hypocone, a mesostyle, and a metacone. The labial protoloph is strong and distolingually oriented. Contrary to the straight and complete lingual protoloph, the mure is discontinuous and longitudinal. The anterior arm of the hypocone is more oblique than the labial protoloph and is connected to a mesolophule. The latter shows a transverse and high lingual part and a lower and slightly longer labial part, directed distolabially. Due to its characteristic, its labial part could be a relic of a connection of the third crest with the posteroloph. The two other fossettes of the tooth are one small and mesiolabially-distolingually elongated parafossette and one expanded hypofossette.

M1–3s referred to *Balsayacuy huallagaensis* gen. et sp. nov. are brachydont (Fig. 2k–m, o–v). The M1s are the smallest upper molars, while the M2–3s are quite similar in size. The M3s (MUSM 3371, 3379, and 3938; Fig. 2q, u, v) exhibit a smaller and more labial located hypocone with respect to the protocone than on M1–2 s (Fig. 2k, l, o, p, r–t). On the less worn upper molars (MUSM 3371, 3377, and 3379; Fig. 2q, r, v), the main cusps are usually well defined, especially the cuspate paracone and mesostyle. The metacone can be well defined (MUSM 3371, 3935, and 3938; Fig. 2p, q, u) or crestiform and poorly recognisable from the posteroloph (MUSM 3379 and 3931; Fig. 2o, v). The lingual protoloph is either elevated and complete (MUSM 3371; i.e., non-taeniodont pattern; Fig. 2q), reduced and limited to a tiny posterior arm of the protocone and/or crestule from the labial protoloph-mure junction (MUSM 3377, 3379, 3930, 3931, 3933, 3935, and 3938; i.e., pseudo-taeniodont pattern;

Fig. 2m, o, p, r, s, u, v) or absent (MUSM 3932; i.e., taeniodont pattern; Fig. 2t). MUSM 3377 has a posterior arm of the protocone and crestule from the labial protoloph-mure junction linked at their base, but not at their top (i.e., pattern II of pseudo-taeniodonty; Fig. 2r). The other pseudo-taeniodont upper molars (i.e., pattern I of pseudo-taeniodonty) have either a posterior arm of the protocone, a crestule from the labial protoloph-mure junction, or both. In the latter case, these two crestules remain disconnected. Two upper molars at a moderate stage of wear (MUSM 3378 and 3936; Fig. 2k, l) are non-taeniodont, but they have a thin lingual protoloph. They may have been pseudo-taeniodont when pristine and at earlier stages of wear. The protocone is mesiolingually-distolabially pinched and connected to a strong anteroloph. This mesial transverse crest runs labially and is separated from the paracone by a medium-sized furrow (MUSM 3371, 3379, 3933, and 3935; Fig. 2p, q, s, v) or connected to the mesial base of this cusp (MUSM 3378, 3931, 3932, and 3938; Fig. 2k, o, t, u). The labial protoloph is slightly oblique, whereas the mure is longitudinal (i.e., parallel to the mesiodistal axis of the tooth; except on MUSM 3932; Fig. 2t). The mesostyle is mesially and distally isolated from the paracone and metacone, respectively. The third transverse crest is straight and strongly linked to the mesostyle in most of cases. This crest is usually formed by either a long mesoloph connected to a mesolophular spur (MUSM 3371, 3378, 3933, and 3935; Fig. 2k, p, q, s) or only by a long mesoloph lingually free (MUSM 3377 and 3930; Fig. 2m, r). On MUSM 3931 and 3938, the configuration of the third crest is different: a long and straight mesolophule runs labially and remains isolated from the mesostyle (MUSM 3931; Fig. 2o) or tightly connected to a tiny mesoloph spur (MUSM 3938; Fig. 2u). The metaloph is absent except on the MUSM 3938 M3, in which it is tiny but clearly distinct (Fig. 2u). On that tooth, there are two very short crestules originate from the posteroloph more lingually. The more lingually located crestule is recognized as a posteroloph spur. A posteroloph spur is also recognized on MUSM 3371 (Fig. 2q) and MUSM 3378 (Fig. 2k). MUSM 3371, 3378, and 3935 have accessory structures (i.e., crestule(s) and/or cusp-shaped structures; Fig. 2k, p, q) between the third crest and the posteroloph, which are not interpreted as remnants of metaloph. These structures can be associated to a posteroloph spur (MUSM 3371 and 3378). They can be either isolated (MUSM 3371; Fig. 2q) or linked to the third crest (MUSM 3935; Fig. 2p) or to the third crest and posteroloph spur (MUSM 3378; Fig. 2k). The two worn upper molars, MUSM 3932 (Fig. 2t) and MUSM 3936 (Fig. 2l), show a small and rounded enlargement of the anterolingual enamel margin, which may correspond to a posteroloph spur or/and accessory structures. The hypocone bears a low posterior arm, which faintly connects to the longer posteroloph.

*Comparisons*. By its brachydonty, bunolophodonty, thin and roughly transverse loph(-id)s, tetralophodont lower molars, with a strong posterior arm of the metaconid, mesostylid and complete second transverse cristid, the presence of a mesostyle and third transverse crest on upper teeth, and the presence of a metacone on upper molars, the morphology of *Balsayacuy* is strongly reminiscent of that found in several Paleogene caviomorphs. By its upper molars with a strong reduction or absence of the metaloph, *Balsayacuy* recalls *Cachiyacuy* cf. *contamanensis* 2 and *Pozomys ucayalensis* (CTA-29 and Santa Rosa; Boivin et al. 2017a; Arnal et al. 2020), *Eoespina woodi*, *Eosachacui lavocati*, and '*Eosallamys*' *simpsoni* (Santa Rosa; Frailey and Campbell 2004; Arnal et al. 2020). On MUSM 2832 attributed to *Cc*. cf. *contamanensis* 2 from CTA-29, the metaloph is longer than MUSM 3938, the unique upper molar of *Balsayacuy* with a metaloph. On LACM 143374 and 143398 of '*Es*.' *simpsoni*, the metaloph is connected to the posteroloph or very close to the posteroloph spur, respectively, contrary to MUSM 3938. The morphology of the MUSM 3936 P4 attributed to *Balsayacuy* is closer to that of *Eoespina*. Particularly, the LACM 143459 P4 of *Eoespina* is characterized by an incomplete third crest disconnected to the mesostyle, and by a thin lingual protoloph as in *Balsayacuy*. Moreover, no metaloph is distinct on LACM 143459, like on MUSM 3936, but the posteroloph is thicker and may be fused with a metaloph contrary to MUSM 3936. Some upper molars of *Cc*. cf. *contamanensis* 2 from CTA-29, *Eosachacui* and *Pozomys* can have a long mesoloph, more or less connected to a very short mesolophule, as some M1–2s from TAR-55/TAR-55bis assigned to *Balsayacuy*. Particularly, the LACM 159207 M1 or M2 of *P. ucayalensis* (Arnal et al. 2020: 203, fig. 4C) displays the mesoloph less connected to the mesolophule, and in addition with a tiny crestule on its distolingual extremity directed towards (but not linked to) a posteroloph spur, a configuration close to the morphology of some upper molars of *Balsayacuy*. The lower and upper molars of *Balsayacuy* shows a tendency toward the taeniodonty (particularly on its upper molars), a character found in *P. ucayalensis*, as well as in *Eobranisamys* (CTA-27 and Santa Rosa; Frailey and Campbell 2004; Boivin et al. 2017a). Nevertheless, the latters usually show a taeniodont pattern much more achieved. Moreover, lower molars of *Balsayacuy* strongly differ from those of *P. ucayalensis* in having a very thin discontinuity of the metalophulid I, which is connected to the protoconid. *Balsayacuy* also differs from *Pozomys* in having a third crest on P4s; from *Eoespina* and '*Es*.' *simpsoni* in having P4s with transverse lingual protoloph; from *Eoespina* in having a stronger connection of the labial structures at moderate stage of wear; from *Eobranisamys* and *Eoespina* in having rounded P4s; from *Eobranisamys* and *Eosachacui* with a complete mure on P4s; from *Eosachacui* and '*Es*.' *simpsoni* in having a reduced third crest on P4s; and from *Eobranisamys* in displaying upper molars with either a reduced metaloph, or devoid of this crest. The presence of accessory crestules between the third transverse crest and the posteroloph on upper molars is a character also found in two basal caviomorphs from Peru: *Cachiyacuy* and *Eosallamys* (Eocene localities of Contamana, Balsayacu-Juanjui, and Santa Rosa; Frailey and Campbell 2004; Antoine et al. 2012; Boivin et al. 2017a; Assemat et al. 2019; Arnal et al. 2020). Besides, *Cachiyacuy* and *Eosallamys* can exhibit a long mesoloph faintly connected to a mesolophular spur, as well as a reduction of the metaloph. Although the more frequent configuration in *Cachiyacuy contamanensis* is a long metaloph terminating very close to the crestules between the third crest to the posteroloph (it can be connected to both crests or only to the posteroloph), some upper molars of this species have a more or less reduced metaloph, and the latter can be absent (MUSM 2744; Boivin et al. 2017a) as in *Balsayacuy*. Upper molars of *Cachiyacuy* cf. *contamanensis* from Santa Rosa (Arnal et al. 2020) have a reduced metaloph, but the latter is always more developed than on molars of *Balsayacuy*. In *Eosallamys paulacoutoi* (Santa Rosa; Frailey and Campbell 2004; Arnal et al. 2020), the metaloph can be more reduced as on MUSM 3938 from TAR-55/TAR-55bis. However, the upper molars of *Cachiyacuy* cf. *contamanensis* and *Es. paulacoutoi* always have a metaloph, and the latter is rarely lingually free. *Balsayacuy* differs from *Cc. contamanensis* and *Eosallamys* in having more rounded P4s; from *Cc. contamanensis* in having a connection of the labial structures (i.e., anteroloph, paracone, mesostyle, and posteroloph) on P4s at an earlier stage of wear; and from *Eosallamys* in having a reduced third crest on P4s. *Cachiyacuy kummeli* (CTA-27 and Santa Rosa; Antoine et al. 2012; Boivin et al. 2017a; Arnal et al. 2020; this work) has upper molars with a metaloph lingually free, well-marked (MUSM 1882 and 1884 [Antoine et al. 2012: fig. 2m, o], LACM 159246 [Arnal et al. 2020: fig. 2T]), reduced (MUSM 1883 [Antoine et al., 2012: fig. 2n], LACM 159244 [Arnal et al. 2020: fig. 2V], and LACM 159250 [Arnal et al. 2020: fig. 2W]) or absent (MUSM 2785 [Boivin et al. 2017a: fig. 4.12]; Fig. 3q). On MUSM 1882, 1884, and LACM 159246, the metaloph is longer than that in *Balsayacuy* (when it is present). Teeth of *Balsayacuy* are smaller than those of *Cc. contamanensis*, *Cc.* cf. *contamanensis* 2 from CTA-29, *Cc.* cf. *contamanensis* from Santa Rosa, *Eobranisamys*, *Es. paulacoutoi* and '*Es.*' *simpsoni*. Their size is similar to that of *Cc. kummeli* and *Canaanimys maquiensis* (CTA-27; Antoine et al. 2012; Boivin et al. 2017a). *Balsayacuy* differs from *Cc. contamanensis*, *Cc.* cf. *contamanensis* 2 from CTA-29,*Cc.* cf. *contamanensis* from Santa Rosa, *Cc. kummeli*, and *Es. paulacoutoi* in having a stronger tendency toward the taeniodonty on molars at early stages of wear, which can develop a pseudo-taeniodont (the more frequent case) or a taeniodont pattern. Some M3s of *Cn. maquiensis* and the LACM 159351 M1 of *Canaanimys* cf. *maquiensis* from Santa Rosa (Arnal et al. 2020: 201, fig. 3A) have a very short metaloph lingually free, but on their other upper molars, this crest turns forward and terminates close to the third crest and can connect to the latter unlike in *Balsayacuy*. Contrary to *Balsayacuy*, *Canaanimys* cf. *maquiensis* has some lower molars with an incomplete second cristid; and P4s with a metaloph, a complete transverse third crest and a slightly oblique lingual protoloph. Finally, *Balsayacuy* differs from *Cachiyacuy* cf. *contamanensis*, *Canaanimys* cf. *maquiensis*, *Eobranisamys*, *Es. paulacoutoi*, *Ep. woodi*, and *P. ucayalensis* in having M1–2s more transverse and from *Cn. maquiensis* in having M1–2s more square-shaped. Some teeth from TAR-55/TAR-55 attributed here to *Balsayacuy* were formerly considered as *Cachiyacuy* cf. *kummeli* (MUSM 3373, 3377, and 3378) or *Canaanimys* aff. *maquiensis* (MUSM 3371 and 3379; Assemat et al. 2019). The discovery of new dental material from TAR-55/TAR-55bis and TAR-77 including new loci has allowed us to refine these attributions. The material defining *Balsayacuy* is characterized by a mosaic of traits principally shared with *Cachiyacuy*, *Canaanimys*, *Eosallamys*, *Eoespina*, and *Pozomys*. This combination of characters and the morphological tendencies of this taxon are somewhat singular, which leads us to propose here a new taxon: *Balsayacuy huallagaensis* gen. et sp. nov.

