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The tarsal-metatarsal complex of caviomorph rodents: Anatomy and functional-adaptive analysis

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Abstract

Caviomorph rodents represent a major adaptive radiation of Neotropical mammals. They occupy a variety of ecological niches, which is also reflected in their wide array of locomotor behaviors. It is expected that this radiation would be mirrored by an equivalent disparity of tarsal-metatarsal morphology. Here, the tarsal-metatarsal complex of Erethizontidae, Cuniculidae, Dasyproctidae, Caviidae, Chinchillidae, Octodontidae, Ctenomyidae, and Echimyidae was examined, in order to evaluate its anatomical variation and functional-adaptive relevance in relation to locomotor behaviors. A qualitative study in functional morphology and a geometric morphometric analysis were performed. We recognized two distinct tarsal-metatarsal patterns that represent the extremes of anatomical variation in the foot. The first, typically present in arboreal species, is characterized by features that facilitate movements at different levels of the tarsal-metatarsal complex. The second pattern, typically present in cursorial caviomorphs, has a set of features that act to stabilize the joints, improve the interlocking of the tarsal bones, and restrict movements to the parasagittal plane. The morphological disparity recognized in this study seems to result from specific locomotor adaptations to climb, dig, run, jump and swim, as well as phylogenetic effects within and among the groups studied.

KEYWORDS

foot, geometric morphometrics, living, locomotion

1 | INTRODUCTION

Caviomorphs (or New World Hystricognathi) constitute a monophyletic group of rodents (e.g., Fabre, Hautier, Dimitrov, & Douzery, 2012; Fabre, Hautier, & Douzery, 2015; Upham & Patterson, 2015; Voloch, Vilela, Loss-Oliveira, & Schrago, 2013), endemic to Central and South America. During their evolutionary history since the late Middle Eocene of Perú (Antoine et al., 2012), caviomorphs developed a noteworthy taxonomic richness that comprises about 250 extant species (e.g., Patton, Pardiñas, & D'Elía, 2015; Woods & Kilpatrick, 2005), which are usually grouped in four main clades (Erethizontoidea, Cavoidea, Octodontoidea and Chinchilloidea; e.g., Upham & Patterson, 2015). Extant South American species belong to ten families: Erethizontidae (Neotropical porcupines or coendús), Abrocomidae (chinchilla rats and arboreal chinchilla rats), Echimyidae (spiny rats, bamboo rats, tree rats, coypus), Octodontidae (degus, rock rats, viscacha rats, coruros), Ctenomyidae (tuco-tucos), Caviidae (cavies, capybaras, Patagonian and Chacoan maras), Dasyproctidae (agoutis and acouchis), Cuniculidae

(pacas), Chinchillidae (chinchillas, plain and mountain viscachas), and Dinomyidae (pacaranas; Ellerman, 1940; Patton et al., 2015; Woods & Kilpatrick, 2005), constituting an important component of the Neotropical mammalian assemblages. Species richness of caviomorphs is accompanied by substantial ecological diversity, which is reflected in their wide array of locomotor behaviors (e.g., cursorials, jumpers, diggers, climbers, swimmers) and substrate preferences (from semiaquatic, terrestrial, fossorial, saxicolous, to scansorial and highly arboreal species). In addition, caviomorphs occupy a wide range of habitats and dwell in very diverse environments (e.g., rainforests, mountain forests, Atlantic forest, semideciduous forests, tropical savannas, Pampas, Monte and adjoining semiarid chaquenean areas, high Andean, and Puna; e.g., Mares & Ojeda, 1982; Patton et al., 2015).

In view of their taxonomic richness, ecological diversity, and extended temporal and geographic range of distribution, living caviomorphs are the result of major adaptive radiation of Neotropical mammals. We hypothesize that this radiation is mirrored by an equivalent postcranial morphological disparity. However, despite the studies on

the postcranium in fossil and living species (e.g., Candela, Rasia, & Pérez, 2012; Candela & Picasso, 2008; Elissamburu & Vizcaino, 2004; Ginot, Hautier, Marivaux, & Vianey-Liaud, 2016; Hildebrand, 1978; Morgan, 2009; Morgan & Verzi, 2011; Prochel, Begall, & Burda, 2014; Rocha-Barbosa, Youlatos, Gasc, & Renous, 2002, 2005; Samuels & Van Valkenburgh, 2008), caviomorphs are not completely understood in terms of their locomotor adaptations.

Several contributions of the postcranium of mammals have recognized that the tarsal-metatarsal bones are informative from functional and phylogenetic points of view (e.g., Abello & Candela, 2010; Argot, 2002; Candela & Picasso, 2008; de Muizon, Cifelli, & Bergqvist, 1998; Flores, 2009; Gebo, Dagosto, Beard, & Qi, 2001; Gebo & Dagosto, 1988; Ginot et al., 2016; Hildebrand, 1985a,b; Lewis, 1980a,b, 1989; Salton & Szalay, 2004; Sargis, 2002; Szalay, 1994; Szalay & Decker, 1974; Szalay & Sargis, 2001, 2006; Weisbecker & Schmid, 2007). The foot, perhaps because its direct contact with the substrate, is the part of the skeleton that supports some of the most complex loads of the body (Salton & Szalay, 2004; Szalay, 1994; Szalay & Sargis, 2001). Because this segment of the limb is a multi-bone system, small changes of its anatomy can reflect changes in its functional ability to support loads (Salton & Szalay, 2004; Szalay, 1994; Szalay & Sargis, 2001). Nevertheless, the foot anatomy of caviomorphs is one of the less studied regions of the postcranium, with only some of its tarsal-metatarsal structures analyzed (Candela & Picasso, 2008; Candela et al., 2012; Ginot et al., 2016; Hildebrand, 1978; Weisbecker & Schmid, 2007) from a functional-adaptive perspective. Moreover, comprehensive phylogenies of caviomorphs are rarely based on foot characters (Horovitz, Sánchez-Villagra, Martin, & Aguilera, 2006).

Given the diverse locomotor behaviors and substrate preferences, we hypothesize that the tarsal-metatarsal anatomy of caviomorphs encompasses different morphological patterns with functional-adaptive value. Here, we examine the tarsal-metatarsal variation in caviomorphs and scrutinize the probable relationship between the foot features, its function, locomotor adaptations and substrate preferences. Consequently, we investigate if the adaptive radiation of the caviomorphs is reflected in their foot anatomy.

2 | MATERIALS AND METHODS

We examined the tarsal-metatarsal complex of at least one specimen of 35 species of caviomorphs (Table 1; Appendix). The morphological variation analyzed correspond to eight families belonging to all higher taxa (i.e., four superfamilies) nested in Caviomorpha (see Fabre, Hautier, Dimitrov, & Douzery, 2012; Fabre, Hautier, & Douzery, 2015; Upham & Patterson, 2015; Voloch, Vilela, Loss-Oliveira, & Schrago, 2013).

Anatomical features were studied from direct observation of the skeletons or from photographs. Diverse contributions on mammalian tarsal bone anatomy on different groups of mammals (e.g., Argot, 2002; Candela & Picasso, 2008; de Muizon et al., 1998; Gebo & Dagosto, 1988; Gebo et al., 2001; Ginot et al., 2016; Hildebrand, 1978; Lewis, 1980a,b, 1989; Salton & Szalay, 2004; Sargis, 2002; Szalay,

1994; Szalay & Decker, 1974; Szalay & Sargis, 2001, 2006), provided an adequate standard of comparison for the analysis of the foot of caviomorphs. The osteological nomenclature used in this study follows that of Salton & Szalay (2004) and Candela & Picasso (2008). Nomenclature of the tarsal-metatarsal complex is illustrated in Figure 1A. The myological nomenclature and the muscular system information was that of McEvoy (1982) for erethizontids and García-Esponda & Candela (2010, 2016) for cavioids.

Primary and secondary locomotor behaviors, as well as substrate preferences of the caviomorph taxa examined are listed in Table 1. Data on these ecological characteristics were taken from Nowak (1991), Lessa, Vassallo, Verzi, & Mora (2008), Ojeda, Novillo, & Ojeda (2015), and Patton et al. (2015). We considered the primary locomotor behavior as the principal mode employed by a species to move on the substrate, and secondary locomotor behaviors as those modes that were used less frequently by that species, e.g., to move on the substrate, to feed, to construct a den, or to evade predators. Data on secondary locomotor behavior were not available for many species. For example, the absence of information on this item in *Myoprocta* does not mean that the species of this genus do not occasionally dig or jump.

We scrutinized the anatomical variation within caviomorphs examined, and evaluated the possible functional relationships between tarsal-metatarsal anatomy and compatible movements of the foot, in association with the locomotor behavior and substrate preference in each case. On this basis, we test if, as in other mammals, morphology and function of the tarsus-metatarsus are distinctive within and between different clades of caviomorphs that show different locomotor habits.

Among tarsal bones, we placed focus on the morphological and functional relationships of the cuboid, navicular, tarsal sesamoids and cuneiforms. We also analyzed the morphological variation of the transverse tarsal joint (TTJ), i.e., the composite joint constituted by the calcaneocuboid (CCJ) and the astragalonavicular joints (ANJ; Figure 1A). We do not describe in details the anatomical characters of the astragalus and calcaneus, which were mainly studied in caviomorphs by Candela & Picasso (2008) and Ginot et al. (2016). As our main objective was to explore the morphological variation of the tarsal-metatarsal complex between different groups of Caviomorpha, the emphasis was on intergeneric or higher taxonomic levels instead of intraspecific anatomical variation. Thus, in the text, all the species analyzed are almost always referred to by their generic names.

We performed a morphological study, a morphometric analyses with linear measurements, and a geometric morphometrics analysis. In the morphometric analysis we measured four variables (Figure 1B,C) on photographs using ImageJ 1.50i software (Schneider, Rasband, & Eliceiri, 2012): navicular body length, plantar process of the navicular length, cuboid length, and third metatarsal length. We calculated two indices: (1) plantar process of the navicular length/navicular body length, and (2) third metatarsal length/ectocuneiform length, and created a box plot for each of them in R software 3.1.5 (R Development Core Team, 2015).

