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ARTICLE

TARSAL MORPHOLOGY AND LOCOMOTOR ADAPTATION OF SOME LATE MIDDLE EOCENE CAVIOMORPH RODENTS FROM PERUVIAN AMAZONIA REVEAL EARLY ECOLOGICAL DIVERSITY

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ABSTRACT—In rodents, and other vertebrates in general, the morphology of tarsal bones, especially the astragalus and calcaneus, has been shown to be tightly linked to locomotor movements. As a result, it has been used to infer locomotor behaviors in extinct species. Recent expeditions in Peruvian Amazonia have led to the discovery of the oldest caviomorph rodent fossils in South America, including two calcanei and one astragalus. The morphologies of these three tarsal bones are described in detail and compared with other extant and extinct caviomorphs. In order to assess and infer the locomotor behaviors of these rodents, linear measurements were taken on these tarsal bones and analyzed via multivariate analyses based on a previously assembled large data set. Both qualitative and quantitative analyses consistently suggest that the osteological adaptations of the astragalus enhance movements for climbing, those of one calcaneus rather enhance movements indicating terrestrial and partly fossorial lifestyle, whereas the other calcaneus may have belonged to a generalist form with a tendency toward a semiaquatic lifestyle. These results fit well with the associated paleoenvironments and hint at ecological diversity early in caviomorph history.

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INTRODUCTION

Vertebrates comprise a large number of species adapted to living in a variety of environments (i.e., aquatic, airborne, terrestrial, arboreal, and subterranean). These species evolve diverse adaptations to their environments, notably from a locomotor perspective. Studies regarding the interplay between form and function in the postcranial skeleton have revealed that postcranial morphology usually has strong ecological and locomotor habit signals (e.g., Reidenberg, 2007; Chatterjee, 2015). These signals are often used to infer locomotor behaviors and lifestyles of extinct taxa using comparative morphology and geometric morphometric techniques (e.g., Samuels et al., 2013; Lires et al., 2016; Tałanda, 2017).

Among rodents, the postcranial skeleton and its relationships with locomotor behaviors has been investigated, especially in caviomorphs (e.g., Szalay, 1985; Biknevicius, 1993; Elissamburu and Vizcaíno, 2004; Weisbecker and Schmid, 2007; Candela and Picasso, 2008; Lessa et al., 2008; Morgan, 2009; Elissamburu and De Santis, 2011; Morgan and Álvarez, 2013; Vianey-Liaud et al., 2015; Ginot et al., 2016). Indeed, the caviomorph clade constitutes a good candidate for analyzing postcranial morphology because of its long and isolated evolutionary history in South America and its wide range of ecomorphological adaptations (including terrestrial, cursorial, fossorial, scansorial, arboreal, and semiaquatic abilities; e.g., Biknevicius, 1993; Elissamburu and Vizcaíno, 2004; Weisbecker and Schmid, 2007; Candela and Picasso, 2008; Lessa et al., 2008; Morgan, 2009; Elissamburu and De Santis, 2011). Many of these studies relate to a pivotal region in locomotion, the ankle joint, and chiefly the calcaneus and astragalus (e.g., Szalay, 1985; Candela and Picasso, 2008; Vianey-Liaud et al., 2015; Ginot et al., 2016). When the foot is considered as a lever system, these two bones correspond to its fulcrum (astragalus) and lever arm (calcaneus) (Carrano, 1997; Davidovits, 2012). Despite the important roles of these bones, few astragali and calcanei of extinct caviomorph taxa have been objects of study (e.g., Quintana, 1994; Sánchez-Villagra et al., 2003; Horovitz et al., 2006; Candela and Picasso, 2008; Candela

et al., 2012; Olivares and Verzi, 2014; Table 1). Only one Paleogene taxon, *Platypittamys brachyodon*, from Argentinian Patagonia (Scarritt Pocket; late early–late Oligocene) is documented by tarsi including astragali and calcanei (Wood, 1949).

Recent field expeditions in Peruvian Amazonia have led to the discovery of the oldest caviomorph occurrences in South America (Antoine et al., 2012, 2016, 2017; Boivin et al., 2017). The fossils were collected from 10 localities near Contamana (Loreto Department, Peru; Antoine et al., 2012, 2016; Boivin et al., 2017). These localities are late middle Eocene in age (Barrancan South American Land Mammal Age [SALMA]; Antoine et al., 2012, 2016). The rodent material from these Contamana localities mainly consists of isolated teeth, but three tarsal bones (one astragalus and two calcanei) were also discovered in two localities (CTA-29 and CTA-27). Both localities are referred to the lower member of the Pozo Formation ('Pozo Sands') and correspond to sandstone lenses of fluvial origin (Antoine et al., 2016). Analyses of their paleontological content suggest that a forested environment prevailed (fossilized wood, pollen, spores, and snakes), crossed by freshwater bodies (freshwater decapods, mollusks, crocodylomorphs, and river stingrays) (Adnet et al., 2014; Antoine et al., 2016; Chabain et al., 2017). Within this context, we provide here (1) an exhaustive analysis (description and comparison) of the three tarsal bones from CTA-29 and CTA-27; (2) propose locomotor inferences for these ankle bones based on comparative morphology and multivariate analyses on a larger data set (Ginot et al., 2016); and (3) discuss the potential ecological diversity of these rodents.

Institutional Abbreviations—**ISEM**, Institut des Sciences de l'Évolution de Montpellier, Montpellier, France; **MNHN**, Musée National d'Histoire Naturelle, Paris, France; **MUSM**, Museo de Historia Natural de la Universidad Nacional Mayor San Marcos, Lima, Peru.

Other Abbreviation—**CTA**, Contamana.