Genus ***Chachapoyamys*** gen. nov.

*Etymology*. From the Andean-Amazonian Chachapoya culture, once developed in the Balsayacu area, and -mys (Greek for mouse).

*Type species*. *Chachapoyamys kathetos* sp. nov.

*Species content*. Only the type species.

*Geographic and stratigraphic distribution*. Contamana (CTA-27), Loreto Department and Balsayacu (TAR-55/TAR-55bis), San Martín Department, Pozo Formation, lower member (late middle–early late Eocene), Peru.

*Generic diagnosis*. As for the type and only known species.

***Chachapoyamys kathetos*** sp. nov.
Figure 3a–n, Table 2

2019 *Cachiyacuy* cf. *kummeli*—Assemat et al.: 707, fig. 3A, B, F, G.

*Etymology*. From κάθετος (kathetos, Greek for vertical, upraised), referring to the vertical layers in which the holotype and referred specimens were found, at TAR-55/TAR-55bis locality.

*Holotype*. MUSM 3918, right M2 (Fig. 3h).

*Referred material*. MUSM 3907 (Fig. 3n), right p4; MUSM 3909, left m1; MUSM 3375 (Assemat et al. 2019: 707, fig. 3F; Fig. 3l), right fragmentary m1; MUSM 3374 (Assemat et al. 2019: 707, fig. 3G; Fig. 3m), right m1; MUSM 3911 (Fig. 3e), left fragmentary dP4; MUSM 3372 (Assemat et al. 2019: 707, fig. 3A; Fig. 3j), left fragmentary P4; MUSM 3912, 3913 (Fig. 3d), right fragmentary P4s; MUSM 3915 (Fig. 3f), 3937 (Fig. 3i), right M1s; MUSM 3916 (Fig. 3c), left M2; MUSM 3917 (Fig. 3b), right M2; MUSM 3919 (Fig. 3a), 3920 (Fig. 3g), right M3s.

*Tentatively referred material*. MUSM 3376 (Assemat et al. 2019: 707, fig. 3B; Fig. 3k), left fragmentary M1.

*Type locality*. TAR-55/TAR-55bis, Balsayacu, San Martín Department, Western Amazonia, Peru.

*Formation and age*. Pozo Formation, lower member, late middle Eocene to early late Eocene (i.e., Barrancan or Mustersan SALMAs).

*Diagnosis*. Small-sized rodent characterized by brachydont, bunolophodont and non-taeniodont teeth. p4s and lower molars with a short posterior arm of the metaconid and a discontinuity of the metalophulid I, which can generate a wide notch. Oval P4s with a third crest connected to the mesostyle and anterior arm of the hypocone, and the presence of a metaloph. Transverse lower and upper molars. M1–2s with an absent or strongly reduced metaloph lingually free or completely isolated on the posterior flexus. M3s with an absent or short metaloph lingually free. Accessory, thin and short enamel structures (posteroloph spur included) almost always present between the third crest and the posteroloph on dP4s and upper molars, and connected to either or both transverse crests on upper molars. Differs from *Cachiyacuy contamanensis*, *Eobranisamys*, *Eosallamys paulacoutoi*, and ‘*Eosallamys*’ *simpsoni* in having a smaller size; from *Balsayacuy*, *Cachiyacuy*, *Canaanimys*, *Eobranisamys*, *Eoespina*, *Eosachacui*, *Es*. *paulacoutoi*, ‘*Es*.’ *simpsoni*, and *Pozomys* in having more transverse lower molars; and from *Balsayacuy*, *Cachiyacuy*, *Eobranisamys*, *Eoespina*, *Eosachacui*, *Es*. *paulacoutoi*, ‘*Es*.’ *simpsoni*, and *Pozomys* in having more transverse upper molars. Differs from *Balsayacuy*, *Eobranisamys*, *Canaanimys*, and *Pozomys* in having teeth always non-taeniodont. Differs from *Pozomys* in having a curved (i.e., mesially concave) second cristid on p4s; from *Eoespina*, *Eosachacui*, *Es*. *paulacoutoi*, and some p4s of *Cc*. *contamanensis* in being devoid of accessory cristulids (mesolophid included) on the anteroflexid and/or mesoflexid on p4s; from *Cachiyacuy*, *Eoespina*, *Es*. *paulacoutoi*, and ‘*Es*.’ *simpsoni* in having a more important discontinuity of the metalophulid I on p4s; from *Balsayacuy*, *Cachiyacuy*, *Canaanimys*, *Eobranisamys*, *Eoespina*, *Eosachacui*, *Es*. *paulacoutoi*, and ‘*Es*.’ *simpsoni* in having lower molars, which can have a more important discontinuity of the metalophulid I; from *Balsayacuy* in having a shorter anterior arm of the metaconid on lower molars, and oval P4s with a third crest connected to the mesostyle and the presence of a metaloph; from *Balsayacuy* and *Es*. *paulacoutoi* in having P4s with a oblique lingual protoloph; from *Balsayacuy* and *Eobranisamys* in having P4s with a paracone, which remains separate from the mesostyle at a moderate stage of wear; from *Eosachacui* and ‘*Es*.’ *simpsoni* in having a metaloph on P4s; from *Eosachacui* in having non-taeniodont P4s; from *Eobranisamys* and *Eosachacui* in having P4s with a complete mure; from *Eoespina* in having P4s with always a third crest connected to the mesostyle; from *Eobranisamys* and ‘*Es*.’ *simpsoni* in having a reduced metaloph disconnected to the posteroloph on dP4s; from *Eosachacui* in having a relictual metaloph on the posterior flexus on dP4s; and from *Balsayacuy*, *Cachiyacuy kummeli*, *Eobranisamys*, *Eoespina*, and *Pozomys* in having some upper molars with more important developed accessory structures between the third crest and the posteroloph, which connect both crests. The metaloph is absent or reduced to a very short crest lingually free on M1–2s of *Chachapoyamys*, differing from the most frequent morphology of this crest in *Cachiyacuy contamanensis*, *Canaanimys*, and *Eobranisamys*, in which the metaloph is longer. Differs from *Es*. *paulacoutoi* in having a metaloph (when present) more reduced and isolated on the posterior flexus on M1s, a shorter metaloph lingually free on M2s and lingually free (when present) on M3s..

*Description*. The MUSM 3907 p4 is moderately eroded and shows digestion marks (Fig. 3n). It has rounded corners. Although being narrower than the talonid, the trigonid is wide, its width being about 77% of that of the talonid. With wear, the four main cuspids (i.e., metaconid, entoconid, protoconid, and hypoconid) are not discernable from the lophids, especially the protoconid and hypoconid areas, which correspond to large dentine platforms. The metaconid and protoconid areas are well separate. The metaconid develops mesiolabially a transverse and short anterior arm being separate from the protoconid by a wide and deep notch. Besides, the metaconid distally bears a very short, but strong posterior arm. There is no anterocingulid. The posterior arm of the metaconid slightly joins a mesostylid, which corresponds with wear to a small and rather round structure of dentine, surrounded by enamel. Stemming from the protoconid area, the second transverse cristid is mostly mesially concave, being distalolingually directed toward the metaconid and mesostylid. The eroded condition of the p4 does not allow to state if a connection is present between these structures. The ectolophid is strong and longitudinal, linking the protoconid to the long and roughly transverse hypolophid. The ectolophid being labially located, it delimits, with the