TABLE 1 Main and secondary locomotor behaviors and substrate preferences of the caviomorph species examined in this study

Taxon	Main locomotor behavior	Secondary locomotor behavior	Main substrate preference
Erethizontoidea			
Erethizontidae			
<i>Erethizon dorsatum</i>	Climbing	Ambulatory	Scansorial
<i>Coendou prehensilis</i>	Climbing		Arboreal
<i>C. spinosus</i>	Climbing		Arboreal
<i>C. insidiosus</i>	Climbing		Arboreal
<i>Chaetomys subspinosus</i>	Climbing		Arboreal
Cavioidea			
Cuniculidae			
<i>Cuniculus paca</i>	Ambulatory	Swimming, digging	Terrestrial
Dasyproctidae			
<i>Dasyprocta azarae</i>	Cursorial	Jumping	Terrestrial
<i>Myoprocta acouchi</i>	Cursorial		Terrestrial
Caviidae			
Caviinae			
<i>Cavia aperea</i>	Ambulatory		Terrestrial
<i>Microcavia australis</i>	Ambulatory	Digging, climbing	Terrestrial
<i>Galea leucoblephara</i>	Ambulatory		Terrestrial
Dolichotinae			
<i>Dolichotis patagonum</i>	Cursorial	Jumping, stotting	Terrestrial
<i>Pediolagus salinicola</i>	Cursorial	Jumping	Terrestrial
Hydrochoerinae			
<i>Hydrochoerus hydrochaeris</i>	Swimming/ambulatory		Semiaquatic
Chinchilloidea			
Chinchillidae			
Chinchillinae			
<i>Chinchilla</i> sp.	Jumping		Saxicolous
<i>Lagidium viscacia</i>	Jumping		Saxicolous
Lagostominae			
<i>Lagostomus maximus</i>	Ambulatory	Digging, jumping	Terrestrial
Octodontoidea			
Octodontidae			
<i>Octomys mimax</i>	Ambulatory	Digging	Saxicolous
<i>Octodontomys gliroides</i>	Ambulatory	Digging, climbing	Terrestrial
<i>Tympanoctomys aureus</i>	Digging		Fossorial
<i>T. kirchnerorum</i>	Digging		Fossorial
Ctenomyidae			
<i>Ctenomys magellanicus</i>	Digging		Subterranean
<i>C. talarum</i>	Digging		Subterranean
<i>C. australis</i>	Digging		Subterranean
Echimyidae			
<i>Myocastor coypus</i>	Swimming	digging	Semiaquatic
<i>Phyllomys pattoni</i>	Climbing		Arboreal
<i>Makalata didelphoides</i>	Climbing		Arboreal
<i>Proechimys guairae</i>	Ambulatory		Terrestrial
<i>P. steerei</i>	Ambulatory		Terrestrial
<i>Trinomys dimidiatus</i>	Ambulatory		Terrestrial
<i>Euryzygomatomys spinosus</i>	Digging		Semifossorial
<i>Clyomys laticeps</i>	Digging		Semifossorial
<i>Lonchothrix emiliae</i>	Climbing		Arboreal
<i>Dactylomys dactylinus</i>	Climbing		Arboreal
<i>Kannabateomys amblionyx</i>	Climbing		Arboreal
<i>Olallamys albicaudata</i>	Undescribed		Undescribed

Data taken from Nowak (1991); Lessa et al., (2008); Ojeda et al., (2015); and Patton et al., (2015).

The geometric morphometric analysis was based on photographs of the tarsus-metatarsus in dorsal view. In these photographs, the specimens were placed with the lateromedial and proximodistal axes of the pes parallel to the camera lens. To minimize deformation due to

the lens, only the central area of the photograph was considered. Fifteen homologous landmarks were chosen to represent the relative size and position of each tarsal bone in the configuration, as well as the degree of elongation and relative orientation of the astragalar neck. To

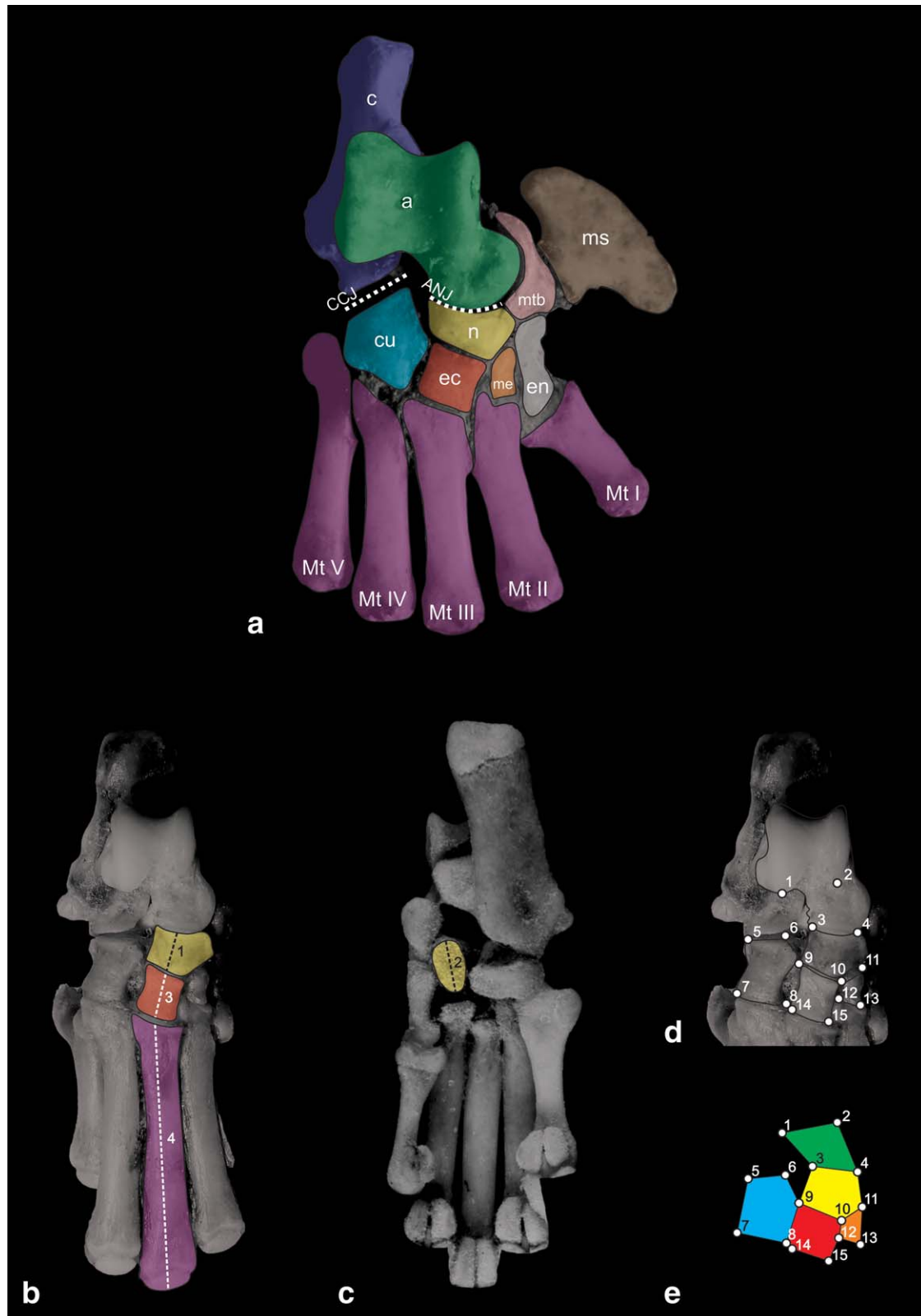


FIGURE 1 (A) nomenclature of the bones and main joints of the tarsal-metatarsal complex; (B and C) measurements used in the construction of indices; (D) landmarks used in the geometric morphometric analysis (landmark definitions are included in Table 2). (E) Landmarks and schematic used in Figures 7 and 8 to show shape changes on the PCA. a: astragalus (green); ANJ, astragalonavicular joint; c, calcaneus (blue); CCJ, calcaneocuboid joint; cu, cuboid (light blue), ec, ectocuneiform (red); en, entocuneiform (grey); me, mesocuneiform (orange); mtb, medial tarsal bone (pink), ms, medial sesamoid (brown); Mt I-V, first to fifth metatarsals (violet); n, navicular (yellow). Measurements: 1, navicular body length; 2, plantar process of the navicular length; 3, cuboid length, and 4, third metatarsal length

TABLE 2 Definitions of the digitized landmarks

Landmark	Definition
1	Most distal point of the lateral lip of the astragalar trochlea
2	Most distal point of the medial lip of the astragalar trochlea
3	Most lateral contact point between the astragalus and the navicular
4	Most medial contact point between the astragalus and the navicular
5	Most lateral contact point between the calcaneus and the cuboid
6	Most medial contact point between the calcaneus and the cuboid
7	Most laterodistal point of the cuboid
8	Most distal contact point between the cuboid and the ectocuneiform
9	Contact point between the navicular, the cuboid and the ectocuneiform
10	Contact point between the navicular, the ectocuneiform and the mesocuneiform
11	Most medial contact point between the navicular and the mesocuneiform
12	Most distal contact point between the ectocuneiform and the mesocuneiform
13	Most mediiodistal point of the mesocuneiform
14	Most laterodistal point of the ectocuneiform
15	Most mediiodistal point of the ectocuneiform

minimize digitation error, these landmarks were digitized by one of us (NAM) and the images were randomized. The landmarks used are shown in Figure 1D–E and their definitions are in Table 2. It has to be noted that the tarsus is not a rigid structure, as it is composed by several bones; for that reason, tarsi with a visible level of torsion or bending were discarded and only those with a straight arrangement were utilized. In addition, complete foot skeletons are scarcely represented in museum collections, and some of the specimens are incompletely cleaned, so that dried tissues do not allow to take some measurements; thus, a few other specimens were not included in the morphometric analyses.

A TPS file was created from a directory with the photograph files in tpsUtil and digitized in tpsDig2 (Rohlf, 2015). The landmark configurations were superimposed to remove the variation that does not correspond to shape. The superimposition was obtained by rotating, translating and scaling the configurations using a Generalized Procrustes Analysis (GPA; Rohlf, 1990). To analyze the shape variation, a Principal Components Analysis (PCA) was used (Manly, 1994). To evaluate the patterns of shape change, the principal component scores were related with the taxonomic and ecological information. The Generalized Procrustes Analysis and PCA were performed with MorphoJ 1.06d (Klingenberg, 2011), and for the visualization of intermediate morphologies TpsRelw (Rohlf, 2015) was used.

3 | RESULTS

3.1 | Linear Morphometrics

The analysis of the plantar process of the navicular length/navicular body length index (Figure 2A) indicates that chinchilloids, octodontoids, and eretizontoids have a relatively short plantar process of the navicular with respect to that of the cavioids. Among the latter group, *Hydrochoerus* exhibits the shortest plantar process while *Pediolagus* and *Dolichotis* the longest one.