MATERIALS AND METHODS

Material

The rodent fossils described in the present work consist of one astragalus (MUSM 3425) from CTA-29 and two calcanei (MUSM 3422 and 3423) from CTA-27, near Contamana, Peruvian Amazonia (Antoine et al., 2016: figs. 1, 2). These two localities are referred to the lower member of the Pozo Formation ('Pozo Sands'; late middle Eocene; for more information regarding the geological context, see Antoine et al., 2016, and Boivin et al., 2017). These three bones were collected during excavations of the localities and/or by wet-screening of the excavated residues (1 to 2 mm meshes).

Description and Comparisons

Osteological nomenclature derives from Ginot et al. (2016; see Fig. 1). The three tarsal bones from Contamana were compared with those of extant and extinct caviomorph taxa based on literature and direct observations on some original specimens housed in the Université de Montpellier osteological collections (Table 1).

Multivariate Analyses

The three fossils described in this article were measured following the protocol of Ginot et al. (2016; see Table 2 and Appendix 1). For the two calcanei, some measurements could not be obtained due to damage (see Fig. 2 and Description and Comparisons, below). These measurements were excluded from subsequent analyses (Table 2 and Appendix 1). To remove the effect of size in the analyses, all measurements were divided by

the geometric mean of all measurements, for each bone, and a log function was applied to produce log shape ratios (Mosimann and James, 1979; Bookstein, 1989; Claude, 2008). Linear discriminant analyses (LDAs) were run using the 'lda' function (Venables and Ripley, 2002) on the full data set of Ginot et al. (2016), with the same six locomotor categories as grouping factors (jumping, cursorial, generalist, fossorial, climber, and semiaquatic), and separately for the calcanei and astragali (Tables S1, S2, S3). The positions of the two fossil calcanei and the astragalus in the LDAs were then calculated using the 'predict' function, to assess the most probable locomotor category to which each specimen could be assigned. All analyses and calculations were run in R (R Core Team, 2017).

DESCRIPTION AND COMPARISONS

Astragalus

Specimen MUSM 3425 from CTA-29 is a well-preserved right astragalus, lacking any apparent postmortem distortion (Fig. 2). Nevertheless, the specimen has suffered some slight abrasions: (i) on the top of the medial ridge of the trochlea (in dorsal view); (ii) on the proximal part of the lateral ridge of the trochlea (in dorsal and anterior views); and (iii) on the medial part of the plantar medial tuberosity (in plantar view). As in the majority of modern caviomorphs observed, the body of the MUSM 3425 astragalus is slightly wider than long. Astragali of some modern taxa (e.g., *Coendou*, *Dolichotis*, and *Myocastor*), however, show accentuation of this character (i.e., much wider than long). The trochlea is asymmetric, with a lateral ridge taller, slightly longer, and much wider (sloping gently) than the medial one, a feature observed on astragali of several other taxa (*Dactylomys*, *Euryzygomatomys*, *Lagostomus*, *Proechimys*, *Octodon*, *Eucelophorus*, *Phoberomys*, and *Platypittamys*) and particularly accentuated on astragali of *Coendou*, *Actenomys*, and *Steiromys*. The trochlea is moderately grooved, as in *Coendou*, *Euryzygomatomys*, *Octodon*, and *Steiromys*. The combined length of the neck and head is shorter than that of the trochlea. The neck is narrow and clearly deflected medially (26.7°), as on astragali of *Coendou*, *Dactylomys*, *Euryzygomatomys*, *Myocastor*, *Proechimys*, *Eumysops*, and *Steiromys*. Conversely, astragali of *Cavia*, *Chinchilla*, *Ctenomys*, *Dinomys*, *Dolichotis*, *Lagostomus*, *Octodon*, *Actenomys*, *Clidomys*, *Eucelophorus*, *Neoreomys*, *Platypittamys*, and *Praectenomys* have a neck that is slightly or not deflected medially. As in *Proechimys*, *Dactylomys*, *Coendou*, and *Steiromys*, the head is rounded, with the astragalo-medial tarsal facet developed on the medial aspect of the neck. In plantar view, this facet and the astragalo-navicular facet are well separated from the sustentacular facet over their entire length. Among the studied taxa, only *Dactylomys*, *Steiromys*, and, to a lesser extent, *Coendou prehensilis*, *Actenomys*, and *Praectenomys* have astragali with separate facets. The sustentacular facet is oriented anteroposteriorly, somewhat oval and curved, with anterior and posterior extremities being lanceolate. It is separated from the ectal facet by a deep and anteriorly narrow sulcus. On astragali of other taxa, these two facets are anteriorly separate or divergent, except in *Coendou*, in which they are connected (*C. villosus*) or in close proximity (*C. prehensilis*). The ectal facet is wide and curved, with a moderate radius of curvature. Its anterior part is not markedly projected laterally (i.e., absence of a well-marked lateral process) as on astragali of *Steiromys*, *Coendou*, *Dactylomys*, and *Proechimys* sp. (MN 31451; but not in *P. cuvieri*). Although the medial plantar tuberosity is damaged, it was unambiguously well marked. In lateral and medial views, the astragalar body is moderately tall and the rims of the trochlea are circular, with a small radius of curvature.

TABLE 1.   Extant and extinct caviomorph taxa used for comparisons in this study.