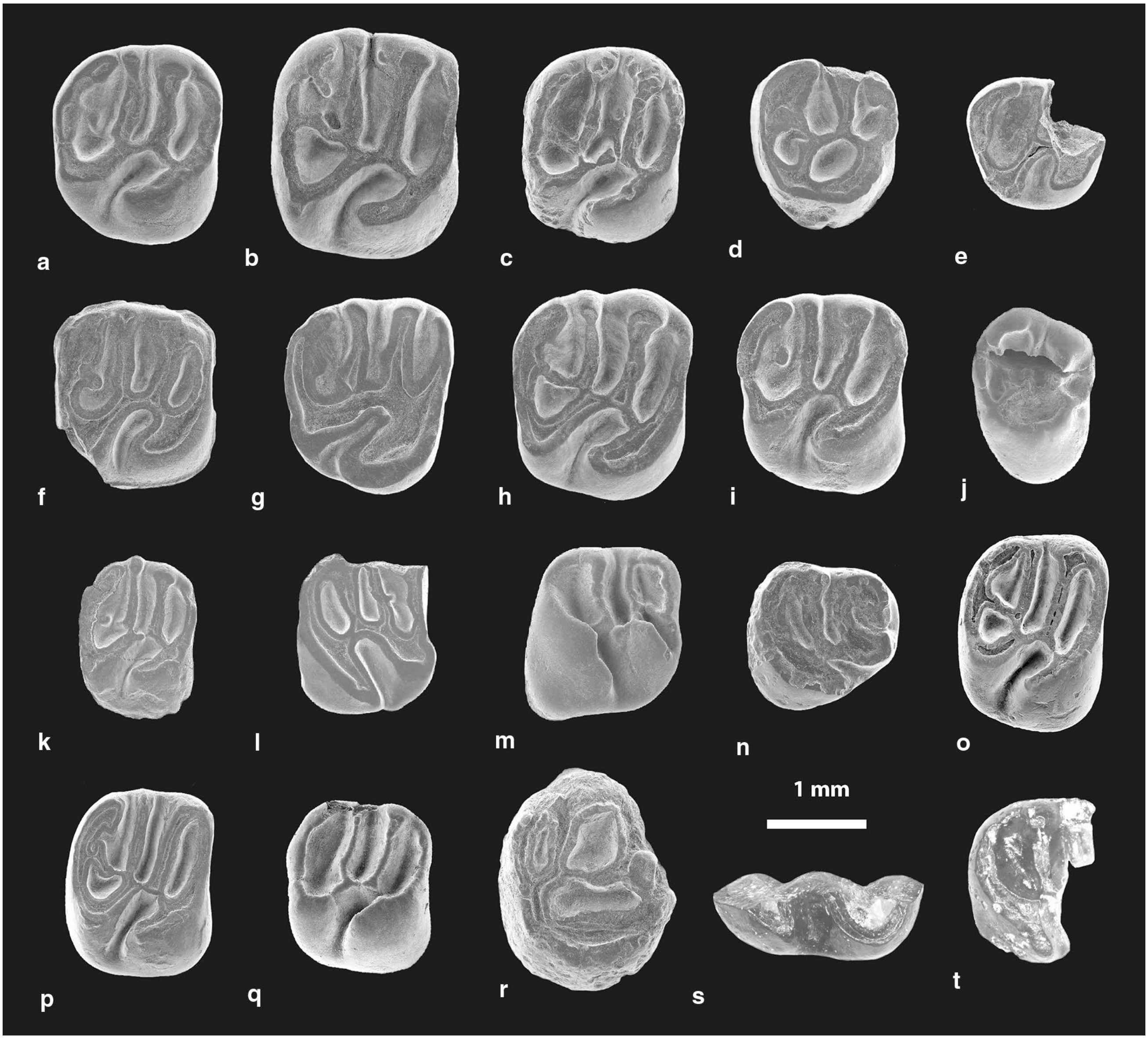


**Fig. 3** Scanning electron microscope images (in occlusal view) of fossil caviomorph teeth from the Eocene Peruvian localities (CTA-27, TAR-55/TAR-55bis, and TAR-76). **a–n** *Chachapoyamys kathetos* from TAR-55/TAR-55bis. **o, p** *Chachapoyamys* cf. *kathetos* from CTA-27. **q, r** Caviomorpha gen. et sp. indet. 1 from TAR-55/TAR-55bis. **s, t** Caviomorpha gen. et sp. indet. 2 from TAR-76. **u** *Cachiyacuy kummeli* from CTA-27. **a** MUSM 3919, right M3; **b** MUSM 3917, right M2; **c** MUSM 3916, left M2 (reversed); **d** MUSM 3913, right P4; **e** MUSM 3911, left dP4 (reversed); **f** MUSM 3915, right M1; **g** MUSM 3920, right M3; **h** MUSM 3918, right M2 (holoype); **i** MUSM 3937, right M2; **j** MUSM 3372, left P4 (reversed); **k** MUSM 3376, left M1 (reversed); **l** MUSM 3375, right m1; **m** MUSM 3374, right m1; **n** MUSM 3907, right p4; **o** MUSM 2786, left M1 or M2 (reversed); **p** MUSM 3943, left M1 or M2 (reversed); **q** MUSM 2785, left M2 (reversed); **r** MUSM 3940, left P4 (reversed); **s** MUSM 3939, labial fragment of right m or lingual fragment of left M; **t** MUSM 3941, posterior fragment of left dp4 or p4 (reversed)

protoconid, the hypoconid, and its anterior outgrowth, a small hypoflexid, poorly extended labiolingually. A very short anterior arm of the hypoconid seems to be faintly connected to the hypolophid (i.e., non taeniodont pattern). The distal cristid formed by the fusion of the hypoconid, its anterior outgrowth and a strong and curved posterolophid, runs lingually and reaches the posterior arm of the entoconid. Moreover, a short cristulid on the metaflexid links the anterior margin of the posterolophid to the hypolophid. As a result of this double connection of the posterolophid with the entoconid-hypolophid, the metaflexid is lingually closed and divided into two subfossettids, a small and round lingual one and a labial one, more labiolingually extended.

The lower molars are brachydont and rectangular, being wider than long (Fig. 3l, m). Contrary to the p4s, the trigonid and talonid are roughly similar in width, although the trigonid can be slightly narrower than the talonid (MUSM 3374; Fig. 3m). All lower molars are tetralophodont and non-taeniodont. The metaconid, protoconid and hypoconid are crestiform, whereas the entoconid and mesostylid are in contrast highly cuspate. On the unworn MUSM 3374 m1 (Fig. 3m), the protoconid, distolabially-mesiolingually pinched, is the highest cuspid of the tooth. The lower and smaller metaconid is positioned on the mesial margin of the tooth, and is mesiodistally compressed. This cuspid bears a strong, short and curved posterior arm faintly linked to a small mesostylid. On MUSM 3909, the protoconid and metaconid are linked by a strong and complete metalophulid I. On MUSM 3375 (Fig. 3l), the latter is formed by two cristids, a lingual long anterior arm of the metaconid connecting to a shorter labial anterior arm of the protoconid. On MUSM 3374 (Fig. 3m), the protoconid is well separated from the anterior arm of the metaconid by a large and deep notch. The anterior arm of the protoconid seems to be absent, but it is possible that it would appears on the labial slope of the anterior arm of the metaconid at a more advanced stage of wear. At the junction between the two anterior arms, a short cristid runs distolingually on the anteroflexid and then ends close to the base of a spur on the mesial margin of the second transverse cristid. MUSM 3375 also shows a very short spur on the mesial margin of the second transverse cristid (Fig. 3l). The second cristid, connecting the mesostylid to the protoconid, is quite thin and S-shaped on MUSM 3374 (Fig. 3m), and distolingually directed on MUSM 3375 (Fig. 3l). The ectolophid can be roughly longitudinal (i.e., parallel to the mesiodistal axis of the tooth; MUSM 3374 and 3375; Fig. 3l, m) or more oblique (MUSM 3909). The hypolophid is strong and transverse (MUSM 3375 and 3909; Fig. 3l) or slightly curved (MUSM 3374; Fig. 3m). It is connected labially to a thin but high and complete anterior arm of the hypoconid. The hypoconid has a long and mesiolabially oriented outgrowth. The entoconid is more mesially positioned with respect to the hypoconid, and bears a strong and short posterior arm on MUSM 3374 (Fig. 3m). The posterolophid reaches the posterior arm of the entoconid and thus the metaflexid is closed lingually, forming a broad metafossettid.

The dP4 (MUSM 3911; Fig. 3e) is damaged and moderately worn. The paracone, labial protoloph, and most of the anteroloph are missing. Although damaged, the distal margin of this tooth and the preserved lingual part of its mesial margin suggest that this tooth would have been trapezoidal. Among the present cusps/styles, only the mesostyle on the labial margin is clearly visible. The mesostyle is mesially and distally separate from the paracone and the labial extremity of the posteroloph. The protocone corresponds to a large dentine platform due to wear. A lingual protoloph is strong and links the protocone to the mure (i.e., non-taeniodont pattern). The latter is complete and oblique, but not aligned with the anterior arm of the hypocone. The probable third transverse crest is straight and continuous. The metacone is not discernable, entirely subsumed within the posteroloph. The latter is long and curved. On the posterior flexus (i.e., confluence of the distal mesoflexus with the metaflexus), there is a wide structure corresponding to a thin dentine line, surrounded by massive enamel layer. It is mesiolabially directed, contiguous to the distal part of the third crest and to the mesial slope of the metacone. This structure is probably a part of the metaloph and/or relictual connections of this loph with the third crest and the posteroloph.

Three specimens are fragmented P4s (MUSM 3372, 3912, and 3913; Fig. 3d, j). Being slightly broken on its labial margin, MUSM 3913 is the most complete of the three (Fig. 3d). MUSM 3912 is damaged labially and lingually and the central part of MUSM 3372 is missing (Fig. 3j). MUSM 3372 and 3913 are oval in occlusal outline. With its paracone more lingually situated than the mesostyle and metacone, MUSM 3372 (Fig. 3j) shows a mesial part narrower than its distal part. The labial cusps/styles are well defined, whereas the protocone and hypocone are strongly crestiform. Via its long and curved posterior outgrowth, the protocone is twinned with the hypocone, forming a protocone-hypocone complex that closes the hypoflexus lingually. The anteroloph, low and short, remains separate from the paracone (MUSM 3372 and 3913) or reaches the base of this cusp (MUSM 3912). The paracone is clearly the largest cusp and displays a strong and oblique labial protoloph. The lingual extremity of the labial protoloph is mesially connected to a complete and distolabially directed lingual protoloph and distally to a high and longitudinal mure. On MUSM 3372 (Fig. 3j), the mesostyle and metacone are equal-sized. The mesostyle is separate from the paracone by a very thin furrow and it is faintly connected to the labial extremity of the posteroloph. The metacone, slightly less distinct, is subsumed within the long posteroloph. Due to the advanced stage of wear of MUSM 3913 (Fig. 3d), the mesostyle, metacone and their potential associated lophs (i.e., mesoloph and metaloph, respectively) are fused on this tooth. They are probably subsumed within the posteroloph, forming a posterior broad dentine platform. On this P4, there are two short crestules on the anterior arm of the hypocone: anteriorly a mesolophule and posteriorly a neocrestule lingually free. The mesolophule appears to have two connections with the posterior platform, which could be with a mesoloph stemming from the mesostyle and a metaloph from the metacone. Despite of its fragmentary state, MUSM 3372 (Fig. 3j) shows a third transverse crest, connected to the mesostyle and the anterior arm of the hypocone, a metaloph, and a tiny damaged crest on the anterior arm of the hypocone backward to the third crest. This damaged crest being aligned with the metaloph, which seems to be unconnected to the posteroloph, might be a rest of a connection of the metaloph with the anterior arm of the hypocone. Another hypothesis is that it could be a neocrest lingually free as on MUSM 3913 (Fig. 3d).