Values of the third metatarsal length/ectocuneiform length index (Figure 2B) indicate that eretizontoids have relatively short metatarsals, octodontoids and cavioids show a great range of variation of this

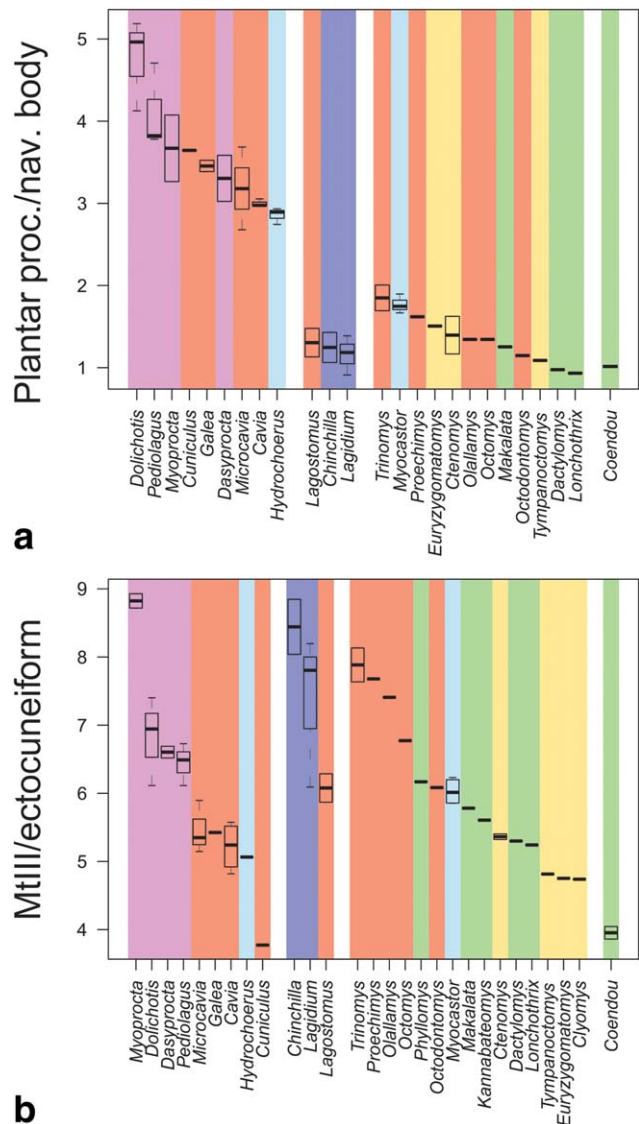


FIGURE 2 Box plots of morphological indices of the pes in caviomorph rodents. (A) Plantar process of the navicular length/navicular body length index; (B) third metatarsal length/ectocuneiform length index. Violet, cursorial; red, ambulatory; light blue, swimming; blue, jumping; green, climbing; yellow, digging. Taxa are arranged by main clades (superfamilies) and then sorted in descending order by mean value

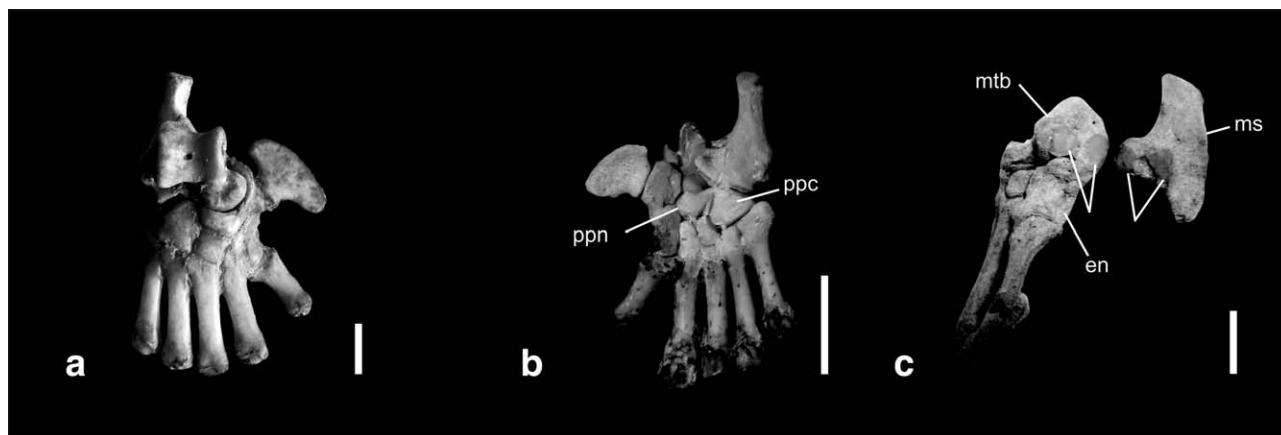


FIGURE 3 Tarsal-metatarsal complex of Erethizontidae showing detail of the articular surfaces of the medial tarsal bone and medial sesamoid (arrows). (A) *Coendou prehensilis* (MLP1086, mirrored), dorsal view; (B) *C. spinosus* (MPS-Z 185, mirrored), plantar view; (C) *C. prehensilis* (MN 4925, mirrored), medial view, Scale: 10 mm. en, entocuneiform; mtb, medial tarsal bone, ms, medial sesamoid; ppc, plantar process of the cuboid; ppn, plantar process of the navicular. Arrows indicate articular surfaces of the mtb and ms

index, and chinchilloids show middle and high values. Among octodontoids, the metatarsals of digging and climbing species are relatively shorter than those of the ambulatory and swimming taxa. Among chinchillids, *Chinchilla* and *Lagidium* show the longest metatarsals. Among cavioids, the ambulatory taxa have the shortest metatarsals while the cursorial species have the longest (*Cuniculus* has the shortest metatarsals while *Myoprocta* has the longest).

3.2 | The Tarsal-Metatarsal Complex in Caviomorphs: Anatomical Variation

3.2.1 | Erethizontoids

The astragalus is mediolaterally extended (Figure 3). The astragalus head is large and medially oriented with respect to the proximo-distal axis of the foot. The astragalus neck is relatively short with respect to the astragalus length (Figure 3A). The navicular facet of the astragalus head is continued medially by a large and convex astragalomediotarsal facet for the medial tarsal bone (=first sesamoid), that spreads on the medial region of the astragalus head. The medial tarsal bone also articulates with the navicular and the entocuneiform, completely wrapping the astragalomediotarsal facet. The medial tarsal bone is wide and large compared with the navicular size. The medial sesamoid (=second sesamoid) is hypertrophied in *Coendou* and *Chaetomys* more than in *E. dorsatum*, and articulates with the medial tarsal bone through two well distinguished facets (Figure 3C). The sustentaculum of the calcaneus is close to the calcaneocuboid facet, so that the distal portion of this bone is short. The latter feature is related with the position of the ANJ and the CCJ, which are located at the same level. The plantar process of the navicular is barely developed (Figures 2A and 3B). The cuboid is larger than the ectocuneiform (Figure 3A), its plantar process is moderately developed (Figure 3B), and surrounds a shallow groove for the tendon of the peroneus longus muscle. The ectocuneiform is obliquely orientated (in a medioproximal-lateralodistal direction) with respect to the longitudinal axis of the Mt III. The entocuneiform is subrectangular in shape. This bone is at least twice as long as the mesocuneiform and

extends distally beyond the level of the distal border of the ectocuneiform (Figure 3A,C).

The metatarsals are not close-packed and are relatively short when compared with the ectocuneiform length (Figure 2B); thus, the length of the Mt III is about four times that of the ectocuneiform. In *Coendou* and *Chaetomys* the Mt I is more medially oriented than in *E. dorsatum*. The Mt V is slightly shorter than the Mt IV (Figure 3).

3.2.2 | Chinchilloids

In *Chinchilla*, *Lagidium* and *Lagostomus* the astragalus is longer than it is wide (Figure 4). The astragalus head is rather parasagittally oriented with respect to the astragalus body. The astragalus head is relatively small, compared with that of the erethizontids, and separated from the astragalus body by a relatively long neck. The navicular facet of the astragalus head is rounded and less lateromedially extended than in cavioids (see below). This facet is continued medioventrally by the astragalomediotarsal facet for the medial tarsal bone. The latter facet is located on the medial plantar portion of the astragalus head. The medial tarsal bone, although well developed, is relatively smaller than that of erethizontids. The calcaneocuboid facet of the calcaneus is distally located with respect to the sustentaculum, so that the distal portion of this bone is long. This feature expresses the distal location of the CCJ with respect to the ANJ. The plantar process of the navicular is distinctive but relatively short with respect to the navicular body (Figure 2A); it does not extend beyond the distal border of the cuboid (Figure 4). The cuboid is subequal (*Lagidium* and *Chinchilla*; Figure 4A,B) or smaller (*Lagostomus*; Figure 4C) than the ectocuneiform; its plantar process is markedly developed. The ectocuneiform is oriented in line with respect to the longitudinal axis of the Mt III. In *Chinchilla* and *Lagidium* the entocuneiform is elongate and narrow (the entocuneiform length is at least three times that of the mesocuneiform), extending beyond the distal border of the ectocuneiform and subequal in width to the mesocuneiform. In *Lagostomus*, the entocuneiform is somewhat smaller than in *Lagidium* and *Chinchilla* (Figure 4). The plantar aspect of the base of the Mt II possesses a large tubercle (Figure 4C) lateroproximally

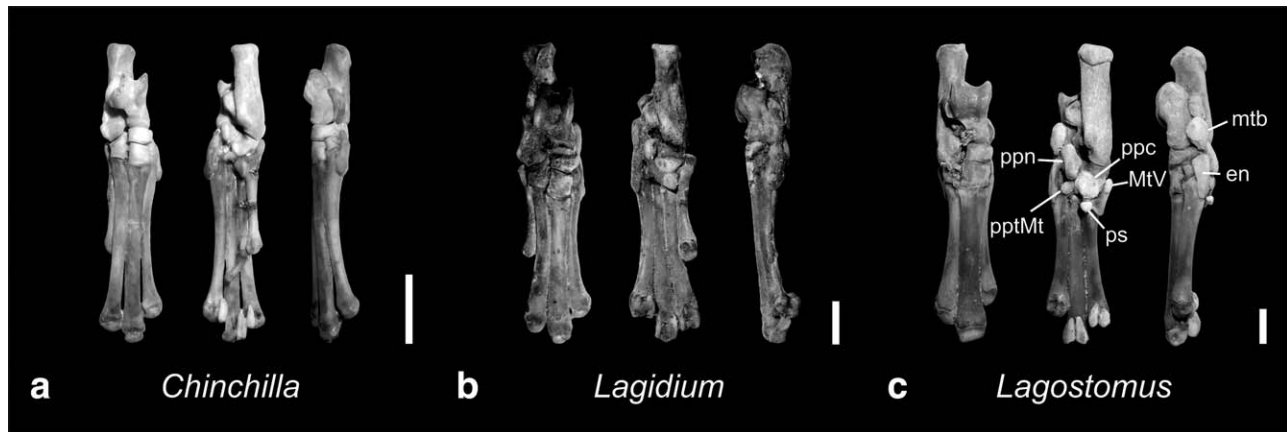


FIGURE 4 Tarsal-metatarsal complex of Chinchillidae in dorsal, ventral and plantar views. (A) *Chinchilla* sp. (MLP 31.XII.02.37, mirrored); (B) *Lagidium viscacia* (MLP 2021); (C) *Lagostomus maximus* (MPS-Z 200, mirrored). Scale: 10 mm. en, entocuneiform; mtb, medial tarsal bone; ppc, plantar process of the cuboid; ppn, plantar process of the navicular; pptMtII, plantar proximal tubercle of the MtII; ps, plantar sesamoid; MtV, metatarsal V

oriented toward the plantar process of the cuboid. In all genera, there is a plantar sesamoid bone, located distally to the plantar face of the cuboid.