Taxon	Collection number	Bone	Age	Observed original material	Reference
Erethizontoidea					
Coendou villosus	MCN 2681	astragalus and calcaneus	recent		Candela and Picasso, 2008
Coendou prehensilis	UM N-481	astragalus and calcaneus	recent		Ginot et al., 2016
Steiromys duplicatus	MACN-A 10055-78	astragalus and calcaneus	early Miocene		Candela and Picasso, 2008; Candela et al., 2012
Cavioidea					
Dolichotis patagonum	MLP 208	astragalus and calcaneus	recent		Candela and Picasso, 2008
Cavia aperea	MLP 11.VII.99.54	astragalus and calcaneus	recent		Candela and Picasso, 2008
Cavia porcellus	UM 558 V	astragalus and calcaneus	recent	X	Ginot et al., 2016
Neoreomys australis	MPM-PV 3517	astragalus and calcaneus	late early Miocene		Candela et al., 2012
Chinchilloidea					
Dinomys branickii	LACM 90854	astragalus and calcaneus	recent		Horovitz et al., 2006
'Scleromys' schurmanni	UCMP 39916	astragalus and calcaneus	late middle Miocene		Fields, 1957
'Scleromys' colombianus	UCMP 40563, UCMP 37951	astragalus and calcaneus	late middle Miocene		Fields, 1957
Drytomomys aequatorialis	UCMP 39969, UCMP 40055	astragalus and calcaneus	late middle Miocene		Fields, 1957
Phoberomys pattersoni	UNEFM-VF-020	astragalus and calcaneus	late Miocene		Sánchez-Villagra et al., 2003; Horovitz et al., 2006
Lagostomus maximus	MLP 27.IV.95.1	astragalus and calcaneus	recent		Candela and Picasso, 2008
Chinchilla laniger	UM 498 V	astragalus and calcaneus	recent	X	Ginot et al., 2016
Chinchilla sp.	MLP 31.XII.02.37	astragalus and calcaneus	recent		Candela and Picasso, 2008
Octodontoidea					
Octodon degus	UM 500 V	astragalus and calcaneus	recent	X	Ginot et al., 2016
Ctenomys australis	MMP 2533	astragalus and calcaneus	recent		Reig and Quintana, 1992
Eucelophorus zaratei	MMP 603-S	astragalus	late Pliocene–early Pleistocene		Reig and Quintana, 1992
Eucelophorus chapadmalalensis	MACN 7294	calcaneus	late Pliocene		Reig and Quintana, 1992
Actenomys priscus	MMP ?	astragalus and calcaneus	early Pliocene		Reig and Quintana, 1992
Praectenomys rhombidens	GB 012	astragalus and calcaneus	Pliocene		Quintana, 1994
Dactylomys sp.	MN s/n	astragalus and calcaneus	recent		Candela and Picasso, 2008
Euryzygomatomys spinosus	MN 31531	astragalus and calcaneus	recent		Candela and Picasso, 2008
Proechimys cuvieri	UM 705 N	astragalus and calcaneus	recent	X	
Proechimys cuvieri	UM 1054 V	astragalus and calcaneus	recent		Ginot et al., 2016
Proechimys sp.	MN 31451	astragalus and calcaneus	recent		Candela and Picasso, 2008
Myocastor coypus	s/n	astragalus and calcaneus	recent		Candela and Picasso, 2008
Myocastor coypus	MNHN 1959-148	astragalus and calcaneus	recent		Ginot et al., 2016
Eumysops gracilis	MMP 798M	astragalus and calcaneus	early Pliocene		Olivares and Verzi, 2015
Clidomys osborni	UF 27401	astragalus	Pleistocene		MacPhee, 1984
Platypittamys brachyodon	AMNH 29601	astragalus	late early Oligocene–late Oligocene		Wood, 1949