The upper molars referred here to *Chachapoyamys kathetos* are brachydont, transverse and non-taeniodont (Fig. 3a–c, f–i, k). M2s are larger than M1s and M3s, and M1s are the smallest upper molars. The M3s differ from other upper molars in having a hypocone clearly displaced much more labially. On the nearly pristine M2 (MUSM 3916; Fig. 3c), the protocone, strongly mesiolingually-distolabially pinched, is not discernable from its anterior arm and its posterior outgrowth, forming a high curved crest on the mesiolingual corner of the tooth. This crest, as well as the hypocone and its anterior and posterior arms, are the highest structures of the tooth. The anterior arm of the protocone and posterior arm of the hypocone are connected to a low and long anteroloph and posteroloph, respectively. The anteroloph can remain separate from the paracone by a tiny and shallow furrow (MUSM 3376, 3916–3918 and 3937; Fig. 3b, c, h, I, k) or can be faintly connected to this cusp (MUSM 3919; Fig. 3a). On MUSM 3917 (Fig. 3b), the labial extremity of the anteroloph is enlarged and could correspond to a parastyle. With wear, the posterior outgrowth of the protocone becomes longer especially on M2s and M3s. As a result of the development of a long posterior outgrowth of the protocone on these molars, the hypoflexus is more mesiodistally constricted. The lingual protoloph is always strong and complete. The labial protoloph is slightly oblique (i.e., mesiolabially directed) and the third transverse crest can be straight or parallel to the labial protoloph (MUSM 3919; Fig. 3a). The third crest is composed of a long mesoloph stemming from the mesostyle associated with a mesolophular spur originating on the anterior arm of the hypocone. The mure is usually roughly longitudinal, but it can be more oblique as on M3s (Fig. 3a, g) and MUSM 3916 (Fig. 3c). On MUSM 3376 (Fig. 3k) and 3916 (Fig. 3c), the mure is incomplete because disconnected to the labial protoloph. On the labial margin, the mesostyle and the paracone are well defined and bulbous, the latter cusp being very large and protruding. These two cusps remain separate on all upper molars by a tiny furrow. On MUSM 3916 (Fig. 3c), there is an additional cusp-shaped structure between the labial protoloph and the third crest. On MUSM 3917 (Fig. 3b), a metacone is present on the distolabial corner of the tooth and displays thin anterior and posterior arms as well as a short metaloph lingually free. On other upper molars, there is no distinct metacone, the latter being probably subsumed within the posteroloph. On MUSM 3918 (Fig. 3h) and 3920 (Fig. 3g), a thin metaloph lingually free is anteriorly oriented. MUSM 3937 displays a rounded structure on the posterior flexus, which probably corresponds to a residual metaloph (Fig. 3b). There is no metaconule. The posteroloph bears a posteroloph spur, almost incipient (MUSM 3916; Fig. 3c) or more developed (MUSM 3917, 3918, and 3919; Fig. 3a, b, h). It can reach an accessory crestule or a net of accessory crestules connected to the mesoloph-mesolophule junction (MUSM 3917 and 3918; Fig. 3b, h) or can be free (MUSM 3916 and 3919; Fig. 3a, c). In the latter case, it can end close to the accessory crestule stemming from the mesoloph-mesolophule junction (MUSM 3916; Fig. 3c).

*Remarks*. Although the MUSM 3376 M1 (Fig. 3k) is fragmentary, it has a smaller size with respect to the other M1s assigned to *Chachapoyamys kathetos*. Owing its characters similar to the other upper molars of *Ch. kathetos* (i.e., brachydonty, transversality, non-taeniodonty, third crest corresponding to a long mesoloph associated with a mesolophular spur, and accessory crestules between the third crest and the posteroloph), we consider that MUSM 3376 would have documented a small individual of this taxon.

*Comparisons*. By its brachydonty, bunolophodonty, thin and roughly transverse loph(-id)s, tetralophodont p4s and lower molars, with a posterior arm of the metaconid, mesostylid and complete second transverse cristid, the presence of a mesostyle, metacone and complete third transverse crest on upper teeth, and the presence of the metaloph (although strongly reduced) on some upper teeth, the morphology of *Chachapoyamys* from TAR-55/TAR-55bis is strongly reminiscent of that found in several Paleogene caviomorphs, particularly five basal caviomorph representatives: *Cachiyacuy*, *Canaanimys*, *Eoespina*, *Eosachacui*, and *Eosallamys* from Peru (Eocene localities of Contamana, Balsayacu-Juanjui, and Santa Rosa; Frailey and Campbell 2004; Antoine et al. 2012; Boivin et al. 2017a; Assemat et al. 2019; Arnal et al. 2020), as well as *Balsayacuy huallagaensis* gen. et sp. nov. described above. By its non-taeniodonty, an important development of crestules (crestule from the third crest and posteroloph spur included) between the third transverse crest and the posteroloph on dP4s and upper molars, which can connect these two transverse crests on some upper molars, this species from TAR-55/TAR-55bis is close to *Cachiyacuy contamanensis* from CTA-27 (Contamana, Peru; late middle Eocene; Antoine et al. 2012; Boivin et al. 2017a), *Cachiyacuy* cf. *contamanensis* and *Eosallamys paulacoutoi* from Santa Rosa (Peru, ?late Eocene/early Oligocene; Frailey and Campbell 2004; Arnal et al. 2020). The M1–2 s of *Cc. contamanensis* usually have a well-marked metaloph longer than on MUSM 3917, the unique upper molar of *Chachapoyamys* that distinctly bears this crest. In most cases, *Cc. contamanensis* has upper molars bearing a metaloph that ends very close to the crestules linking the third crest to the posteroloph (it can be connected to them), or that is only connected to the posteroloph (via crestules or not). Conversely, the short metaloph, which remains lingually free on MUSM 3917, is remote from these crestules. However, in *Cc. contamanensis*, the M3s show more frequently a reduction of the metaloph, whereas its M1–2s exhibit a high morphological variation of this crest in terms of development and connections. Indeed, on some M1–2s, the metaloph can be reduced to a short crest or a very short spur, or absent (MUSM 2744), and can be lingually free and far from the crestules between the third crest and the posteroloph (MUSM 2742), as in *Chachapoyamys*. The length of the metaloph of M1–2s of *Cachiyacuy* cf. *contamanensis* from Santa Rosa is shorter than the most frequent configuration of this crest in *Cc. contamanensis* but usually longer than in *Chachapoyamys*, in which the metaloph has a development more similar to the configuration of *Es. paulacoutoi*. The LACM 159241 M1 or M2 of *Cachiyacuy* cf. *contamanensis* and several upper molars of *Es. paulacoutoi* (LACM 143267, 144302, 149494, and 160206) show a similar morphology to that of MUSM 3917 from TAR-55/TAR-55bis and MUSM 2742 from CTA-27 in having a reduced metaloph remote from the crestules between the third crest and the posteroloph. Nevertheless, neither *Cachiyacuy* cf. *contamanensis* nor *Es. paulacoutoi* have an upper molar without metaloph, contrary to MUSM 3916 and 3919 from TAR-55/TAR-55bis. Unlike *Chachapoyamys*, the other upper molars of *Cachiyacuy* cf. *contamanensis* and *Es. paulacoutoi* have a metaloph connected to both the third crest and the posteroloph (LACM 143376, 143380, 159245 and the LACM 143422 M2–3), or only to the third crest (LACM 159243, 159240, 143363 and the LACM 143422 M1). *Chachapoyamys* differs from *Cc. contamanensis*, *Cachiyacuy* cf. *contamanensis*, *Es. paulacoutoi*, as well as from *Eobranisamys* (CTA-27 and Santa Rosa) and '*Eosallamys*' *simpsoni* (Santa Rosa; Frailey and Campbell 2004; Boivin et al. 2017a; Arnal et al. 2020), in having a smaller size, similar to that of *Cc. kummeli*, *Canaanimys maquiensis* from CTA-27 (Antoine et al. 2012; Boivin et al. 2017a) and *B. huallagaensis*. The metaloph of *Cc. kummeli* is reduced or almost absent and lingually free on M2s, and more developed and tends to connect to the posteroloph (via a potential very short posteroloph spur) on M1s and M3s (Antoine et al. 2012; Boivin et al. 2017a; Arnal et al. 2020; this work). On upper molars of this species, there is no crestule that tend to link the third crest to the posteroloph. On M1–2s of *Cn. maquiensis*, the metaloph is long, turned forward and ends close to the third crest, and can connect to the latter. *Chachapoyamys* differs from *Es. paulacoutoi* and some p4s of *Cc. contamanensis* in having no accessory cristulid on the anteroflexid and/or mesoflexid (mesolophid included) on p4s; from *Es. paulacoutoi* in having P4s with a oblique lingual protoloph; and from *Canaanimys* cf. *maquiensis* from CTA-27 (Arnal et al. 2020) in having P4s with a more oblique lingual protoloph and lower molars with always a complete second cristid. In comparison to *Ch. kathetos*, *B. huallagaensis* from the same locality show a tendency toward a taeniodont pattern in having a pattern II of pseudo-taeniodonty on lower molars and a more frequent pattern I of pseudo-taeniodonty on upper molars; a rounded P4 with a transverse lingual protoloph, a connection of its labial structures at a moderate stage of wear, a third crest disconnected to the mesostyle and without metaloph; a longer posterior arm of the metaconid on lower molars; a tendency to have a mesoloph disconnected to the anterior arm with the reduction/absence of the mesolophule on M1–2s; and a reduction or more frequent absence of the crestules between the third crest and the posteroloph By its upper molars with a strong reduction or absence of the metaloph, *Chachapoyamys* recalls *Eoespina woodi*, *Eosachacui lavocati*, and '*Es.*' *simpsoni* (Santa Rosa; Frailey and Campbell 2004; Arnal et al. 2020), as well as *Pozomys ucayalensis* (CTA-29 and Santa Rosa; Boivin et al. 2017a; Arnal et al. 2020), *Chachapoyamys* differs from all taxa mentioned above in having more transverse lower molars; from all taxa mentioned above (except *Cc. maquiensis*) in having more transverse upper molars; from *Cn. maquiensis*, *Eobranisamys*, and *P. ucayalensis* in having non-taeniodont teeth; from *P. ucayalensis* in having a curved (i.e., mesially concave) second cristid on p4s; from *Eoespina* and *Eosachacui* in having no accessory cristulids on the anteroflexid and/or mesoflexid (mesolophid included) on p4s; from *Cachiyacuy*, *Eoespina*, *Es. paulacoutoi*, and '*Es.*' *simpsoni* in having a more important discontinuity of the metalophulid I on p4s; from all taxa mentioned above (except *P. ucayalensis*) in having lower molars, which can have a more important discontinuity of the metalophulid I close to the protoconid; from *Eobranisamys* and '*Es.*' *simpsoni* in having a reduced metaloph disconnected to the posteroloph on dP4s; from *Eosachacui* in having a rest of metaloph on the posterior flexus on dP4s; from *Eoespina* in having always a third crest connected to the mesostyle on P4s; from *Eosachacui* and '*Es.*' *simpsoni* in having a metaloph on P4s; from *Eobranismys* and *Eosachacui* in having P4s with a complete mure; from *Eosachacui* in having non-taeniodont P4s; from *Eobranismys* in having P4s with paracone, which remains separate the mesostyle at a moderate stage of wear, and a shorter or absent metaloph on upper molars; and from *Eobranismys*, *Ep. woodi* and *P. ucayalensis* in having some upper molars with a connection between the third crest and the posteroloph. Some teeth from TAR-55/TAR-55 attributed here to *Chachapoyamys kathetos* were previously referred to *Cachiyacuy* cf. *kummeli* (MUSM 3372 and 3374–3376; Assemat et al. 2019). The discovery of new dental material from TAR-55/TAR-55bis including new loci has allowed us to refine the former attributions. The upper molars of *Chachapoyamys* are included in the morphological variation of *Cc. contamanensis*, *Cachiyacuy* cf. *contamanensis*, and *Es. paulacoutoi*. Owing an absent or more reduced metaloph than the most frequent morphology of this crest in these taxa, its transverse molars, the discontinuity of the metalophulid I on p4s and lower molars with a short posterior arm of the protoconid, we attribute this material from TAR-55/TAR-55bis to a new taxon: *Chachapoyamys kathetos* gen. et sp. nov.