In *Chinchilla* and *Lagidium*, the metatarsals are relatively long with respect to the length of the ectocuneiform (Figure 2B), more than in *Lagostomus*. Mt I is absent in all three genera. In *Chinchilla* and *Lagidium* Mt V is well developed (Figure 4A,B), extending about half the length of Mt III, whereas in *Lagostomus*, Mt V is reduced to its proximal portion (Figure 4C). In all genera, the metatarsals are proximally closed-packed, but in *Lagostomus* the metatarsals are more strongly united at the distal ends.

3.2.3 | Octodontoids

In arboreal echimyids (Figure 5A), as well as in the semiaquatic *Myocastor* (Figure 5E), the astragalar head resembles that of erethizontids in its medial displacement and relatively globular shape, although not to the degree observed in the porcupines (Figure 5). On the other hand, in the terrestrial *Proechimys*, *Trinomys*, and the semifossorial *Euryzygomatomys* and *Clyomys* (Figure 5C,D), the astragalar head is somewhat less medially oriented than that of the arboreal taxa. In some arboreal taxa (e.g., *Dactylomys*, *Kannabateomys*), there is a relatively large medial tarsal bone (Figure 5A) that articulates with the navicular, entocuneiform, and the astragalomediotarsal facet of the astragalar head. In *Myocastor* (Figure 5E) and the arboreal taxa (Figure 5A,B), the sustentaculum of the calcaneus is close to the calcaneocuboid facet, so that the distal portion of this bone is short, although not to the same degree as in erethizontids. Consequently, the ANJ and CCJ are located approximately at the same level. Conversely, the terrestrial *Proechimys* and *Trinomys* show a more elongated and narrow distal calcaneal portion than that of the arboreal echimyids. The plantar process of the navicular is short (Figure 2A), not extending beyond the distal border of the cuboid. The cuboid is relatively larger than or subequal to the ectocuneiform (Figure 5). The latter is obliquely oriented with respect to the longitudinal axis of the Mt III. In *Proechimys*, *Euryzygomatomys*, *Clyomys* and *Myocastor* the cuboid is relatively smaller than that of the arboreal forms (Figure

5C,E). In all echimyids, the entocuneiform is subrectangular in shape, extending distally beyond the level of the distal border of the ectocuneiform. The plantar process of the cuboid is moderately developed (Figure 5A,E).

The metatarsals of the terrestrial *Trinomys* and *Proechimys* are lengthened (Figure 2B), so that the Mt III is approximately eight times longer than the ectocuneiform. In *Olallamys*, the Mt III has a similar value to that of terrestrial echimyids. On the contrary, the arboreal *Makalata*, *Lonchothrix*, *Phyllomys*, *Dactylomys* and *Kannabateomys* show metatarsals relatively shorter (Figure 2B), but not as much as in erethizontids. In these genera, Mt III length is between five and six times the ectocuneiform length. In addition, the metatarsals of *Trinomys* and *Proechimys* are close-packed (Figure 5C), especially at its proximal and medial portions, while in the arboreal echimyids the metatarsals are spread (Figure 5A,B). *Myocastor* has metatarsals longer than those of the arboreal echimyids, with the exception of *Phyllomys* (Figure 2B). In the semifossorial *Clyomys* and *Euryzygomatomys*, the metatarsals are even shorter than those of the arboreal forms.

In echimyids, the Mt I is not medially orientated. The Mt I of the arboreal taxa is relatively longer than that of the terrestrial forms (more than half the length of the Mt III). In *Trinomys* and *Proechimys* the Mt I is approximately half the length of Mt III (Figure 5C). The length of the Mt V of the echimyids examined is variable. In the arboreal *Makalata*, for example, the Mt V is relatively long (more than half the length of Mt III), a similar condition to that observed in *Phyllomys* and *Lonchothrix*. In the terrestrial *Proechimys* (and in a lesser degree in *Trinomys*) the Mt V is relatively shorter than that of the arboreal genera. As in terrestrial echimyids, in the semifossorial *Euryzygomatomys* the Mt I and Mt V are relatively shorter than those of the arboreal taxa.

The Ctenomyidae *Ctenomys* (Figure 5F) shows several tarsal features similar to those of arboreal echimyids. In addition, this genus has robust metatarsals and the Mt V relatively short with respect to Mt III.

Octodontidae (Figure 5G–I) have an elongated astragalus, a relatively long astragalar neck, and a narrow and elongated ectocuneiform. The cuboid is also elongated. The astragalar head is slightly medially

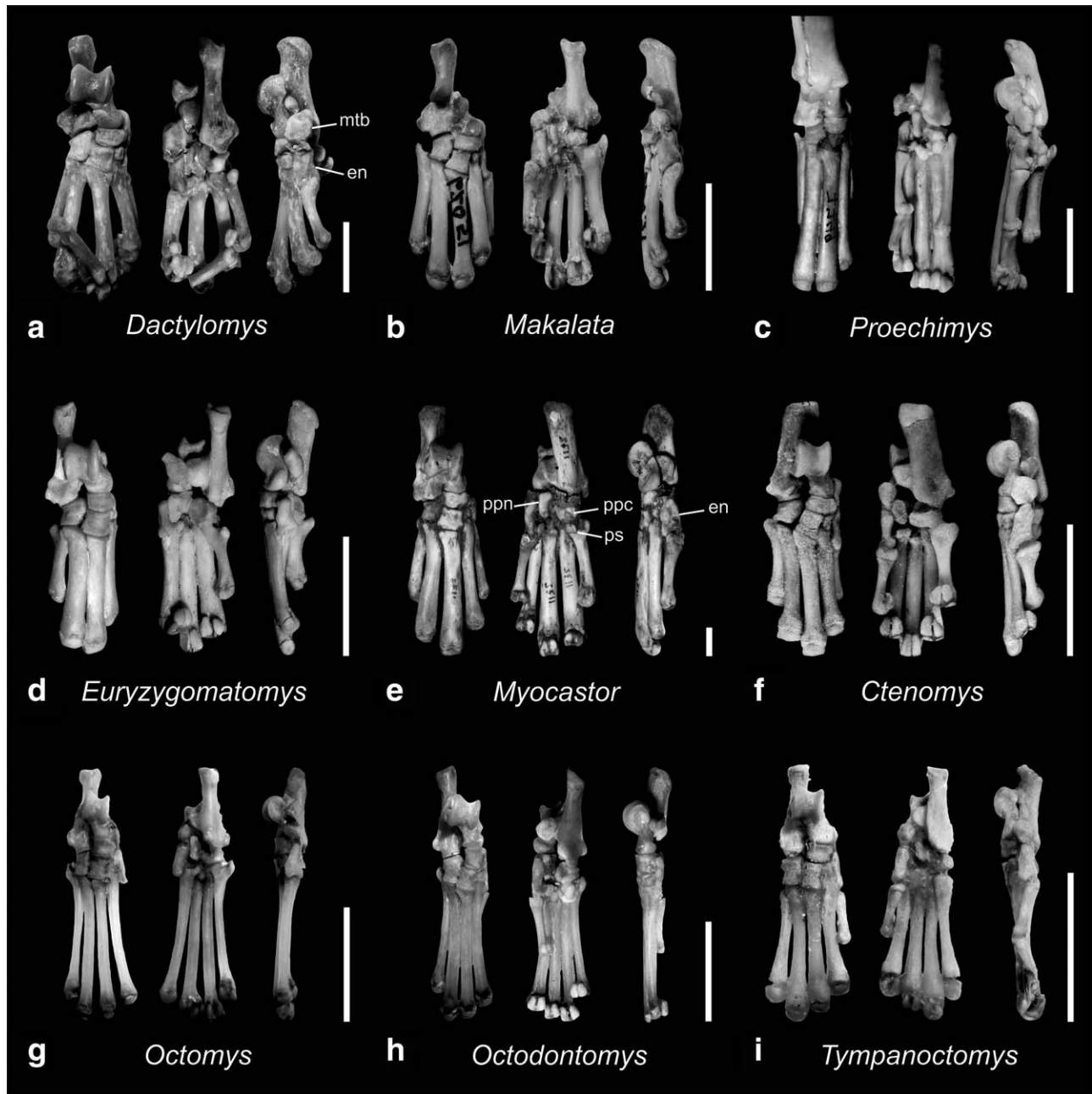


FIGURE 5 Tarsal-metatarsal complex of Octodontoidea in dorsal, plantar and medial views. (A) *Dactylomys dactylinus* (YPM 1391); (B) *Makalata didelphoides* (FMNH 62051; mirrored, lacking astragalus); (C) *Proechimys guairae* (MLP 22.II.00.7, mirrored); (D) *Euryzygomatomys spinosus* (MLP 16.VII.02.11, mtb displaced); (E) *Myocastor coypus* (MLP 1172, mirrored, mtb is lacking); (F) *Ctenomys talarum* (MLP 2507, mirrored); (G) *Octomys mimax* (IADIZA CM 03785, mirrored); (H) *Octodontomys gliroides* (MACN 25.197, mirrored); (I) *Tympanoctomys kirchnerorum* (CNP 1819, mirrored). Scale: 10 mm. en, entocuneiform; mtb, medial tarsal bone; ppc, plantar process of the cuboid; ppn, plantar process of the navicular; ps, plantar sesamoid

displaced with respect to the astragalar trochlea. The CCJ is somewhat distally located with respect to the ANJ. The plantar process of the navicular (Figure 2A) does not extend beyond the distal border of the cuboid, and the ectocuneiform is less obliquely orientated with respect to the longitudinal axis of the Mt III than in *Ctenomys*.

There is certain variation on the relative length of the metatarsals (Figure 2B). *Octodontomys* and *Octomys* has elongated and gracile, whereas *Tympanoctomys* has shorter and more robust metatarsals (Fig-

ure 2B). In these genera, the Mt V is not as shortened as in terrestrial echimyids.