Institutional abbreviations: **AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **GB**, Servicio Geológico de Bolivia, La Paz, Bolivia; **LACM**, Museum of Natural History Los Angeles County, Los Angeles, California, U.S.A.; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MCN**, Fundaçao Zoobotânica do Rio Grande do Sul, Museu de Ciencias Naturais, Porto Alegre, Brazil; **MLP**, Museo de Ciencias Naturales de La Plata, La Plata, Argentina; **MMP**, Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Seaglia,' Buenos Aires, Argentina; **MN**, Museu Nacional, Rio de Janeiro, Brazil; **MNHN**, Musée National d'Histoire Naturelle, Paris, France; **MPM-PV**, Museo Regional Padre Manuel Jesus Molina, Rio Gallegos, Argentina; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **UF**, Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.; **UM**, Université de Montpellier, Montpellier, France; **UNEFM**, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela.
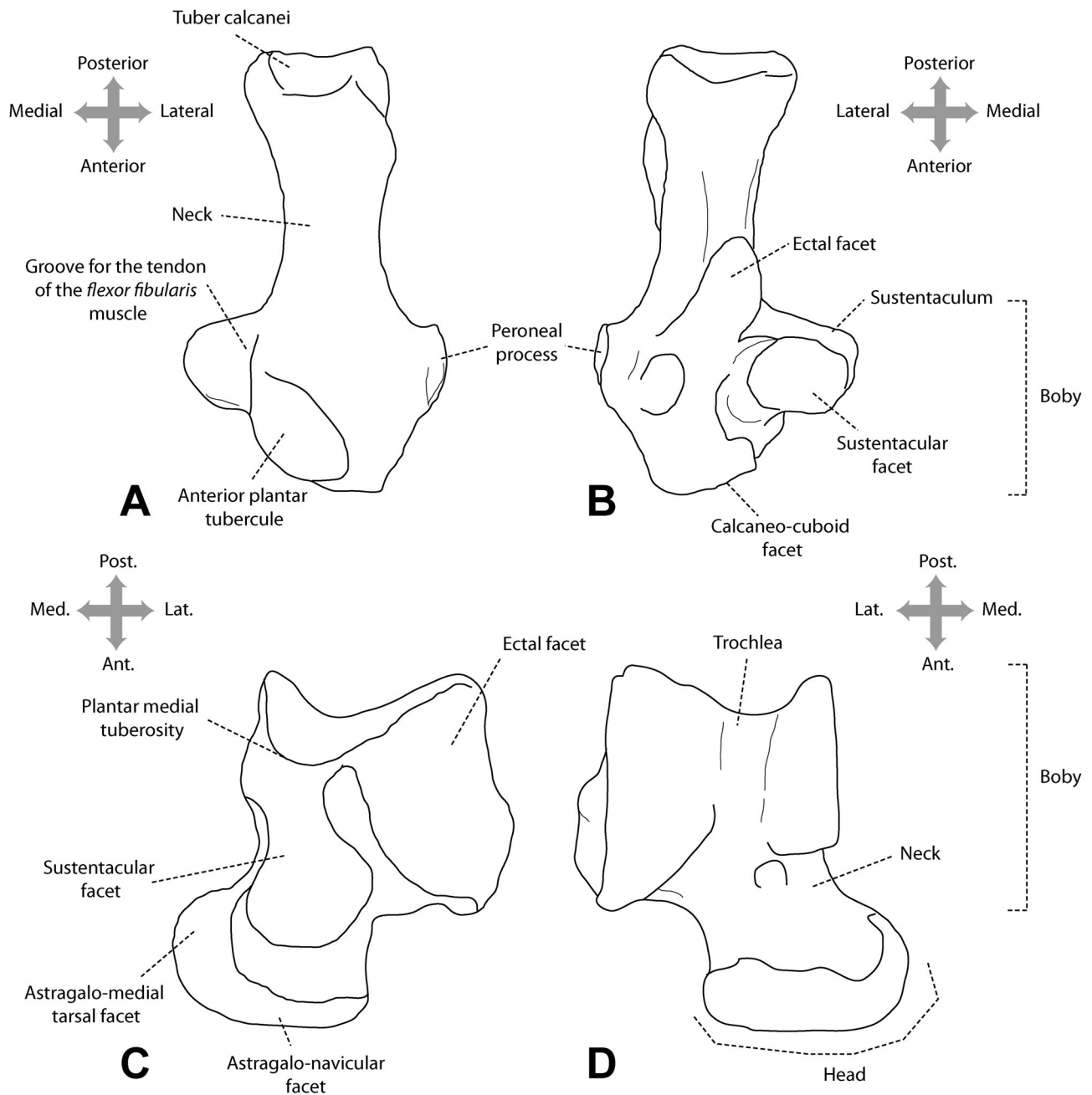
FIGURE 1. Nomenclature used for describing rodent tarsal bones, modified from Ginot et al. (2016). **A**, **B**, for calcaneus; **C**, **D**, for astragalus. **A**, **C**, plantar views; **B**, **D**, dorsal views.

Calcanei

MUSM 3422—Specimen MUSM 3422 from CTA-27 (Fig. 2) is a right calcaneus lacking the tuber and most of the posterior part of the neck. It shows minor damage at the level of the sustentaculum, the peroneal process, the lateral base of the ectal facet, and on the anterior part of the neck (in plantar view). The body is stout, wide, and with a prominent sustentaculum, which is longer than it is wide. The robustness of the sustentaculum is a character also found in the calcanei of *Coendou*, *Dinomys*, *Myocastor*, *Actenomys*, and *Steiromys*. On the calcaneus of *Chinchilla*, the sustentaculum is very long in dorsal view, but with a mediolateral shortening anteriorly (associated with the anterior elongation of the sustentacular facet), a configuration not present on MUSM 3422. In the latter, the sustentaculum is anteriorly positioned, as in *Coendou* and *Steiromys*. The sustentacular facet is not well defined either medially (due to postmortem breakage) or laterally. It is parallel to the main axis of the bone, as on calcanei of *Myocastor*, *Octodon*, and *Proechimys*. In plantar view, the groove for the tendon of the flexor fibularis muscle is well marked anteriorly, as on the calcaneus of *Proechimys*. Yet, in the latter taxon, this groove is deep throughout its length. The anterior plantar tubercle is well defined and adjoins a slight depression on the anteromedial part of the body, as observed on calcanei of *Octodon* and *Proechimys*. This depression is slightly deeper

TABLE 2. Measurements (in millimeters) of the astragalus and calcanei from two Eocene localities of Contamana (CTA-27 and CTA-29).

Specimen	ABW	AmTL	ATL	ATW	EL	EW	HH	HW	LBH	LTL	MBH	MTL	NL	SL	SW	TW
MUSM 3425	3.989	1.835	6.427	5.346	2.814	2.111	2.143	2.390	2.807	3.857	2.662	3.777	3.620	3.968	2.039	3.079
	CAL	CCH	CCW	CTW	EL	EW	MH	NH	NW	PPL	PPW	SL	SW			
MUSM 3422	3.433	2.266	2.590	4.775	2.826	1.517	3.247	2.531	1.537	1.559	0.767	1.736	1.410			
MUSM 3423	1.714	0.871	0.861	2.614	1.612	1.012	1.918	1.752	1.074	1.012	0.131	1.035	1.010			

For abbreviations, see Appendix 1 and Ginot et al. (2016).

than in *Octodon* and markedly shallower than in *Proechimys*. Although partly broken, the peroneal process is anteriorly positioned. It appears to have been well developed, as is the case on calcanei of *Coendou*, *Octodon*, and *Proechimys*, but less than in *Praectenomys*. In anterior view, the calcaneo-cuboid facet is mediolaterally developed and oval. The shape of this facet is similar to that observed on the calcaneus of *Coendou prehensilis*. This facet has a slightly concave surface. It is moderately tilted following an anterolateral-posteromedial axis and with an angle close to that measured on the calcaneus of *Octodon*. In contrast, the calcaneo-cuboid facet is clearly more tilted in calcanei of *Cavia*, *Chinchilla*, and *Proechimys*. On MUSM 3422, the neck is much narrower than the body. Although the posterior part is missing, the neck appears to be narrower centrally, as on calcanei of *Coendou*, *Dactylomys*, *Euryzygomatomys*, and *Proechimys*. The ectal facet is concave and mostly oriented anterolaterally-posteromedially, whereas its posterior part is parallel to the long axis. This facet displays a strong dorsoplantar inclination and is separated from the sustentacular facet by a wide groove. In lateral view, the ectal facet is rounded, a condition similar to that observed on calcanei of *Chinchilla* or *Octodon*.