***Chachapoyamys*** **cf.** ***kathetos***
Figure 3o, p

2017a *Cachiyacuy kummeli*—Boivin et al.: 8, fig. 4.13.

*Referred material*. MUSM 2786 (Boivin et al. 2017a: fig. 4.13; Fig. 3o), 3943 (Fig. 3p), left M1 or M2.

*Locality*. CTA-27, Contamana, Loreto Department, Western Amazonia, Peru.

*Formation and age*. Pozo Formation, lower member, late middle Eocene (i.e., Barrancan or Mustersan SALMAs).

*Description*. MUSM 2786 and 3943 are brachydont and transverse-shaped (Fig. 3o, p). The transverse crests (anteroloph, protoloph, mesolophule/mesoloph, and posteroloph) are thin. There is no metaconule. Lingually, the protocone is massive and distolabially-mesiolingually compressed. On MUSM 2786 (Fig. 3o), the protocone displays a short distolabially directed posterior arm, which reaches a longer crestule from the labial protoloph-mure junction. These two crestules are joined at their base, but remain separate at their top by a very tiny and shallow notch (i.e., pattern II of pseudo-taeniodont). MUSM 3943 (Fig. 3p) shows a complete posterior arm of the protocone (i.e., non-taeniodont pattern). However, the latter is slightly connected to the labial protoloph-mure junction. Hence, it is possible that MUSM 3943 had a pseudo-taeniodont pattern at earlier stages of wear (Fig. 3p). The anteroloph is long and barely curved. From the protocone, the anteroloph runs labially and reaches the paracone. The parafossette is labiolingually well extended. The labial protoloph is long and slightly oblique. The mure connects the anterior arm of the hypocone to the protoloph lingually. The mure is thin and longitudinal on MUSM 3943 (Fig. 3p), whereas it is thicker and oblique on MUSM 2786 (Fig. 3o). The third transverse crest, strongly developed, links the anterior arm of the hypocone to a strong mesostyle, centrally situated in the labialmost margin of the crown. This crest is formed by the union of a long and straight mesoloph with a short and slightly distolabially oblique mesolophule. The mesostyle is mesially isolated from the paracone (or from its posterior arm). This style is clearly disconnected to the metacone on MUSM 3943 (Fig. 3p), while its posterior arm links to the metacone on MUSM 2786 (Fig. 3o). Due to the moderate stage of wear of the teeth, the metacone is not visible and seems to be fused with the posteroloph. At the level of the metacone area, MUSM 2786 has a thickening of the posteroloph, without metaloph (Fig. 3o). On MUSM 3943, a tiny spur, stemming from the metacone and interpreted as a relic of the metaloph, is present on the mesial slope of the posteroloph (Fig. 3p). Both upper molars are characterized by a connection between the third crest and the posteroloph on the posterior flexus (i.e., confluence of the distal mesoflexus with the metaflexus). On MUSM 2786, this connection is formed by two accessory crestules: a mesial crestule from the third crest joining a posteroloph spur (Fig. 3o). On MUSM 3943, these two accessory crestules appear to be present, as well as a third accessory crestule, which would be longer, stronger and mesiolingually directed (Fig. 3p). It is faintly connected mesially to the crestule from the third transverse crest, and distally to the posteroloph and its spur. This crestule may be a part of relictual connections of the metaloph (and a part of this loph?) to the third transverse crest and posteroloph.

*Comparisons*. By their brachydonty, bunolophodonty, thin and roughly transverse lophs, the presence of a mesostyle, metacone and complete third transverse crest, the morphology of MUSM 2786 and 3943 is strongly reminiscent of that found in several Paleogene caviomorphs. By the presence of a long lingual protoloph, and a connection, via crestule(s) between the third transverse crest and the posteroloph, MUSM 2786 and 3943 recall upper molars of the basal caviomorphs from Peru, *Cachiyacuy* and *Eosallamys* (Eocene localities of Contamana and Balsayacu-Juanjui, and Santa Rosa; Frailey and Campbell 2004; Antoine et al. 2012; Boivin et al. 2017a; Assemat et al. 2019; Arnal et al. 2020), as well as upper molars of *Chachapoyamys kathetos* gen. et sp. nov. from TAR-55/55-bis. MUSM 2786 and 3943 are closer to *Chachapoyamys kathetos* in being transverse and in having a very minute or absent metaloph. The size of MUSM 2786 and 3943 is similar to that of the M1s of *Chachapoyamys kathetos*. However, MUSM 2786 and 3943 are more transverse than the upper molars of *Chachapoyamys kathetos*. Moreover, these two specimens from CTA-27 have mesiodistally thinner flexi, a stronger connection between the anteroloph and the paracone, and a slight reduction of the lingual protoloph (pattern II of pseudo-taeniodonty, at least for MUSM 2786). MUSM 2786 and 3943 differ from the upper molars of *Cachiyacuy contamanensis* and *Eosallamys* in being more transverse; from the upper molars of *Eosallamys* and the most of upper molars of *Cc. contamanensis* in having a much shorter metaloph or an absence of this loph. MUSM 2786 and 3943 recall the M2s of *Cachiyacuy kummeli* from CTA-27 and Santa Rosa (Antoine et al. 2012; Boivin et al. 2017a; Arnal et al. 2020; Fig. 3u) in having a similar size and in bearing an incipient or absent metaloph (see below). However, the upper molars of *Cc. kummeli* have a paracone strongly separate from the anteroloph and do not show similar crestules located between the third transverse crest and the posteroloph. The upper molars of *Balsayacuy huallagaensis* gen. et sp. nov. can have crestules located between the third transverse crest and the posteroloph, but they are shorter. Unlike MUSM 2786 and 3943, the M1–2s of *Balsayacuy* are square-shaped with mesiodistally well-expanded flexi. Owing to the differences between MUSM 2786 and 3943 and the upper molars of *Chachapoyamys kathetos* and the low quantity of this material from CTA-27, we prefer keeping it in open nomenclature, as *Chachapoyamys* cf. *kathetos*.

Genus ***Cachiyacuy*** Antoine, Marivaux, Croft, Billet, Ganerød, Jaramillo, Martin, Orliac, Tejada, Altamirano, Duranthon, Fanjat, Rousse, and Salas-Gismondi, 2012

*Type species*. *Cachiyacuy contamanensis* Antoine, Marivaux, Croft, Billet, Ganerød, Jaramillo, Martin, Orliac, Tejada, Altamirano, Duranthon, Fanjat, Rousse, and Salas-Gismondi, 2012.

*Species content*. The type species and *Cachiyacuy kummeli* Antoine, Marivaux, Croft, Billet, Ganerød, Jaramillo, Martin, Orliac, Tejada, Altamirano, Duranthon, Fanjat, Rousse, and Salas-Gismondi, 2012.

***Cachiyacuy kummeli*** Antoine, Marivaux, Croft, Billet, Ganerød, Jaramillo, Martin, Orliac, Tejada, Altamirano, Duranthon, Fanjat, Rousse, and Salas-Gismondi, 2012
Figure 3q

*Holotype*. MUSM 1882, left M1 (in Antoine et al. 2012: 1322, fig. 2m).

*Referred material*. MUSM 2785 (Boivin et al. 2017a: fig. 4.12; Fig. 3q), left M2.

*Locality*. CTA-27, Contamana, Loreto Department, Western Amazonia, Peru.

*Formation and age*. Pozo Formation, lower member, late middle Eocene (i.e., Barrancan SALMA).

*Description*. MUSM 2785 is a pristine M2, labially broken at the level of the mesostyle (Fig. 3q). It is brachydont, transverse-shaped, fully tetralophodont and characterized by a pattern II of pseudo-taeniodonty. The protocone is the most massive cusp. The latter, as well as the hypocone and the metacone (see below), are crestiform, whereas the paracone is more bulbous. There is no metaconule. The transverse crests (anteroloph, protoloph, mesolophule/mesoloph, and posteroloph) are thin. The first loph and posteroloph are long and curved, anteriorly convex or concave, respectively. Conservely, the labial protoloph and the third crest are straight, roughly parallel and slightly oblique (i.e., mesiolabially directed). The protocone has a long anterior arm, which is separate from the anteroloph by a very tiny and shallow notch. The labial part of the anteroloph is isolated from the paracone and enlarged, thus it probably corresponds to a parastyle. The mure is rather longitudinal and divided into two equal-sized crestules: a mesial crestule stemming from the labial protoloph and a distal one from the third crest-anterior arm of the hypocone junction. The third crest, strongly developed, links the mesostyle to the anterior arm of the hypocone. This crest is formed by a long mesoloph and a shorter and distolabially oblique mesolophule. There is neither metaloph nor distinct metacone. However, considering the other upper molar attributed to this taxon (Antoine et al. 2012; Arnal et al. 2020), this cusp is probably fused with the posteroloph. The hypocone has a short, but strong, posterior arm slightly connected to the posteroloph. Labially, the paraflexus and probably the mesial mesoflexus are opened, whereas the posterior flexus (i.e., confluence of the distal mesoflexus and metaflexus) is closed and forms a well-extended fossette.

*Remarks*. MUSM 2785 has a size and general morphology similar to that the other upper molars attributed to this taxon (Antoine et al. 2012; Arnal et al. 2020). MUSM 2785 was originally described as a M1 by Boivin et al. (2017a). However, other M1s of *Cachiyacuy kummeli* (MUSM 1882 [Antoine et al. 2012: fig. 2m] and LACM 159246 [Arnal et al. 2020: fig. 2T]) are characterized bu a well-marked metaloph, a loph absent on MUSM 2785. The metaloph is almost absent on M2s of *Cc. kummeli* (MUSM 1883 [Antoine et al. 2012: fig. 2n], LACM 159244 [Arnal et al. 2020: fig. 2V], and LACM 159250 [Arnal et al. 2020: fig. 2W]), reduced to a minute cups-shaped structure on the posterior flexus. Furthermore, the rectangular shape of MUSM 2785 is more similar to that of the MUSM 1883 M2 than the holotype (the MUSM 1882 M1). Based on these two characters (i.e., absence of metaloph and rectangular shape), we consider MUSM 2785 as being a M2 instead of a M1.

**Caviomorpha** gen. et sp. indet. 1
Figure 3r, s, Table 2

*Referred material*. MUSM 3939 (Fig. 3r), right labial fragment of lower molar or left lingual fragment of upper molar; MUSM 3940 (Fig. 3s), left P4.

*Locality*. TAR-55/TAR-55bis, Balsayacu, San Martín Department, Western Amazonia, Peru.

*Formation and age*. Pozo Formation, lower member, late middle Eocene to early late Eocene (i.e., Barrancan or Mustersan SALMAs).