3.2.4 | Cavioids

Most cavioids share a particular set of foot features: astragalar head parasagittally orientated, lateromedially extended navicular facet of the astragalar head, well-developed plantar process of the navicular, relatively large ectocuneiform with respect to the cuboid, distal portion of

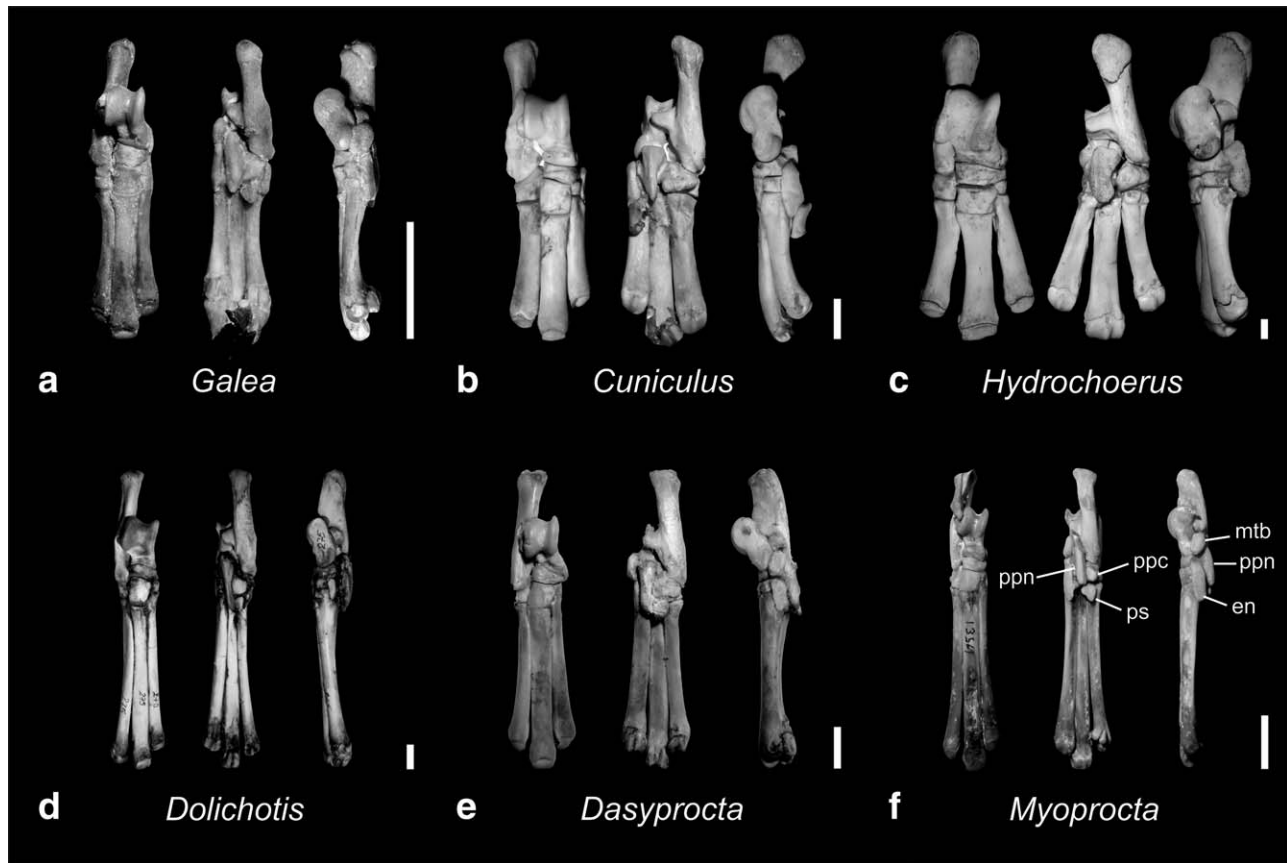


FIGURE 6 Tarsal-metatarsal complex of Caviioidea in dorsal, ventral, and medial views. (A) *Galea leucoblephara* (MLP 1928, mirrored); (B) *Cuniculus paca* (MACN-Ma 49.396, mirrored, ps and mtb, MtV are lacking); (C) *Hydrochoerus hydrochaeris* (MACN 43.43, mtb, en, ps, MtV are lacking); (D) *Dolichotis patagonum* (MLP 275, mtb is lacking); (E) *Dasyprocta azarae* (CNP 790, mirrored); (F) *Myoprocta acouchi* (YPM 1360). Scale: 10 mm. en, entocuneiform; mtb, medial tarsal bone; ppc, plantar process of the cuboid; ppn, plantar process of the navicular; ps, plantar sesamoid

the calcaneus elongated, reduced medial tarsal bone, elongated metatarsals, absence or marked reduction of Mt I and Mt V (Figure 6).

The astragalus is longer than it is wide, but shows certain variability. In *Hydrochoerus*, it is wider than in the other genera, being almost as wide as long (Figure 6C); it is relatively more elongated in *Cuniculus* (Figure 6B), and markedly long in the dasyproctids *Dasyprocta* and *Myoprocta*, and in the caviids *Dolichotis* and *Pediolagus* (Figure 6D,F). The astragal neck is relatively short in *Hydrochoerus* and caviines (Figure 6A,C); dasyproctids show the longest astragal necks. The astragalo-metatarsal facet for the medial tarsal bone is narrow and ventrally located on the medial region of the astragal head. This feature is in association with the small size of the medial tarsal bone.

The CCJ is distally located with respect to the ANJ (a feature related to the elongated distal region of the calcaneus). In most cavioids, the plantar process of the navicular is keel-shaped and highly developed, extending both proximally and distally, largely overpassing the distal border of the cuboid. In *Cuniculus* this process is robust, but it slightly overpasses the distal border of the cuboid. In *Hydrochoerus* it is very wide and just overpasses the distal border of the cuboid. *Pediolagus* and *Dolichotis* have the longest navicular process (Figure 2A). The

cuboid has a well-developed groove for the tendon of the peroneus longus muscle. In most cavioids, the entocuneiform is orientated parallel or slightly oblique with respect to the longitudinal axis of the Mt III. In *Cuniculus*, the entocuneiform is well developed, whereas it is small in the other cavioids, a feature associated with the absence of the digit I. The major reduction of the entocuneiform is seen in dasyproctids and dolichotines, in which this bone is scale-shaped with a small or absent contact with the medial tarsal bone (Figure 6D,F). In *Dolichotis* and *Pediolagus*, the medial tarsal is also reduced. In all cavioid genera, there is a well-developed plantar sesamoid bone that is located distally to the plantar face of the cuboid.

The metatarsals are relatively elongated (more than six times the entocuneiform length; Figure 2B). The semiaquatic *Hydrochoerus* shows relatively shorter metatarsals compared with the other cavioids. Among terrestrial forms, *Cuniculus* shows the shortest metatarsals. In this taxon, the entocuneiform articulates with a complete but short Mt I-digit I; the Mt V is short and robust, and the digit V is small. The remaining cavioids lack Mt I. Mt V is vestigial in *Hydrochoerus* and much reduced in Dasyproctidae, Caviinae and Dolichotinae. In Caviidae (with exception of *Hydrochoerus*) and Dasyproctidae, Mt II, III and IV are close-packed.

TABLE 3 First eight principal components

PC	Eigenvalues	% Var.	Cum. Var. %
1	0.00919349	42,306	42,306
2	0.00534452	24,594	66,900
3	0.00135452	6,233	73,134
4	0.00120173	5,530	78,664
5	0.00077879	3,584	82,247
6	0.00066905	3,079	85,326
7	0.00052586	2,420	87,746
8	0.00049783	2,291	90,037

PC, principal component; % Var., percent of variance explained by each PC; Cum. Var. %, Cumulative variance percent.

3.3 | Geometric Morphometrics

The first eight principal components of the PCA account for ~90% of cumulative variance; as observed in Table 3, after PC2 there is little explained variation by each PC. Principal component 1 (PC1) and Principal component 2 (PC2; Figure 7) account for ~67% of cumulative

variance. On PC1 (~42%) there is a variation from a tarsus relatively wide, a relatively large cuboid, wide ectocuneiform, calcaneocuboid joint at the same level as the astragalonavicular joint and a medially oriented astragalar head in negative values, to a relatively narrow tarsus, a relatively small cuboid, narrow ectocuneiform, CCJ distally located with respect to the ANJ and more parasagittally oriented astragalar head in positive values. On PC2 (~24%) there is a variation from a large cuboid, relatively small ectocuneiform, and long navicular and astragalar neck on negative values, to a small cuboid, large ectocuneiform, and short navicular and astragalar neck (Figure 7).

Figure 8A shows the same PCA, but emphasizing the visualization of the superfamilies. The obtained grouping seems to be indicative of a strong taxonomic influence: the Erethizontoidea occur in the negative values of PC1 and extreme negative values of PC2, the Octodontoidea occur principally in the negative values of PC2, the Cavioida occur principally in the positive values of PC2, and the Chinchilloidea occur in middle-positive values of PC1 and negative values of PC2. There is a gradient of variation shared by the Cavioida and the Octodontoidea (principally in PC1 but also in PC2), from lower PC1 and higher PC2 values to higher PC1 and lower PC2 values. In the case of the Octodontoidea, the change goes from the Echimyidae to the Octodontidae,