MUSM 3423—This specimen is also a right calcaneus (Fig. 2) from CTA-27. It is smaller than MUSM 3422 (Table 2), and its neck is broken posteriorly. In addition, this bone shows a damaged calcaneo-cuboid facet on its lateral aspect and lacks the peroneal process. Even though the peroneal process is lacking, the body is wider than long. The sustentaculum is narrow, notably anteriorly, and less developed than on MUSM 3422. The shape and proportions of this structure recall the condition found on calcanei of *Dactylomys* and *Octodon*. The sustentaculum is more posterior than on MUSM 3422, but more anterior than in calcanei of *Cavia*, *Dolichotis*, *Lagostomus*, *Actenomys*, and *Eucelophorus*. The sustentacular facet is well defined and circular, and it overlaps the whole plantar surface of the sustentaculum. This facet is inclined following a postero-dorsal-anteroplantar axis, with an angle close to that observed on the calcaneus of *Cavia*. In plantar view, the groove for the tendon of the flexor fibularis muscle is deep throughout its length, as on the calcaneus of *Octodon*. As on MUSM 3422, there is a slight depression of a similar depth on the anteromedial aspect of the body, next to a well-marked anterior plantar tubercle. The calcaneo-cuboid facet is weakly inclined anterolaterally-posteromedially, and it is slightly developed medially. Due to wear of this facet, the shape of its medial part is unclear on MUSM 3423. The neck is wider than the body, but it seems to be straight without narrowing in its central part, contrary to the condition found on MUSM 3422. The ectal facet is ovoid, particularly wide, especially in its anterior part, and less dorsally projected than on MUSM 3422. On MUSM 3423, the ectal facet is stout and comparable to that developed on calcanei of *Coendou* and *Myocastor*. However, the shape of the ectal facet on MUSM 3423 is closer to that of the calcaneus of *Coendou*. On MUSM 3423, a wide and shallow groove separates the ectal facet from the sustentacular one, contrary to what is observed on the calcaneus of *Coendou villosus*, in which both facets are connected.

FUNCTIONAL INTERPRETATION AND TAXONOMIC INFERENCES

Astragalus

The MUSM 3425 astragalus displays a suite of anatomical details suggesting enhanced mediolateral movement: (i) asymmetric trochlea; (ii) ectal facet not projected laterally; (iii) medial deflection of the neck; (iv) well-rounded head with the astragalo-medial tarsal facet developed on the medial aspect of
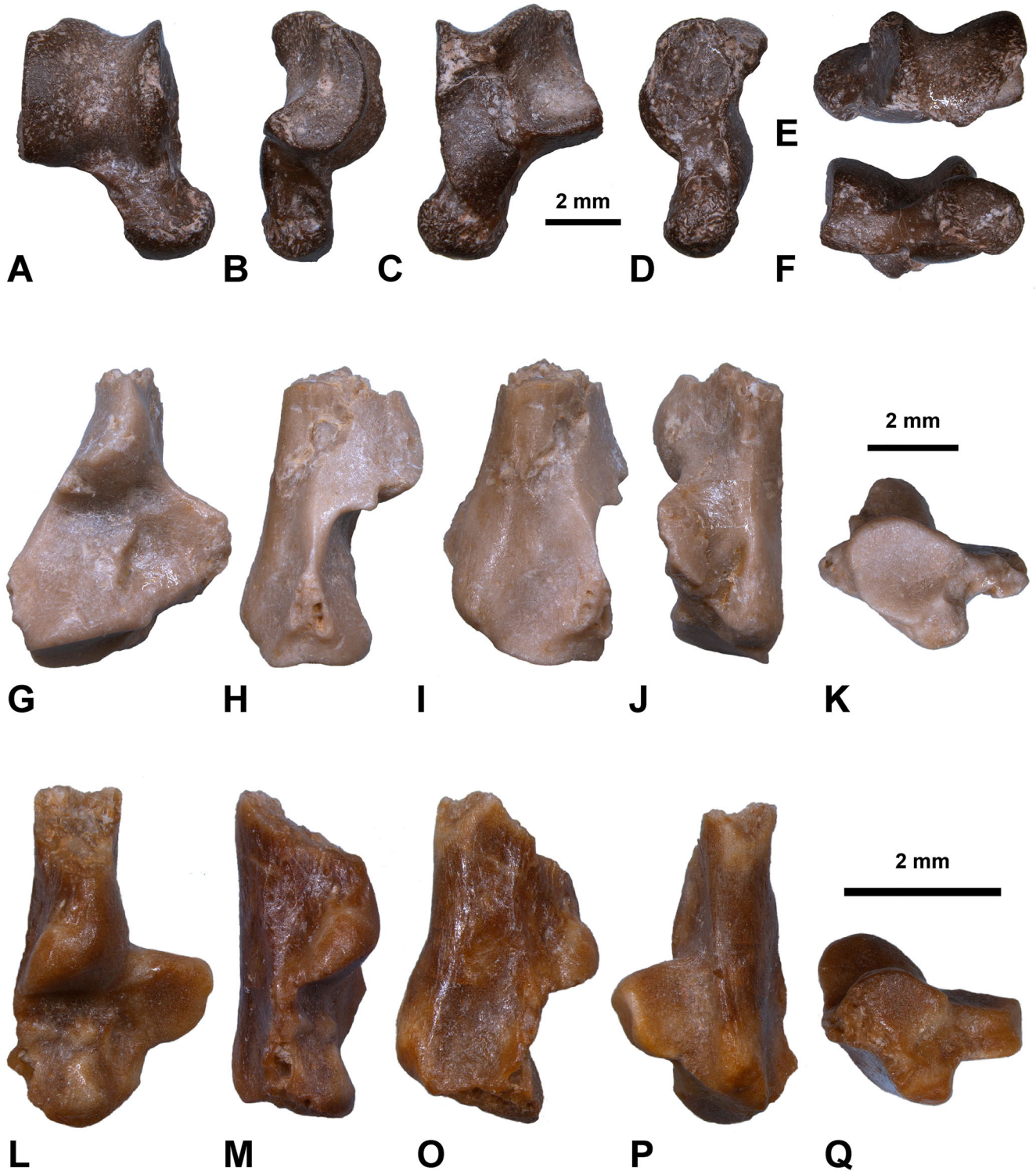
FIGURE 2. Caviomorph rodent tarsal bones from the late middle Eocene of Contamana (Peruvian Amazonia). **A–F**, MUSM 3425, a right astragalus from CTA-29; **G–K**, MUSM 3422, a right calcaneus from CTA-27; **L–Q**, MUSM 3423, a right calcaneus from CTA-27. **A**, **G**, **L**, dorsal views; **B**, **H**, **M**, lateral views; **C**, **I**, **O**, plantar views; **D**, **J**, **P**, medial views; **E**, posterior view; **F**, **K**, **Q**, anterior views.