*Description*. MUSM 3939 is a right labial fragment of a moderately worn lower or upper molar, in which only the protoconid/hypocone area, the parts of the hypoflexid/hypoflexus and the anterior outgrowth of the hypoconid/posterior outgrowth of the protocone are preserved (Fig. 3r). The anterior outgrowth of the hypocone/posterior outgrowth of the protocone seems to be mostly labially/lingually directed and the hypoflexid/hypoflexus does not show any mesiodistal constriction. These characters suggest that this damaged tooth could be a labial fragment of lower molar instead of a lingual fragment of upper molar.

MUSM 3940 is an eroded, labially broken and moderately worn P4 (Fig. 3s). The anteroloph, paracone, and the labial part of the labial protoloph are missing. MUSM 3940 is non-taeniodont and could be tetralophodont. The protocone displays a strong posterior arm (or lingual protoloph) connected to the labial protoloph and a long and curved posterior outgrowth. The latter reaches the anterior arm of a minute hypocone. As it is not confluent with the paraflexus and given it is lingually closed, the hypoflexus forms a fossette mesiodistally extended. The mure is long, longitudinal, and composed of two linked crests, a strong mesial one stemming from the labial protoloph and a thinner distal one that runs from the oblique anterior arm of the hypocone. The third transverse crest is straight and distally situated, close to the posteroloph. Because of the position of the third crest, the mesial mesoflexus is well expanded. Conversely, the posterior flexus is strongly reduced (i.e., confluence of the distal mesoflexus with the metaflexus). All the preserved labial structures are connected, and thus, the mesial mesoflexus and the posterior flexus form two fossettes.

*Comparisons*. Despite their very fragmentary nature, these two specimens document the presence of a medium-sized species, which is the largest taxon to be recorded at TAR-55/TAR-55bis. The MUSM 3939 and 3940 are comparable in size to the material attributed to *Eobranisamys javierpradoi* from CTA-27 (Contamana, Peru; late middle Eocene; Boivin et al. 2017a). By its characters (i.e., possible tetralophodont pattern, transverse crest distally positioned, and a labial link between the labial protoloph, the third crest and the posteroloph), the MUSM 3940 P4 has a morphological pattern close to that of the P4s of *Eb. javierpradoi* (Antoine et al. 2012: 1322, fig. 2a'; Boivin et al. 2017a) in having a similar oval occlusal outline, and a mesial mesoflexus mesiodistally well-extended and labially closed in moderate stage of wear. However, a typical character of *Eb. javierpradoi*, the taeniodonty of its upper molars, is not present on MUSM 3940. In addition, the P4s of *Eb. javierpradoi* are characterized by an incomplete mure, while it is complete on MUSM 3940. Some taxa can show tetralophodont and non-taeniodont P4s as MUSM 3940: *Balsayacuy huallagaensis* gen. et sp. nov. (MUSM 3936), *Cachiyacuy contamanensis* (MUSM 2725), *Cachiyacuy* aff. *kummeli* from TAR-47 (Juanjui; MUSM 3523), *Eoespina woodi* (LACM 143459), *Eosallamys paulacoutoi* (LACM 143415), and '*Eosallamys*' *simpsoni* (LACM 149451; Frailey and Campbell 2004; Boivin et al. 2017a; Assemat et al. 2019; Arnal et al. 2020). MUSM 3940 differs from P4s of all these taxa in having a more mesiodistally extended mesial hypoflexus; all these taxa except to *Cc*. aff. *kummeli* from TAR-47 in having a more mesiodistally extended mesial mesoflexus; of *Cc*. aff. *kummeli* from TAR-47 and *Ep*. *woodi* in having a complete third crest; from other P4s of *Es*. *paulacoutoi* (LACM 143422 and 159214) in having no metaloph. Owing to the fragmentary state of these teeth and the poor quantity of material, we provisionally refer the material of TAR-55/TAR-55bis to as Caviomorpha gen. et sp. indet. 1.

**Caviomorpha** gen. et sp. indet. 2
Figure 3t, Table 2

*Referred material*. MUSM 3941 (Fig. 3t), left posterior fragment of dp4 or p4.

*Locality*. TAR-76, Balsayacu, San Martín Department, Western Amazonia, Peru.

*Formation and age*. Pozo Formation, lower member, late middle Eocene to early late Eocene (i.e., Barrancan or Mustersan SALMAs).

*Description*. MUSM 3941 is a fragment corresponding to the posterior part of a p4, bearing digestion marks (Fig. 3t). Only the entoconid, hypolophid, hypoconid, its anterior arm and outgrowth, and the posterolophid are preserved. Mesially, the tooth shows a rest of a transverse cristid, probably of a neomesolophid or posterior arm of the protoconid. The area of the mesostylid is broken. The entoconid is bulbous and bears a roughly straight hypolophid. The anterior arm of the crestiform hypoconid and the labial extremity of the hypolophid are separate at their top, but connected at their base (i.e., pattern II of pseudo-taeniodonty). The anterior outgrowth of the hypoconid is very short, strong, with a strong labially-directed component. MUSM 3941 is characterized by a posterolophid strongly curved and connected to the posterior slope of the entoconid. The latter characters (i.e., short anterior outgrowth of the hypoconid, labially directed, and posterolophid strongly curved) suggest that this damaged tooth would be a distal fragment of right dp4 or p4.

*Comparisons*. By its brachydonty, bunolophodonty, thin and roughly transverse lophids, the presence of a posterior arm of the metaconid, mesostylid and complete second transverse cristid, the morphology of MUSM 3941 is strongly reminiscent of that found in several Paleogene caviomorphs. MUSM 3941 shows a pattern II of pseudo-taeniodonty as *Balsayacuy huallagaensis* gen. et sp. nov. In the case of that specimen would be a p4, its size would be similar to that of *B. huallagaensis* and *Chachapoyamys kathetos* gen. et sp. nov. from TAR-55/TAR-55bis. However, in the case of that specimen would be a dp4, its size would be clearly larger than that of these taxa, and perhaps could be similar to that of Caviomorpha gen. et sp. indet. 1 described above. The fragmentary nature of MUSM 3941 does not allow to conclude regarding the determination of this material as *B. huallagaensis*, *Chachapoyamys kathetos*, Caviomorpha gen. et sp. indet. 1, or another early caviomorph.

## Discussion

### A single caviomorph assemblage at TAR-55/TAR-55bis, TAR-76 and TAR-77

Two taxa were previously described at TAR-55/TAR-55bis: *Cachiyacuy* cf. *kummeli* and *Canaanimys* aff. *maquiensis* (Assemat et al. 2019). The study of the new material from these localities has allowed for a taxonomic revision of the rodent fauna from TAR-55/TAR-55bis. Three taxa are currently recognized: *Balsayacuy huallagaensis* gen. et sp. nov. (coinciding fully with *Canaanimys* aff. *maquiensis* sensu Assemat et al. 2019 and partly with *Cachiyacuy* cf. *kummeli* sensu Assemat et al. 2019), *Chachapoyamys kathetos* gen. et sp. nov. (partly synonymous with *Cachiyacuy* cf. *kummeli* sensu Assemat et al. 2019) and Caviomorpha gen. et sp. indet. 1. *Balsayacuy huallagaensis* also occurs at TAR-77. The material from TAR-76, here referred to as Caviomorpha gen. et sp. indet. 2, could be attributed to both *B. huallagaensis* and *Chachapoyamys kathetos*. Nevertheless, this material could also document other early caviomorphs and its fragmentary nature and advanced stage of wear do not allow us to conclude on their taxonomic determination. This taxonomic uniformity is compatible with the existence of short time interval between all the localities from the upper part of the stratigraphic section (within a 90 m-thick section), as suggested by similar conditions, based on lithology (see Assemat et al. 2019). Hence, the concerned assemblages caviomorph samples are likely to document a single local faunal assemblage. *Balsayacuy huallagaensis*, *Chachapoyamys kathetos* and Caviomorpha gen. et sp. indet. 1. share dental characters, considered as plesiomorphic in caviomorphs: small size; brachydonty; bunolophodonty; thin and transverse loph(-id)s; tetralophodont p4s and lower molars with a posterior arm of metaconid, mesostylid and complete second transverse cristid; presence of a mesostylid and third transverse crest on upper teeth; presence of a metacone on upper molars; and presence of a metaloph, although very reduced, on some upper molars (Antoine et al. 2012; Boivin et al. 2017a, 2019b; Boivin and Marivaux 2020). These three taxa show strong morphological affinities with basal caviomorphs found in pre-Deseadan localities of Peru, especially in CTA-27 (Contamana, late middle Eocene; Antoine et al. 2012; Boivin et al. 2017a) and, to a lesser extent, Santa Rosa (Frailey and Campbell 2004; Arnal et al. 2020). By having some upper molars bearing accessory structures between the third transverse crest and the posteroloph, and which tend to connect to both transverse crests, *Balsayacuy* and *Chachapoyamys* are particularly close to *Cachiyacuy* and *Eosallamys* from CTA-27 and Santa Rosa. However, contrary to *Balsayacuy* and *Chachapoyamys*, in which the metaloph is absent or strongly reduced and lingually free, *Cachiyacuy contamanensis* and *Eosallamys paulacoutoi* have a longer metaloph, which ends very close to these accesory structures or that is connected to them in most cases. Within caviomorphs, a connection between the third crest and the metaloph is unusual, and otherwise found only in *Canaanimys maquiensis* from CTA-27, *Canaanimys* cf. *maquiensis* from Santa Rosa and on one upper molar of *Eosachacui* from Santa Rosa (LACM 143292; Frailey and Campbell 2004; Antoine et al. 2012; Boivin et al. 2017a; Arnal et al. 2020). As previously noted (Antoine et al. 2012; Boivin et al. 2017a), in non-caviomorph hystricognathous rodents, some earliest African–Asian hystricognaths ("protophiomyines", "baluchimyines", and "bugtimyids"; Marivaux and Boivin 2019) are characterized by this connection (e.g., *Baluchimys*, *Hodsahibia*, *Bugtimys*, *Protophiomys*, *Walsamys*), but some others "phiomyids" also have a double connection of the metaloph with the third crest and the posteroloph (e.g., *Acritophiomys*, *Phiomys*, *Phenacophiomys*). As a result, these species from CTA-27 (i.e., *Cn. maquiensis* and *Cc. contamanensis*) and to a lesser extent some taxa from Santa Rosa (i.e., *Canaanimys* cf. *maquiensis*, *Cachiyacuy* cf. *contamanensis*, and *E. paulacoutoi*; because they have M1–2 s with a more reduced metaloph than in species from CTA-27) appear to be the caviomorph taxa so far known with a strongly reminiscent occlusal morphology with these African-Asian basal hystricognaths. Moreover, *Balsayacuy* and *Chachapoyamys* share some characters with other taxa from CTA-29 (another Eocene locality from Contamana) and Santa Rosa: *Eoespina woodi*, *Eosachacui lavocati*, '*Eosallamys*' *simpsoni* and *Pozomys ucayalensis* (Frailey and Campbell 2004; Boivin et al. 2017a; Arnal et al. 2020). According to the recent phylogenetic analyses of Boivin et al. (2019b), these species are resolved as basal representatives of caviomorphs (early stem Caviomorpha). Finally, Caviomorpha gen. et sp. indet. 1 from TAR-55/TAR-55bis exhibits some affinities with *Cc. contamanensis*, *Cachiyacuy* aff. *kummeli* from TAR-47 (Juanjui: Assemat et al. 2019), *Ep. woodi*, *Es. paulacoutoi*, and '*Es.*' *simpsoni*, as well as with *Eobranisamys javierpradoi* from CTA-27 (Boivin et al. 2017a), a species also recently recognized as a stem caviomorph (Boivin et al. 2019b). In conclusion, all three rodent taxa from TAR-55/TAR-55bis would likely be basal representatives of caviomorphs. *Balsayacuy* and *Chachapoyamys* seem to have slightly more advanced morphology of their M1–2 s over *Cn. maquiensis*, *Cc. contamanensis* and *E. paulacoutoi* by showing a metaloph that is either absent or strongly reduced and lingually free.