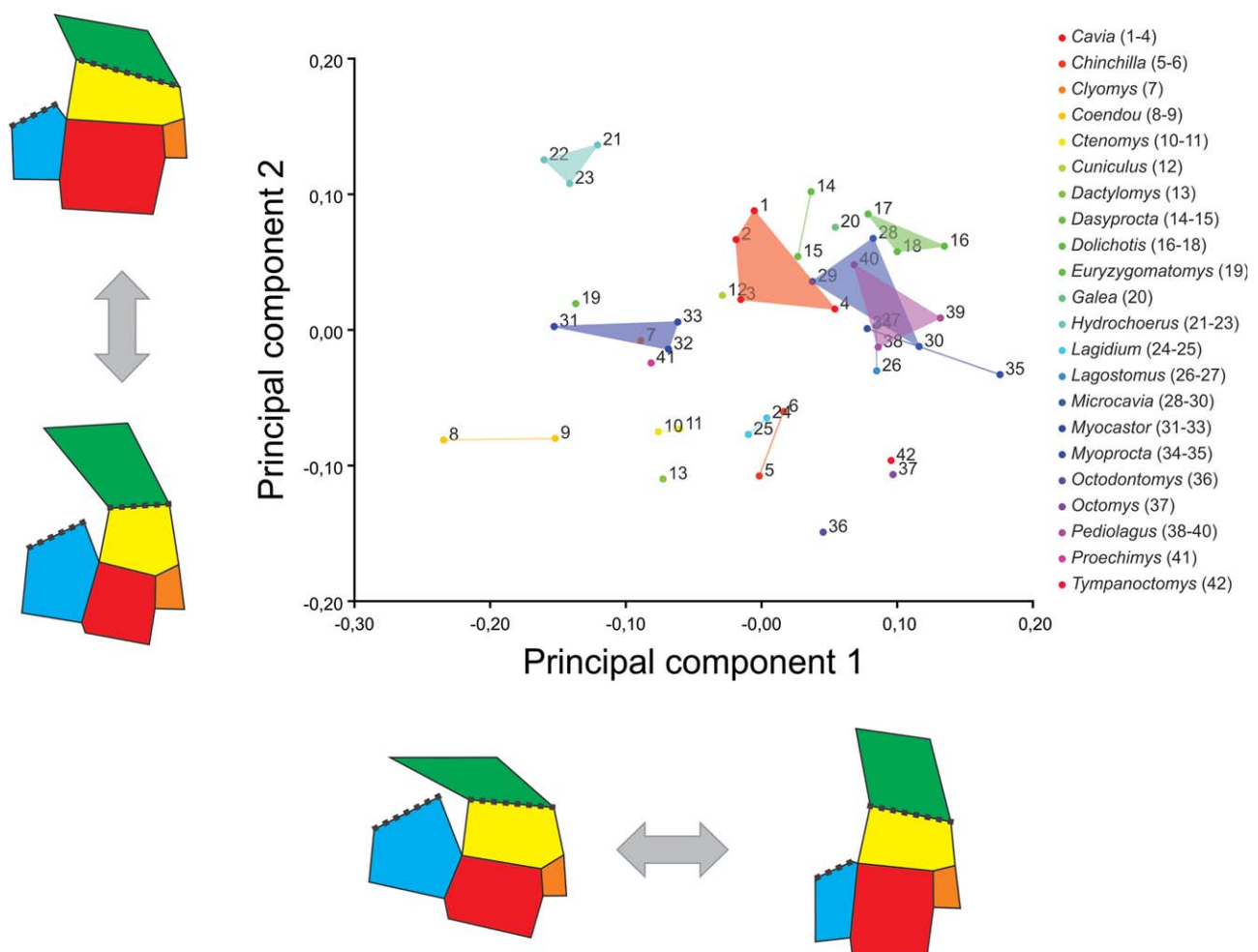


FIGURE 7 Shape variation of the tarsus of caviomorphs in the morphospace defined by the first two PCs

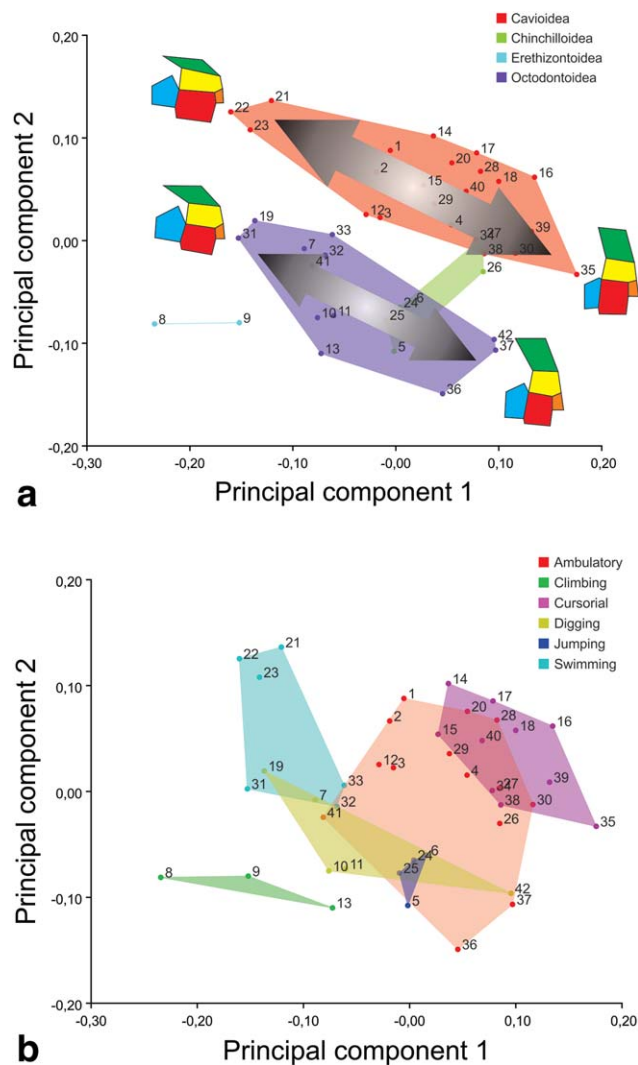


FIGURE 8 Shape variation of the tarsus of caviomorphs in relation to taxonomy and ecology. (A) Same PCA from Figure 7, showing the superfamilies, with special emphasis in the parallelism between Caviioidea and Octodontoidea; (B) same PCA from Figure 7, showing the main locomotor specializations (climbing, swimming, cursorial, digging, jumping, ambulatory)

and in the case of Caviioidea goes from *Hydrochoerus* to the remaining cavioids (with *Cuniculus* in the middle). The principal difference between the two superfamilies (shown mostly in PC2) seems to be a more robust configuration, a more distal located calcaneocuboid joint, and a relatively smaller cuboid in the Caviioidea.

The Chinchilloidea present two strikingly different morphologies, with *Chinchilla* and *Lagidium* sharing the morphospace with the Octodontoidea and *Lagostomus* closer to the Caviioidea.

In the Figure 8B, the main locomotor specializations are plotted over the same PCA. Climbers display negative values of PC1 and PC2, swimmers have negative values of PC1 and mid-positive values of PC2, cursorial taxa have positive values of PC1 and PC2, diggers have mainly negative values of PC2, jumpers have mid values of PC1 and negative values of PC2, and the ambulatory species have mostly positive values for both PC1 and PC2.

4 | DISCUSSION

4.1 | Identifying Tarsal-Metatarsal Patterns

Two distinct tarsal-metatarsal patterns representing the extremes of the observed anatomical variation are recognized in caviomorphs: one is typically present in erethizontids and arboreal echimyids (tarsal-metatarsal pattern I; Figure 9A,B), while the other is characteristic of the most specialized cursorial cavioids (tarsal-metatarsal pattern II; Figure 9 C,D). From a functional-adaptive point of view, these patterns seem to contrast climbing versus cursorial modes of locomotion, although intermediate conditions were also identified.

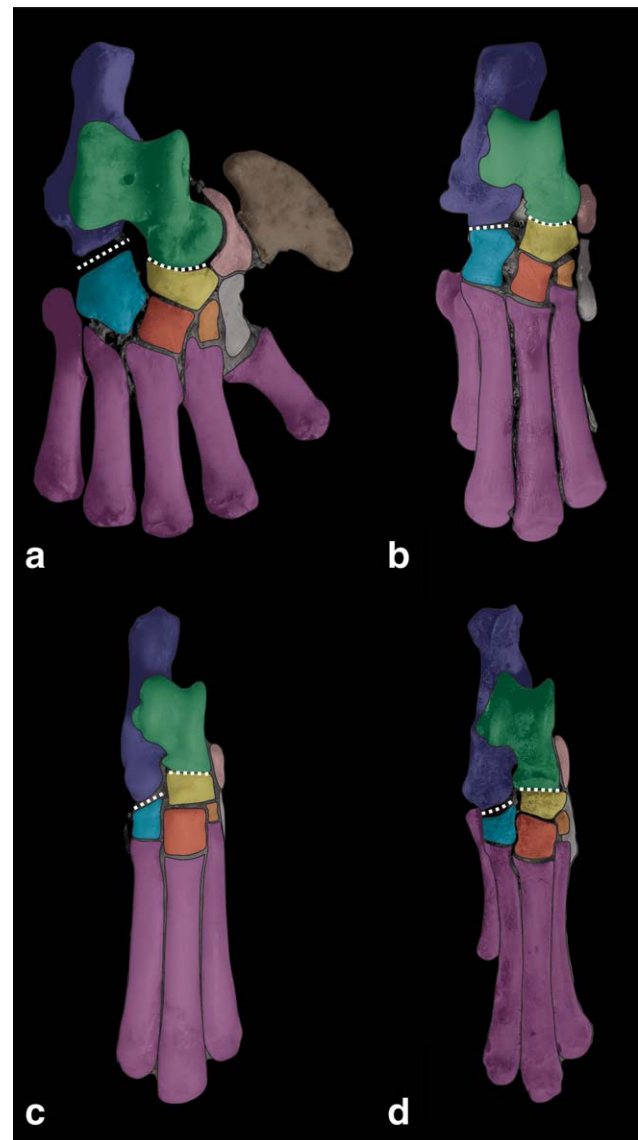


FIGURE 9 Tarsal-metatarsal complex represented in the four superfamilies of caviomorphs. (A and B) Tarsal-metatarsal Pattern I (TMPI); (C and D) tarsal-metatarsal Pattern II (TMPII). (A) Erethizontoidea (*Coendou*); (B) Octodontoidea (*Ctenomys*); (C) Caviioidea (*Cavia*); (D) Chinchilloidea (*Lagidium*). Colours indicate the same bones as those of the figure 1. Scale: 10 mm

4.1.1 | Tarsal-Metatarsal Pattern I (TMPI)

In this pattern (Figure 9A,B) the tarsus is relatively wide with respect to its length. The astragalar body is wide; the astragalar head is large and medially oriented with respect to the astragalar trochlea, and the astragalar neck is relatively short. The CCJ is located at the same level as the ANJ, resulting in a slightly curve TTJ. The medial tarsal bone is large, articulating with the medially extended and large astragalomediotarsal facet of the astragalar head. The plantar process of the navicular is scarcely developed. The cuboid is larger than the ectocuneiform. The latter bone is obliquely orientated with respect to the longitudinal axis of Mt III. The entocuneiform is relatively large, subrectangular, and wider than the mesocuneiform, extending distally beyond the ectocuneiform. Five well developed metatarsals are present. All metatarsals are relatively short with respect to the tarsal-metatarsal length. Mt V is slightly shorter than Mt III. With some variation (see Results), this pattern is also identified in non-arboreal echimyids and ctenomyids.

4.1.2 | Tarsal-Metatarsal Pattern II (TMPII)

In this pattern (Figure 9C,D), the tarsus is much narrower and longer than that of TMPI. The astragalus is longer than it is wide, while its head is oriented in a more parasagittal position with respect to the astragalar body. The medial tarsal bone is relatively smaller than that of the arboreal erethizontids and echimyids, contacting with the astragalomediotarsal facet of the astragalar head in a postero-plantar location. The CCJ is located distally with respect to the ANJ, resulting in a TTJ with the aspect of a broken line. The cuboid is smaller than the ectocuneiform; the latter bone is located in line with the proximodistal axis of Mt III. The plantar process of the navicular is strongly developed, extending both proximally and distally. The plantar process of the cuboid is also well developed, but not in the same extent as that of the navicular. The entocuneiform is small, a feature related to the reduction or absence of Mt I. Mt II-IV are relatively elongated and close-packed. Mt V is reduced. This pattern typically characterizes the most cursorial cavioids but also, albeit with some variation (especially in *Hydrochoerus* and *Cuniculus*), the remaining members of this clade. Among chinchilloids, *Lagostomus* shows a typical TMPII but *Lagidium* and *Chinchilla* partially depart from this pattern (see Results). Finally, although they share some features with TMPI (medially located astragalar head, short navicular process of the navicular), Octodontids can also be recognized as possessing TMPII.