the neck; and (v) sustentacular facet separated from the astra-galo-navicular facet (Ginot et al., 2016). All these features are present, but are usually more emphasized, on the astragali of arboreal rodents such as *Coendou* or *Dactylomys* (but in the latter these features are less marked than in *Coendou*). In addition, the closeness of the sustentacular and ectal facets, at least anteriorly, on MUSM 3425 recalls the configuration observed on the astragalus of *Coendou*, on which both facets can be connected. Therefore, MUSM 3425 exhibits clear osteolo-gical adaptations for climbing.

The astragalus LDA (Wilks' Λ = 0.46; P < 0.001; 66% correct assignment; Table S3) shows that despite being out of the morphological range of our sample of extant rodents, MUSM 3425 is close to the cursorial/semiaquatic groups along LD1, while being clearly associated with the arboreal climber group on LD2 (Fig. 3A). Although this suggests an intermediate morphology, MUSM 3425 is overall assigned to the climber group with the highest posterior probability (0.986), which is consistent with the characters previously described.

Calcanei

MUSM 3422—The sustentaculum of the MUSM 3422 calcaneus recalls the condition found on calcanei of *Coendou* and *Steiromys*, notably through its robustness and its anterior position. Otherwise, MUSM 3422 shows a mosaic of features found on calcanei of arboreal caviomorphs (e.g., *Coendou*), as well as some found in terrestrial species (e.g., *Octodon* and *Proechimys*). Characters associated with arboreal climbing are (i) a sustentacular facet parallel to the main axis of the bone and (ii) a central narrowing of the neck, although the damage on the bone renders this uncertain. Characters associated with terrestrial forms are (i) a tilted calcaneo-cuboid facet and (ii) an anterior position of the peroneal process. Although the development of the peroneal process is important in climbers (e.g., *Coendou*), it is also found in terrestrial and fossorial species (e.g., *Octodon*; Ginot et al., 2016). Finally, the ectal facet on MUSM 3422 is projected dorsally, a condition notably present on calcanei of terrestrial taxa with cursorial/jumping abilities, such as *Chinchilla* and *Lagostomus*. In any case, in the absence of a complete neck on MUSM 3422, it is difficult to estimate the posterior development of the ectal facet reliably. Taking into consideration all these morphological features, the MUSM 3422 calcaneus might have belonged to a generalist rodent with some climbing and fossorial abilities.

The calcaneus LDA (Wilks' Λ = 0.66; P < 0.002; 27% correct assignment; Table S3) is consistent with these activity and locomotor behavior interpretations, although MUSM 3422 also falls outside of the range of extant species (Fig. 3B). Along the first axis, MUSM 3422 is on the same side as fossorial and arboreal taxa, whereas along the second axis it is closest to the generalist group. Posterior probabilities assign MUSM 3422 to the generalist group (0.675), but with a fairly high probability for fossorial affinities (0.311). The high Wilks' Λ and low proportion of correct assignment in this LDA clearly suggest that the interpretations above should be treated very cautiously.

Even if the MUSM 3422 calcaneus is compatible with the MUSM 3425 astragalus in terms of size (although the astragalus is slightly larger), details of their morphology reveal several points of functional mismatch resulting from distinct locomotor behaviors associated with each specimen. In this context, the possibility exists that these two tarsal bones belonged to two different taxa. Specimen MUSM 3422 could belong to *Cachiyacuy contamanensis* Antoine et al., 2012, which is the most abundant taxon of CTA-27, although the size of this tarsal bone is larger than would be expected given the tooth size of *C. contamanensis* (Antoine et al., 2012; Boivin et al., 2017). Another taxon from CTA-27 that is slightly larger than *C. contamanensis,* could also be a candidate: *Eobranisamys javierpradoi* Boivin et al., 2017. Similarly, based on a size criterion, Cavioidea or Chinchilloidea, gen. et sp. indet., or, to a lesser extent, *Cachiyacuy* cf. *contamanensis* 2, both described and defined from locality CTA-29 (Boivin et al., 2017), could be potential candidates for the identity of the MUSM 3425 astragalus.