### Age of TAR-55/TAR-55bis, TAR-76 and TAR-77

Although three taxa are henceforth recognized at TAR-55/TAR-55bis and they have different names from those described before (see Assemat et al. 2019), they are strongly similar with some basal caviomorph representatives, suggesting an old age for these localities, as proposed by Assemat et al. (2019). According to these authors, these localities would be late middle Eocene in age owing to their species resemblance with the late middle Eocene localities of Contamana (in particular with CTA-27), and in the absence of taxa with more derived dental characters and representatives of modern superfamilies of caviomorphs, even as dental fragments (Boivin et al. 2019b). The younger deposits of the region (TAR-49 and TAR-50, Juanjui area) record taxa evolutionarily more advanced, with an occlusal morphology characterized by a marked obliquity of loph(-id)s (the chinchilloid *Eoincamys*), and some with incisors having already achieved a derived multiserial enamel subtype 2–3 (Assemat et al. 2019). *Eoincamys* was originally described in Santa Rosa (Frailey and Campbell 2004) and subsequently in the localities of the Shapaja section near Tarapoto (Peru; Boivin et al. 2018a; Antoine et al. in revision). The latter section ranges the late Eocene–early Oligocene time interval, based on mammalian biostratigraphy, depositional environment sequence, stratigraphic correlation in the northern Peruvian foreland (Boivin et al. 2018a; Assemat et al. 2019), and chemostratigraphy (Antoine et al. in revision). The age of Santa Rosa is less constrained. Santa Rosa has yielded caviomorph taxa related to those of the Eocene localities of Contamana, as recognized through newly described specimens (Arnal et al. 2020). Santa Rosa unambiguously has a younger signature, however, as suggested by the conspicuous occurrence of at least three of the four modern superfamilies of caviomorphs, such as *Eoincamys* (Chinchilloidea), *Eodelphomys* (Octodontoidea) or *Eopululo* (Erethizontoidea; Frailey and Campbell 2004; De Vries and Seiffert 2017; Boivin et al. 2019b). These genera, or closely related taxa, further occur around the Eocene–Oligocene transition at Shapaja-Tarapoto (Antoine et al. in revision). In accordance with the results of Assemat et al. (2019), the Balsayacu caviomorph record (from TAR-56, TAR-76, TAR-77, and TAR-55/TAR-55bis) attests to the full absence of taxa with such an advanced occlusal morphology in these localities, as well as in TAR-76 and TAR-77 (and TAR-56; see Assemat et al. 2019), even through dental fragments. In addition, we could assign two upper molars from CTA-27 to *Chachapoyamys* cf. *kathetos* (one of them had previously been referred to as *Cc. kummeli*; Boivin et al. 2017a). The presence of somewhat derived characters observed in *Balsayacuy* and *Chachapoyamys* with respect to *Canaanimys maquiensis* and *Cachiyacuy contamanensis* (i.e., a metaloph absent or strongly reduced and lingually free) suggests that TAR-55/TAR-55bis, TAR-76 and TAR-77 document a time interval posterior to CTA-27, i.e., documenting latest middle or early late Eocene.

## Conclusion

The study of new caviomorph material from TAR-55/TAR-55bis, TAR-76 and TAR-77 (Balsayacu) reveals the presence of four caviomorph taxa in these localities: *Balsayacuy huallagaensis* gen. et sp. nov., *Chachapoyamys kathetos* gen. et sp. nov. and Caviomorpha gen. et sp. indet. 1 and 2. The first three taxa show strong affinities with stem Caviomorpha recorded in pre-Deseadan localities in Peru (Eocene localities of Contamana plus Santa Rosa), and thus providing additional information regarding the paleodiversity of early low latitude caviomorphs of South America. In accordance with the results of a previous study (Assemat et al. 2019), we propose an Eocene age for the Balsayacu section, based on the absence of morphologically derived taxa, and notably the absence of representatives of the four modern superfamilies of Caviomorpha (contrary to younger localities such as TAR-49, TAR-50, those of the Shapaja section, and Santa Rosa). In other words, the Balsayacu section may document intermediate between CTA-27 (late middle Eocene) and Santa Rosa/Shapaja/Juanjui assemblages (latest Eocene–early Oligocene. Continuing field efforts in this Amazonian region of the Andean foothills should provide new critical insights into the early evolutionary history and paleodiversity of small South American mammals. Taxonomic-free age constraints such as provided by U/Pb datings on detrital zircon grains or chemostratigraphy would considerably add to the knowledge of the evolutionary dynamics of such puzzling African-Asian Paleogene incomers.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s12542-021-00551-0.

**Acknowledgements** Many thanks to all the people that helped us in the field and in the lab. We are particularly grateful to our drivers Giancarlo, Manuel, and Percy, for their long-standing help during the yearly field seasons in the San Martín Department of Peruvian Amazonia. We warmly thank A. Assemat (ISEM, Montpellier, France) for taking SEM photographs of the original specimens from TAR-55/TAR-55bis collected in 2015–2016; C. Cazeveille (Montpellier RIO Imaging, Institut des Neurosciences de Montpellier, France) for access to a scanning electron microscope facility; and C. Girard (ISEM) for access to her optical stereomicroscope facility. We are indebted to A.-L. Charruault and S. Jiquel (ISEM) for the cast preparation of the rodent material from the Balsayacu section and from other Peruvian localities. We also thank the Editors of the PalZ. Paläontologische Zeitschrift, Thomas Mörs and Mike Reich, as well as M. Arnal (MLP, La Plata, Argentina) and A. Kramarz (MACN, Buenos Aires, Argentina), who provided formal reviews of this manuscript that enhanced the final version. This work was supported by The Leakey Foundation, the National Geographic Society, the "Investissements d'Avenir" grant managed by the "Agence Nationale de la Recherche" (CEBA, ANR-10-LABX-25-01), and by the COOPINTEER CNRS/CONICET (n° 252540) and the ECOS-SUD/FONCyT (n° A-14U01) international collaboration programs. This work was carried out in the frame of the ongoing cooperation agreement between the "Museo de Historia Natural de la Universidad Nacional Mayor San Marcos" (Lima, Peru) and the "Institut des Sciences de l'Évolution de Montpellier-Université de Montpellier" (France). This is ISEM publication 2021-032-Sud.

## References

Antoine, P.-O., R. Salas-Gismondi, P. Baby, M. Benammi, S. Brusset, D. De Franceschi, N. Espurt, C. Goillot, F. Pujos, J. Tejada, and M. Urbina. 2007. The middle Miocene (Laventan) Fitzcarrald fauna, Amazonian Peru. In Proceedings of the 4th EMPSLA, eds. E. Díaz-Martínez, and I. Rábano. *Cuadernos del Museo Geominero* 8: 19–24.

Antoine, P.-O., L. Marivaux, D.A. Croft, G. Billet, M. Ganerød, C. Jaramillo, T. Martin, M.J. Orliac, J. Tejada, A. J. Altamirano, F. Duranthon, G. Fanjat, S. Rousse, and R. Salas-Gismondi. 2012. Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. *Proceedings of the Royal Society of London (B: Biological Sciences)* 279: 1319–1326.

Antoine, P.-O., M. Roddaz, S. Brichau, J. Tejada-Lara, R. Salas-Gismondi, A. Altamirano, M. Louterbach, L. Lambs, T. Otto, and S. Brusset. 2013. Middle Miocene vertebrates from the Amazonian Madre de Dios Subandean Zone, Perú. *Journal of South American Earth Sciences* 42: 91–102.

Antoine, P.-O., M.A. Abello, S. Adnet, A.J. Altamirano Sierra, P. Baby, G. Billet, M. Boivin, Y. Calderón, A. Candela, J. Chabain, F. Corfu, D.A. Croft, M. Ganerød, C. Jaramillo, S. Klaus, L. Marivaux, R.E. Navarrete, M.J. Orliac, F. Parra, M.E. Pérez, F. Pujos, J.-C. Rage, A. Ravel, C. Robinet, M. Roddaz, J.V. Tejada-Lara, J. Vélez-Juarbe, F.P. Wesselingh, and R. Salas-Gismondi. 2016. A 60-million-year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. *Gondwana Research* 31: 30–59.

Antoine, P.-O., R. Salas-Gismondi, F. Pujos, M. Ganerød, and L. Marivaux. 2017. Western Amazonia as a hotspot of mammalian biodiversity throughout the Cenozoic. In Proceedings of the Symposium Cenozoic Evolution of TRopical-Equatorial Mammals (IPC4), eds. P.-O. Antoine, and F. Pujos. *Journal of Mammalian Evolution* 24: 5–17.

Antoine, P.-O., J. Yans, A. Aliaga Castillo, N. Stutz, M.A. Abello, S. Adnet, M. Andriolli Custódio, A. Benites-Palomino, G. Billet, M. Boivin, F. Herrera, C. Jaramillo, C. Mártinez, F. Moreno, R.E. Navarrete, F.R. Negri, F.J. Parra, F. Pujos, J.-C. Rage, A.M. Ribeiro, C. Robinet, M. Roddaz, J. Tejada Lara, R. Varas-Malca, R. Ventura Santos, R. Salas-Gismondi, and L. Marivaux. 2021, in revision. Biotic community and landscape changes around the Eocene−Oligocene transition at Shapaja, Peruvian Amazonia: regional or global drivers? *Global and Planetary Change.*

Arnal, M., A.G. Kramarz, M.G. Vucetich, C.D. Frailey, and K.E. Campbell. 2020. New Palaeogene caviomorphs (Rodentia, Hystricognathi) from Santa Rosa, Peru: systematics, biochronology, biogeography and early evolutionary trends. *Papers in Palaeontology* 6: 193–216.

Assemat, A., M. Boivin, L. Marivaux, F. Pujos, A. Benites-Palomino, R. Salas-Gismondi, J.V. Tejada-Lara, R.M. Varas-Malca, F.R. Negri, A.M. Ribeiro, and P.-O. Antoine. 2019. Restes inédits de rongeurs caviomorphes du Paléogène de la région de Juanjui (Amazonie péruvienne): systématique, implications macroévolutives et biostratigraphiques. *Geodiversitas* 41: 699–730.