4.1.3 | Geometric Morphometrics and Tarsal-Metatarsal Patterns

Several of the features that identify the two main tarsal-metatarsal patterns were analyzed in the PCA: proportions of the tarsus, orientation and obliquity of the astragalar neck, type of TTJ, and the relative size and position of the navicular, cuboid, mesocuneiform and entocuneiform (Figure 1D,E). This allowed identifying typical TMPI and TMPII, and intermediate variation based on the results of the geometric morphometrics analysis. The TMPI can be identified on the negative values of the first two PCs, and the TMPII in the positive values of these PCs. The morphological variation reflected within Octodontoidea described

above (see Results) is partially in agreement with the gradient between TMPI and TMPII. The similar gradient recognized within Caviodea varies from a typical TMPII to a modified TMPII (*Hydrochoerus*). Some of the morphologies that can be related with the main locomotor specializations are: typical TMPI for climbers and TMPII with a robust configuration for cursorial taxa. Diggers mostly have TMPI, with the exception of the octodontid *Tympanoctomys*, with a slender TMPII. The two jumpers *Chinchilla* and *Lagidium* have an intermediate morphology (between TMPI and TMPII) and the ambulatory species present a very wide range of morphologies.

4.2 | Functional Analysis of the Tarsal Complex of Caviomorphs

Several studies on the foot anatomy in mammals have recognized its important functional and phylogenetic implications (e.g., Argot, 2002; de Muizon et al., 1998; Gebo & Dagosto, 1988; Lewis, 1983, 1989; Salton & Szalay, 2004; Sargis, 2002; Szalay, 1994; Szalay & Sargis, 2001). The tarsus supports some of the most complex loads in the body (Szalay, 1994; Szalay & Sargis, 2001); consequently, different arrangements of the tarsal bones, reflect significant changes in the distribution of loadings and the range of movements performed by the foot. Regarding the TTJ, the ANJ reflects the degree to which the distal portion of the foot can be inverted and/or everted (Salton & Szalay, 2004; Szalay, 1994; Szalay & Sargis, 2001, 2006). The CCJ reflects the range of movements and force transmission from the calcaneus to the cuboid, showing either flexion-extension or the ability to rotate (pronate-supinate) this joint (Szalay, 1994; Szalay & Sargis, 2001).

The more distal location of the CCJ with respect to the ANJ, a characteristic arrangement of TMPII (Figures 9C,D and 7A), is more efficient in cursorial and/or saltatorial locomotion, since this configuration severely restricts the mobility at the transverse ankle joint (Candela & Picasso, 2008; Fostowicz-Frelik, 2007; Hildebrand, 1985a; Szalay, 1994; Taylor, 1976). The bones involved in both articulations are interlocked, indicating that lateral movements of the foot are limited while forwards and backwards movements are emphasized. Thus, caviomorphs having TMPII display a TTJ that restricts movements at this joint, such as in other terrestrial mammals (Fostowicz-Frelik, 2007; Hildebrand, 1985a; Szalay, 1994; Taylor, 1976). Considering the foot as a lever system (Carrano, 1997; Maynard Smith & Savage, 1956; Stein, 2000), the resultant force (F_o) exerted by it against the ground could be augmented by increasing the in-lever arm (L_i) or by increasing the magnitude of the force generated by the muscles inserted onto the tuber calcanei (F_i). On the other hand, an increase of the out-lever arm (L_o) would improve speed at the expense of force. In caviomorphs with a TMPII, this later condition results from a lengthening of the distal portion of the calcaneus (a feature that places the CCJ more distally with respect to the ANJ; Candela & Picasso, 2008), as well as from the lengthening of the metatarsals (see below), thus increasing L_o , and consequently the stride length and the speed. In chinchillids and in the octodontoids *Octomys* and *Octodontomys*, in addition to the elongation of distal portion of the calcaneus, the elongation of the tarsus is accompanied by a relative lengthening of the astragalar neck, a condition that

could be related, at least in chinchillines, to their saltatorial locomotion (see also Ginot *et al.*, 2016). Thus, lengthening of the tarsal-metatarsal complex is accomplished through one or more strategies in different species. Conversely, in erethizontids and other caviomorphs having TMPI (e.g., *Dactylomys*), the CCJ and ANJ joints are located approximately at the same level (Figures 9A,B and 7A), a condition that allows a greater range of movements at the TTJ. The CCJ joint indicates the rotational abilities of the foot (Candela & Picasso, 2008; Szalay, 1994). So, the CCJ and the ANJ of the TMPI appear to be designed to allow greater rotational movements, increasing the ability to accommodate the pes to irregular surfaces (Szalay & Sargis, 2001; Szalay, 1994). In addition, the relatively short distal portion of the calcaneus and short metatarsals (i.e., relatively short Lo) provide a more effective Fo, albeit at a lower velocity, which would result in short, and powerful strides during locomotion.

A medially oriented astragalar head, a feature that characterizes TMPI (Figures 9A and 7A), would better assist lateral and rotational movements at the TTJ, enabling the inversion of the foot in arboreal species (Argot, 2002; Candela & Picasso, 2008; Sargis, 2002; Szalay, 1994), so that its plantar side can be medially turned against the arboreal substrate during climbing. Medial orientation of the astragalar head is in turn related to the extensive medially extended astragalomediotarsal facet. This facet provides a broad articulation with the large medial tarsal bone, which would assist inversion of the foot. The wide contact between the astragalar head, the navicular, and the medial tarsal bone, as well as the relative enlargement of the entocuneiform, articulating with a well-developed Mt I, are features that reflect the importance of the medial region of the foot in supporting stress during climbing, while allowing lateral and rotational mobility of these tarsal bones (Argot, 2002; Candela & Picasso, 2008; Szalay, 1994).

In erethizontids the great size of the medial tarsal bone indicates an important insertional area for the tibialis caudalis muscle, an important inverter of the pes in living porcupines (McEvoy, 1982), and possibly in other arboreal caviomorphs. The medial tarsal bone is also well developed in arboreal echimyids and *Ctenomys*. This condition is probably associated with the function of the tibialis caudalis muscle as an inverter and plantarflexor of the foot during climbing and digging.

A relatively large entocuneiform is also consistent with a well-developed area of insertion of the tibialis cranialis muscle, which in erethizontids has an important function in the inversion of the foot (McEvoy, 1982, pp. 406). In arboreal echimyids the relatively large entocuneiform could also be indicative of the significance of the tibialis cranialis muscle as an inverter during climbing. Particularly in erethizontids, the large entocuneiform, hypertrophied medial sesamoid bone, and medial orientation of Mt I strongly indicate a powerful grasping foot, compatible with adaptations to climbing.

The set of features of the TMP II (Figures 9C,D and 7A) of saltatorial and cursorial caviomorphs maximizes stability and facilitates planterflexion-dorsiflexion movements, as it occurs in runners/leapers of other groups of mammals (Hildebrand, 1985a). This feature, along with the small size of the medial tarsal and entocuneiform bones, and the loss of digit I all reflect the reduction of the loading support on the

medial portion of the foot. The reduced size of the medial tarsal bone in the most cursorial caviomorphs, is related with the reduction of the tibialis caudalis muscle and of the very restricted ability to invert the pes. Note that in *Dasyprocta* the tibialis cranialis muscle would act as a dorsiflexor rather than as an inverter of the pes (García-Esponda & Candela, 2010, 2016).

In TMP II, the relative enlargement of the ectocuneiform with respect to the cuboid indicates that the central axis of the tarsus is in line with Mt III and that it could be supporting the main load of the body (Szalay, 1994). Thus, in TMP II loading would probably be concentrated on the astragalar head-navicular-ectocuneiform-Mt III, which build the principal longitudinal axis of the foot. These features are indicative of an emphasized central region of the foot, which may support the main stress during running or leaping (Argot, 2002; Szalay, 1994).

4.3 | Plantar Tarsal-Metatarsal Structures: Functional Considerations

Among caviomorphs with TMP II, the most specialized cursorial cavioids (Figure 6D,F) show a different plantar anatomical pattern from that of the leaper chinchilloids *Chinchilla* and *Lagidium* (Figure 4A,B) and the ambulatory/digger *Lagostomus* (Figure 4C). Nevertheless, all these patterns are interpreted as adaptations to reinforce the proximal plantar region of the foot, required to run, dig and leap. In the specialized cursorials, the extended plantar process of the navicular (Figures 2A and 6D,F) constitutes a buttress-like structure. This process seems to act as a strong pillar within the plantar region of the foot, strengthening the points where the tarsus withstands more thrust during the propulsion stage of the locomotor cycle. A relatively long plantar process of the navicular seems to be an adaptive feature that reaches its highest degree of expression in the cursorial *Dolichotis* (but see Fostowicz-Frelik, 2007 for a different interpretation of the degree of development of this process in Lagomorpha). The plantar region of the tarsus is also reinforced by the presence of a well-developed sesamoid bone located distally and attached to the plantar process of the cuboid (e.g., Figure 6F). In addition, the extended plantar process of the navicular seems to act as a guide for the passage of the tendons of the flexores digitorum medialis and lateralis muscles, which act as plantarflexors of the ankle joint and flexors of the joints of all digits in cavioids (García-Esponda & Candela, 2010, 2016).

In chinchillids, the plantar process of the navicular is relatively less developed than that of the cursorial cavioids (Figures 2B and 4A,C). In this case, the plantar process would not act as a buttress. Instead, the strengthening of the plantar region the tarsus is mainly accomplished by the strongly developed plantar tubercle of the Mt II, which projects toward the plantar process of the cuboid, to finally contact this bone (e.g., Figure 4C). In addition, this tubercle is distally attached or closely located to a well-developed plantar sesamoid bone. Therefore, in chinchillids the plantar tubercle of the Mt II, the well-developed plantar process of the cuboid, and the plantar sesamoid bone build a compact and strengthened anatomical unit. In *Chinchilla* and *Lagidium* this unit seems to be an adaptation to resist the impacts generated in each

jump and to support the forces acting during the movements of the foot on the rocks. In the case of *Lagostomus*, the foot must resist not only the forces generated during jumping, but also those acting when the animal is digging (as for example, the recoil of the body in each movement of digging; see below).