MUSM 3423—With the posterodorsal-anteroplantar inclination of the sustentacular facet and a lack of neck narrowing, the MUSM 3423 calcaneus could belong to a rodent with more cursorial abilities. However, the ectal facet on MUSM 3423 is very similar to that observed on the calcaneus of the arboreal erethizontid *Coendou* in terms of robustness and shape. The reduction and anterior position of the peroneal process, on the other hand, are characteristic of cursorial or semiaquatic rodents (Ginot et al., 2016).

Results from the LDA support a terrestrial locomotor interpretation for this taxon, inasmuch as the MUSM 3423 calcaneus is primarily assigned to the generalist group. However, as can be seen in Figure 3B, it is also placed at the intersection between the cursorial, semiaquatic, and generalist groups. Posterior probability is highest for a generalist type (0.428), but with a relatively high probability for the semiaquatic group
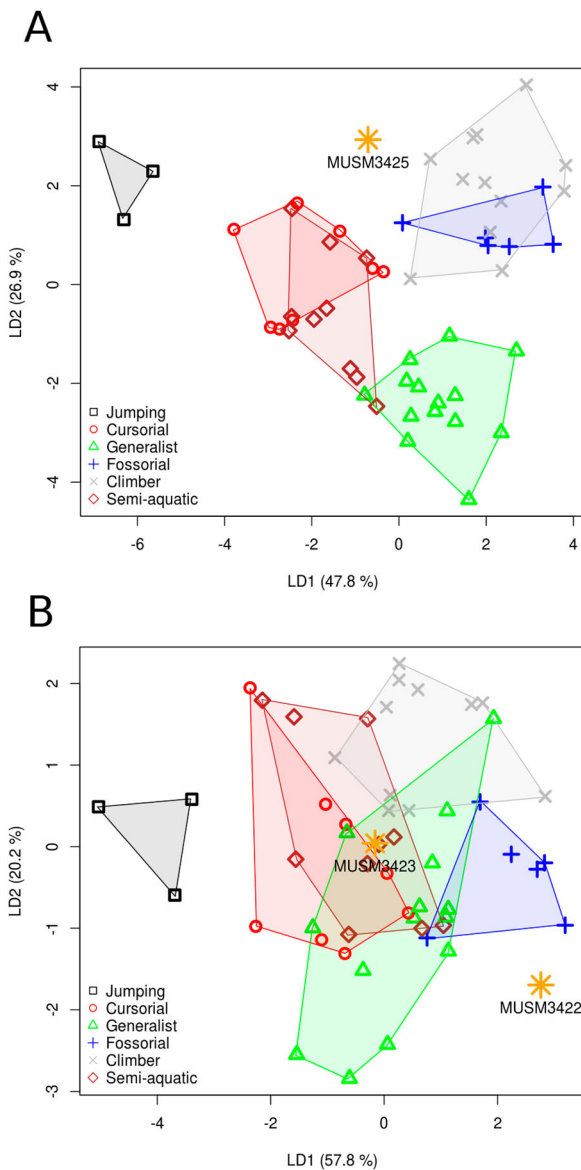

FIGURE 3. Linear discriminant analyses (LDAs) of log shape ratio measurements of rodent tarsal bones, based on the data set of Ginot et al. (2016), with locomotor categories as grouping factors (black squares: jumping; red circles: cursorial; green triangles: generalist; blue crosses: fossorial; gray Xs: climber; brown diamonds: semiaquatic). Fossils described in this article are represented by yellow asterisks. **A**, astragalus LDA; **B**, calcaneus LDA.

(0.292) and cursorial group (0.143). This is consistent with Ginot et al. (2016) who proposed that, due to similar anteroposterior movements of the hind limb, the tarsal bones of semiaquatic and cursorial taxa should show convergent morphologies. As with the previous specimen, the high Wilks' Λ and low proportion of correct assignment in the calcaneus LDA prevent any confident interpretations.

Based on its divergent morphology and smaller size than the other tarsal bones studied here, the MUSM 3423 calcaneus corresponds to a taxon distinct from the taxa associated with the MUSM 3422 calcaneus and the MUSM 3425 astragalus. Other taxa documented in CTA-27, *Cachiyacuy kummeli* Antoine et al., 2012, *Canaanimys maquiensis* Antoine et al., 2012, and cf. *Eoespina* sp., are smaller in size than *C. contamanensis* and *E. javierpradoi* and as such could be potential candidates (Antoine et al., 2012). Given that the dental material from CTA-27 referable to *C. kummeli* is more abundant than that of the two other tiny species, referral of MUSM 3423 to *C. kummeli* could be a plausible taxonomic option.

PALEOECOLOGY

Due to the fragmentary state of preservation and the mosaic of morphological traits that characterize the calcanei from CTA-27, as well as the low predictive power of our especially for the calcanei, the functional inferences regarding the mobility possibilities of these tarsal bones, and the associated locomotor behaviors, remain only tentative. Despite these limitations, we have shown that the three tarsal bones display distinct morphologies, which indicate various locomotor types, thereby illustrating different species of the caviomorph rodent community from Contamana. Going further, these different locomotor types could reflect occupation of different ecological niches by these rodents. The record of a taxon with preferentially arboreal abilities and a generalist, which might have had cursorial or swimming abilities, would suggest forested conditions associated with aquatic environments. These biotope types fit well with what is reconstructed for the Pozo Formation in terms of paleoenvironmental conditions (Antoine et al., 2016; Chabain et al., 2017).