Bianucci, G., O. Lambert, R. Salas-Gismondi, J. Tejada, F. Pujos, M. Urbina, and P.-O. Antoine. 2013. A Miocene relative of the Ganges River dolphin (Odontoceti, Platanistidae) from the Amazonian basin. *Journal of Vertebrate Paleontology* 33: 741–745.

Boivin, M., and L. Marivaux. 2020. Dental homologies and evolutionary transformations in Caviomorpha (Hystricognathi, Rodentia): new data from the Paleogene of Peruvian Amazonia. *Historical Biology* 32: 528–554.

Boivin, M., L. Marivaux, M.J. Orliac, F. Pujos, R. Salas-Gismondi, J. V. Tejada-Lara, and P.-O. Antoine. 2017a. Late middle Eocene caviomorph rodents from Contamana, Peruvian Amazonia. *Palaeontologia Electronica* 20.1.19A: 1–50.

Boivin, M., L. Marivaux, A.M. Candela, M.J. Orliac, F. Pujos, R. Salas-Gismondi, J.V. Tejada-Lara, and P.-O. Antoine. 2017b. Late Oligocene caviomorph rodents from Contamana, Peruvian Amazonia. *Papers in Palaeontology* 3: 69–109.

Boivin, M., L. Marivaux, F. Pujos, R. Salas-Gismondi, J.V. Tejada-Lara, R.M. Varas-Malca, and P.-O. Antoine. 2018a. Early Oligocene caviomorph rodents from Shapaja, Peruvian Amazonia. *Palaeontographica (A: Paläozoologie und Stratigraphie)* 311: 87–156.

Boivin, M., S. Ginot, L. Marivaux, A.J. Altamirano-Sierra, F. Pujos, R. Salas-Gismondi, J.V. Tejada-Lara, and P.-O. Antoine. 2018b. Tarsal morphology and locomotor adaptation of some late middle Eocene caviomorph rodents from Peruvian Amazonia reveal early ecological diversity. *Journal of Vertebrate Paleontology* 38: e1555164.

Boivin, M., L. Marivaux, R. Salas-Gismondi, E.C. Vieytes, and P.-O. Antoine. 2019a. Incisor enamel microstructure of Paleogene caviomorph rodents from Contamana and Shapaja (Peruvian Amazonia). *Journal of Mammalian Evolution* 26: 389–406.

Boivin, M., L. Marivaux, and P.-O. Antoine. 2019b. L'apport du registre paléogène d'Amazonie sur la diversification initiale des Caviomorpha (Hystricognathi, Rodentia): implications phylogénétiques, macroévolutives et paléobiogéographiques. *Geodiversitas* 41: 143–245.

Bond, M., M.F. Tejedor, K.E. Campbell, L. Chornogubsky, N. Novo, and F. Goin. 2015. Eocene primates of South America and the African origins of New World monkeys. *Nature* 520: 538–541.

Bowdich, T.E. 1821. *An analysis of the natural classifications of Mammalia: for the use of students and travellers*. Paris: J. Smith.

Campbell, K.E. 2004. The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru. *Natural History Museum of Los Angeles County, Science Series* 40: 1–163.

Campbell, K.E., C.D. Frailey, and L. Romero-Pittman. 2000. The Late Miocene gomphothere *Amahuacatherium peruvium* (Proboscidea: Gomphotheriidae) from Amazonian Peru: implications for the

Great American Faunal Interchange. *Boletín del Ingemmet* 23: 1–152.

Campbell, K.E., M. Heizler, C.D. Frailey, L. Romero-Pittman, and D.R. Prothero. 2001. Upper Cenozoic chronostratigraphy of the southwestern Amazon Basin. *Geology* 297: 595–598.

Campbell, K.E., C.D. Frailey, and L. Romero-Pittman. 2006. The Pan-Amazonian Ucayali Peneplain, Late Neogene sedimentation in Amazonia, and the birth of the modern Amazon River system. *Palaeogeography Palaeoclimatology Palaeoecology* 239: 166–219.

Campbell, K.E., D.R. Prothero, L. Romero-Pittman, F. Hertel, and N. Rivera. 2010. Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. *Journal of South American Earth Sciences* 29: 619–626.

Chabain, J., P.-O. Antoine, A.J. Altamirano-Sierra, L. Marivaux, F. Pujos, R. Salas Gismondi, and S. Adnet. 2017. Cenozoic batoids from Contamana (Peruvian Amazonia) with focus on freshwater potamotrygonins and their paleoenvironmental significance. *Geobios* 50: 389–400.

Croft, D.A., J.J. Flynn, and A.R. Wyss. 2008. The Tinguiririca Fauna of Chile and the early stages of "modernization" of South American mammal faunas. *Arquivos do Museu Nacional* 66: 191–211.

De Vries, D., and E.R. Seiffert. 2017. Bayesian Tip-dating of Caviomorph Rodent Phylogenies provides New Age Estimates for South America's oldest Platyrrhines. Program of the 86th Annual Meeting of the American Association of Physical Anthropologists (New Orleans, Unites States). *American Journal of Physical Anthropologists* 162: 161–162.

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

Frailey, C.D., and K.E. Campbell. 2004. Paleogene rodents from Amazonian Peru: the Santa Rosa local fauna. In *The Paleogene Mammalian Fauna of Santa Rosa*, Amazonian Peru, ed. K.E. Campbell. *Natural History Museum of Los Angeles County, Science Series* 40: 71–130.

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

Goin, F.J., and A.M. Candela. 2004. New Paleogene marsupials from the Amazon Basin of Eastern Peru. In *The Paleogene Mammalian Fauna of Santa Rosa*, Amazonian Peru, ed. K.E. Campbell. *Natural History Museum of Los Angeles County, Science Series* 40: 15–60.

Hoorn, C., F.P. Wesselingh, H. Ter Steege, M.A. Bermúdez, A. Mora, J. Sevink, I. Sanmartín, A. Sanchez-Meseguer, C.L. Anderson, J.P. Figueiredo, C. Jaramillo, D. Riff, F.R. Negri, H. Hooghiemstra, J. Lundberg, T. Städler, T. Särkinen, and A. Antonelli. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330: 927–931.

Huchon, D., F.M. Catzeflis, and E.J.P. Douzery. 2000. Variance of molecular datings, evolution of rodents, and the phylogenetic affinities between Ctenodactylidae and Hystricognathi. *Proceedings of the Royal Society of London (B: Biological Sciences)* 267: 393–402.

Jenkins, C.N., P.L. Stuart, and L.N. Joppa. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences* 110: E2602–E2610.

Kay, R.F. 2015. New World monkey origins. *Science* 347: 1068–1069.

Kerber, L., F.R. Negri, A.M. Ribeiro, N. Nasif, J.P. Souza-Filho, and J. Ferigolo. 2017. Tropical fossil caviomorph rodents from the southwestern Brazilian Amazonia in the context of the South American faunas: systematics, biochronology, and paleobiogeography. *Journal of Mammalian Evolution* 24: 57–70.

Marivaux, L., and M. Boivin. 2019. Emergence of hystricognathous rodents: Palaeogene fossil record, phylogeny, dental evolution and historical biogeography. *Zoological Journal of the Linnean Society* 187: 929–964.

Marivaux, L., R. Salas-Gismondi, J. Tejada, G. Billet, M. Louterbach, J. Vink, J. Bailleul, M. Roddaz, and P.-O. Antoine. 2012. A platyrrhine talus from the early Miocene of Peru (Amazonian Madre de Dios Sub-Andean Zone). *Journal of Human Evolution* 63: 696–703.

Marivaux, L., S. Adnet, A.J. Altamirano-Sierra, M. Boivin, F. Pujos, A. Ramdarshan, R. Salas-Gismondi, J.V. Tejada-Lara, and P.-O. Antoine. 2016a. Neotropics provide insights into the emergence of New World monkeys: new dental evidence from the late Oligocene of Peruvian Amazonia. *Journal of Human Evolution* 97: 159–175.

Marivaux, L., S. Adnet, A.J. Altamirano-Sierra, F. Pujos, A. Ramdarshan, R. Salas-Gismondi, J.V. Tejada-Lara, and P.-O. Antoine. 2016b. Dental remains of cebid platyrrhines from the earliest late Miocene of Western Amazonia, Peru: macroevolutionary implications on the extant capuchin and marmoset lineages. *American Journal of Physical Anthropology* 161: 478–493.

Marivaux, L., W. Aguirre-Diaz, A. Benites-Palomino, G. Billet, M. Boivin, F. Pujos, R. Salas-Gismondi, J.V. Tejada-Lara, R.M. Varas-Malca, and P.-O. Antoine. 2020. New record of *Neosaimiri* (Cebidae, Platyrrhini) from the late Middle Miocene of Peruvian Amazonia. *Journal of Human Evolution* 146: 102835.

Negri, F.R., J. Bocquentin-Villanueva, J. Ferigolo, and P.-O. Antoine. 2010. A review of Tertiary mammal faunas and birds from western Amazonia. In *Amazonia, landscape and species evolution: a look into the past*, eds. C. Hoorn and F.P. Wesselingh, 245–258. Hoboken: Blackwell-Wiley.

Pujos, F., R. Salas-Gismondi, G. Baby, P. Baby, C. Goillot, J. Tejada, and P.-O. Antoine. 2013. Implication of the presence of *Megathericulus* (Xenarthra: Tardigrada: Megatheriidae) in the Laventan of Peruvian Amazonia. *Journal of Systematic Palaeontology* 11: 973–991.

Seiffert, E.R., M.F. Tejedor, J.G. Fleagle, N.M. Novo, F.M. Cornejo, M. Bond, D. De Vries, and K.E. Campbell. 2020. A parapithecid stem anthropoid of African origin in the Paleogene of South America. *Science* 368: 194–197.

Shockey, B.J., R. Hitz, and M. Bond. 2004. Paleogene notoungulates from the Amazon Basin of Peru. In *The Paleogene Mammalian Fauna of Santa Rosa*, *Amazonian Peru*, ed. K.E. Campbell. *Natural History Museum of Los Angeles County, Science Series* 40: 61–70.

Stebbins, G.L. 1974. *Flowering plants: evolution above the species level*. Cambridge: The Belknap Press of Harvard University Press.

Tejada-Lara, J.V., R. Salas-Gismondi, F. Pujos, P. Baby, M. Benammi, S. Brusset, D. De Franceschi, N. Espurt, M. Urbina, and P.-O. Antoine. 2015. Life in protoamazonia: Middle Miocene mammals from the Fitzcarrald Arch (Peruvian Amazonia). *Palaeontology* 58: 341–378.

Tullberg, T. 1899. Ueber das System der Nagethiere: eine phylogenetische Studie. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* 18: 1–514.

Vucetich, M.G., E.C. Vieytes, M.E. Pérez, and A.A. Carlini. 2010. The rodents from La Cantera and the early evolution of caviomorphs in South America. In *The Paleontology of Gran Barranca, Evolution and Environmental Change through the Middle Cenozoic of Patagonia*, eds. R.H. Madden, A.A. Carlini, M.G. Vucetich, and R.F. Kay, 189–201. Cambridge: Cambridge University Press.

Wood, A.E. 1955. A revised classification of the rodents. *Journal of Mammalogy* 36: 165–187.

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