Considering the moderate generic/specific diversity characterizing caviomorphs recorded from the late middle Eocene of Contamana (CTA-27 and CTA-29; Boivin et al., 2017), and their low morphological disparity regarding dental patterns, limited ecological diversity could be expected. However, ecological information deriving from the functional attributes of these few tarsal bones indicates that these rodents may have occupied various ecological niches, as reflected by their diverse locomotor adaptations. Because these rodents from the late middle Eocene of Contamana exhibit dental patterns reminiscent of those of their Paleogene African counterparts, they are viewed as representing the earliest stages of caviomorph evolution (i.e., initial diversification; Antoine et al., 2012; Boivin, 2017; Boivin et al., 2017). The various locomotor behaviors recorded among these rodents (at least as we interpret them here) suggest that early caviomorphs (stem-Caviomorpha) diversified rapidly after their arrival in South America, both in terms of specific diversity and ecological disparity.

Several hypotheses could be proposed to explain this potential ecological diversification: (i) an event related to their relatively recent dispersal to South America, a landmass they had begun to colonize; (ii) the absence of direct competitors; (iii) they were stronger competitors than other groups; and/or (iv) environmental changes. In the middle Eocene, caviomorphs were the only rodent group in South America, the history of

representatives of the squirrel-related clade (Sciuridae) and mouse-related clade (Castorimorpha, Sigmodontidae, Cricetidae, and Muridae) on this continent being much more recent (i.e., late Neogene and Quaternary, except maybe for the Neotropical pygmy squirrel; Roth and Mercer, 2008; Patton et al., 2015). A conspicuous scansorial and arboreal South American mammal group, i.e., platyrrhine primates, had probably not dispersed into South America by the late middle Eocene (Antoine et al., 2017). Other taxonomic groups documented in the ancient localities of Amazonia (e.g., Eocene Contamana, Santa Rosa) could have competed with caviomorphs, notably those with a similar diet to caviomorphs (herbivorous or frugivorous), such as sauropsids, paucituberculate and polydolopimorph metatherians, perhaps gondwanatheres, and/or small typothere notoungulates (Campbell, 2004; Antoine et al., 2016, 2017). However, it is worth noting that these pre-Deseadan Amazonian assemblages likely only yield a limited part of the faunas due to taphonomic biases. In addition, these localities are scarce and scattered, which does not allow for a realistic picture of these mammalian guilds. Regarding the environmental changes in the middle Eocene, a global climatic warming (the Middle Eocene Climatic Optimum [MECO]; Bohaty and Zachos, 2003; Bohaty et al., 2009) and an intense Andean uplift phase (the Incaic phase; Steinmann, 1929; Jaillard and Soler, 1996) could have played a role in the early diversification of caviomorphs (see Boivin, 2017). The biotopes of CTA-27 and CTA-29, inferred from biological and geological data (Antoine et al., 2012, 2016), indicate warm and wet conditions, which could be linked to MECO effects. The overall palynoflora in the Amazonian Paleogene shows fluctuations in forest diversity that correlate with global temperatures. Forest diversity increased during periods of global warming and decreased during periods of cooling (Jaramillo et al., 2006, 2010). However, unlike the high latitudes of South America (e.g., Barreda and Palazzesi, 2010), the low latitudes may not show environmental heterogeneity (Jaramillo et al., 2010). This statement must be confirmed with better constrained local and regional paleoenvironmental data. Paleontological field efforts must also be sustained in the Paleogene of South America in order to further document and deepen our understanding of the ecology of early caviomorph rodents and other groups. With such data, it will be interesting to explore the modalities of the emergence of ecological diversity in caviomorphs and determine the correlative effects of biotic and abiotic factors on the appearance of different locomotor behaviors in this group of rodents.

CONCLUSIONS

The three tarsal bones from the CTA-29 and CTA-27 localities (Contamana) described here provide new key elements, which further our understanding of the early evolutionary history of caviomorphs. Indeed, they are the oldest known tarsal bones documenting this rodent group. Additionally, they contribute to improvement of the caviomorph postcranial record, which was only known from limited material from the Paleogene. Our results show that the astragalus from CTA-29 (MUSM 3425) has clear osteological adaptations that enhance movements for climbing. One of the calcanei from CTA-27 (MUSM 3422) displays a mosaic of morphological characters suggesting a terrestrial and partly fossorial lifestyle, whereas the other calcaneus (MUSM 3423) may represent a generalist form with a tendency for a potential semiaquatic lifestyle. Given these observations, these three tarsal bones could correspond to three distinct species, which would have occupied different ecological niches. Accordingly, these results suggest that the earliest caviomorphs underwent

a rapid adaptive radiation after their arrival in South America, during which they colonized different ecological niches.

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APPENDIX 1. Abbreviations of dimensions of measurements used in this study (in alphabetical order). Based on Ginot et al. (2016).

Abbreviation	Dimension
ABW	astragalus body width
AmTL	astragalo-medial tarsal facet length
ATL	astragalus total length
ATW	astragalus total width
CAL	calcaneus anterior length
CCH	calcaneo-cuboid facet height
CCW	calcaneo-cuboid facet width
CTW	calcaneus total width
EL	ectal facet length
EW	ectal facet width
HH	head height
HW	head width
LBH	lateral body height
LTL	lateral trochlear length
MBH	medial body height
MH	maximum height
MTL	medial trochlear length
NH	neck height
NL	neck length
PPL	peroneal process length
PPW	peroneal process width
SL	sustentacular facet length
SW	sustentacular facet width
TW	trochlear width