In sum, in specialized cursorial and leaping forms, as well as in *Lagostomus*, the proximal plantar region of the tarsus constitutes an integrative functional unit adapted to different locomotor behaviors and substrate preferences, all of which require a strong and compact foot. These findings demonstrate multiple anatomical solutions to the same challenge (see Losos, 2011; Wainwright, 2007, and bibliography therein, for a discussion on many-to-one mapping of form to function).

The anatomical configuration of the plantar region of octodontoids and erethizontids (Figures 3 and 5), are indicative of a mobile and easily adjustable tarsus that involve a wide range of movements of the foot.

4.4 | Metatarsals: Functional Considerations

4.4.1 | Metatarsal length

The elongation of the metatarsals, seen in fast-running mammals, is perhaps the feature that most entirely reflects cursoriality (e.g., Fostowicz-Frelik, 2007; Gambaryan, 1974; Hildebrand, 1985a). Such as was observed in others groups of mammals (e.g., Argot, 2002; Samuels, Meachen, & Sakai, 2013), in cursorial caviomorphs, the lengthened metatarsals, accentuated in the Dasyproctidae *Dasyprocta* and *Myoprocta* and in the Caviidae *Dolichotis* and *Pediolagus* (Figure 2B) improve speed as well as the stride length during locomotion at the expense of force (Carrano, 1997; Maynard Smith & Savage, 1956). On the other hand, short metatarsals in *Cuniculus paca* indicate that this species is not highly specialized for running or leaping habits. In *Hydrochoerus* the short metatarsals and low pes length index (Mt III length/femur length) are features associated with its quadrupedal paddling swimming habits (García-Esponda & Candela, 2016).

In *Chinchilla* and *Lagidium* (Figure 2B), the lengthening of the metatarsals increases the stride length during leaping, as observed in other saltatorial mammals (Emerson, 1985). Likewise, the elongated metatarsals of the octodontoids *Proechimys*, *Trinomys*, *Octodontomys*, and *Octomys* (Figure 2B) would increase the stride length and the speed during locomotion. Thus, terrestrial echimyids and octodontids seem to parallelize the pattern observed in cursorial cavioids. The elongated metatarsals of the semiaquatic *Myocastor* would facilitate the length of the paddling limb, like in other hindlimb paddling semiaquatic rodents (Samuels & Van Valkenburgh, 2008). Consequently, elongated metatarsals are present in different lineages of caviomorphs that have different locomotor habits, including echimyids, octodontids, caviids, dasyproctids, and chinchillids.

In contrast, relatively short metatarsals, a feature characteristic of the highly arboreal erethizontids, and the arboreal and semifossorial echimyids (Figure 2B), would provide a more effective resultant force for locomotion, although at lower velocity, which would result in short and powerful strides.

4.4.2 | Close-Packing of the Central Metatarsals

Another character functionally associated with leaping or cursoriality is the degree of close-packing (i.e., degree of contact) between the metatarsals. In erethizontids and arboreal echimyids, wide and not close-packed metatarsals provide room for functional interosseus muscles (Taylor, 1976), allowing independent digital movements. On the contrary, in terrestrial echimyids, leaping chinchillids and specialized cursorial dasyproctids and caviines, the close-packed metatarsals seem to increase the rigidity of the plantar sole, allowing the metatarsals to act as a single unit, a condition that would be particularly optimal during running or leaping (Argot, 2002).

4.4.3 | The Lateral and Medial Metatarsals (Mt V and Mt I)

While variable, erethizontids and echimyids have well-developed and relatively long Mt I and Mt V. The divergent and relatively short Mt I of *Coendou* and *Chaetomys* emphasizes the grasping ability of their feet (McEvoy, 1982). The relative shortening of Mt I and Mt V in terrestrial echimyids with respect to those of the arboreal forms, could indicate that the central metatarsals exert the principal function in load-support during locomotion, as in cavioids.

With the exception of *Cuniculus*, all cavioids bear only three functional digits, concentrating the loadings on Mt III, which constitutes the principal axis of the foot.

The well-developed Mt V in *Chinchilla* and *Lagidium* is probably related to its function in the stabilization of the CCJ, and to emphasize the plantarflexor role of the peroneus brevis muscle, which is required for leaping (Argot, 2002). In *Lagostomus*, the presence of Mt V, although very reduced in length, could be reflecting its function in the stabilization of the CCJ.

4.5 | Considerations on Digging Abilities and Foot Anatomy

Adaptive significance of the morphological features in fossorial and subterranean rodents have been intensively investigated (e.g., Hildebrand, 1985b; Lessa, 1990; Lessa et al., 2008; Morgan & Verzi, 2011; Stein, 2000; and bibliography therein). In general, it is recognized that the highly digging species show marked modifications, such as the acquirement of shorter and thicker extremities than related epigeous species, with the consequent mechanical advantages proportioned by shorter lever arms.

Here, we discuss the anatomy of the foot of caviomorphs that display different degrees of fossoriality and digging abilities (*sensu* Lessa et al., 2008): *Ctenomys*, *Tympanoctomys*, *Octodontomys*, *Octomys*, *Euryzgomatomys*, *Clyomys*, and *Lagostomus*.

All *Ctenomys* species have a subterranean style of life (i.e., they spent most of their life underground and have the ability to construct complex burrows; Lessa et al., 2008). As expected, adaptations for subterranean life in *Ctenomys* appear to be reflected in their foot anatomy, which is characterized by short robust metatarsals (Figure 2B) and a marked stepped metatarsal pattern (i.e., Mt III is longer than Mt IV, and the latter is longer than Mt V; Figure 5F). As observed in the hand (Morgan & Verzi, 2011), the main axis of the foot of *Ctenomys* (Figure

5F) is concentrated onto Mt III (mesaxony), which would act bracing the body against the backward forces generated during digging. In addition to their strengthened metatarsals, the tarsal features of *Ctenomys* (Figures 5F and 8A) are compatible with a relatively wide ability of movements (e.g., ANJ and CCJ located at the same level, plantar process of the navicular scarcely developed, astragalar head somewhat medially orientated).

Among Octodontidae, *Tympanoctomys* species construct complex burrow systems with several branches and openings (Lessa et al., 2008; Patton et al., 2015). The foot anatomy of *Tympanoctomys* (Figure 5I) does not show any anatomical modification that is functionally related to digging, apart from its relatively short metatarsals (Figure 2B). Thus, in agreement with previously established observations (Lessa et al., 2008), the construction of complex burrows does not appear to require substantial morphological modifications of the foot.

Octodontomys gliroides is able to dig simple burrows (Lessa et al., 2008). This taxon can be classified as a fossorial species because individuals spend a substantial fraction of their life outside their burrows (Lessa et al., 2008). In agreement with previous studies that indicate that this species has no obvious morphological adaptations for a fossorial life style (Lessa et al., 2008), the foot of *O. gliroides* does not have any feature that can be functionally related to digging. The tarsus of *O. gliroides* (Figures 5H and 8A) with the CCJ distally located with respect to ANJ, gracile, relatively long (Figure 2B) and not close-packed metatarsals (Figure 5H), and with Mt IV slightly longer than Mt III (paraxony), suggest a stable tarsal-metatarsal complex at the TTJ, but being able to agile movements. The relatively well developed cuboid and its alignment with Mt IV, suggest that the main forces generated during locomotion would be uniformly distributed, through both rays III and IV. These features would allow the foot to acquire medial and lateral postures to accommodate their anatomical structures to irregular surfaces, typical of rocky environments.

Octomys mimax is a saxicolous and surface dwelling species with digging ability (Lessa et al. 2008; Patton et al., 2015). According to previous authors there is no evidence that this species modifies daytime resting sites through digging and its activity was associated with the utilization of simple burrows (Lessa et al., 2008). The foot of *Octomys mimax* has no features related to digging. Its long, delicate and not closely-packed metatarsals (Figures 2B and 5G) are in agreement with rapid and agile movements. Gracile bones reduce the inertia of the limb, increasing rotational velocity and thus stride rate (Gambaryan, 1974; Hildebrand, 1985a; Samuels et al., 2013). As noted for *O. gliroides*, the set of features of *O. mimax* (indicate a stable TTJ and agile movements of the metatarsals to accommodate the foot to irregular surfaces and move on rocky environments).

The semifossorial echimyids *Euryzygomatomys* and *Clyomys* differ from *Ctenomys* by having a more robust tarsus and a relatively larger ectocuneiform, which is more parasagittally oriented with respect to Mt III (Figures 5D and 8A). The metatarsals are relatively shorter and more robust than those of the terrestrial *Proechimys* showing a stepped pattern, but to a lesser degree than in *Ctenomys* (Figure 2B). These features would provide an advantage to resist the forces generated during

digging (such as was inferred for the carpal-metacarpal features of these genera; Morgan & Verzi, 2011).

Finally, the chinchillid *Lagostomus maximus* has tarsal-metatarsal features (Figures 2B and 4C) related to restricted movements. The closely-packed metatarsals would constitute a functional unit, which is more compact than that of the digging octodontoids and saltatorial chinchillines. This pattern seems to be an adaptation to resist the forces generated during digging, acting as a strong and secure support to anchor firmly in the substrate.

5 | INTEGRATIVE ANALYSIS AND CONCLUSIONS

5.1 | Adaptations and Phylogeny

According to our results, there is substantial anatomical variation of the caviomorph foot that reflects their diverse locomotor behaviors. Morphological variation also seems to include a strong phylogenetic influence at different taxonomic levels. As noted above, we recognized two distinct tarsal-metatarsal patterns, which represent the extremes of this anatomical variation (Figure 7), one present in arboreal erethizontids and echimyids (TMPI; Figures 7A,B and 8), and the other in the most specialized cursorial cavioids (TMPII; Figures 7C,D and 8). The remaining caviomorph species display intermediate tarsal-metatarsal arrangements, but can also be assigned to one of these two patterns.

Erethizontoids have the typical TMPI, characterized by a highly mobile tarsal-metatarsal complex adapted to climb, showing some distinctive features (very large medial sesamoid, Mt I medially oriented,) that are not identified in other superfamilies. The foot of the different species of porcupines examined displays an essentially similar morphology that is congruent with their homogenous locomotor ecology.

Among octodontoids, a gradient of morphological variation from Echimyidae to Octodontidae was observed (Figure 8A). Echimyids fit in TMPI (Figures 9B and 8A), but display some intrafamilial morphological disparity (Figure 8A). The arboreal forms (*Kannabateomys*, *Makalata*, *Dactylomys*, *Phyllomys*, *Lonchotrix*) have a typical TMPI, similar to that of erethizontids, whereas the terrestrial (*Trinomys*, *Proechimys*), the semifossorial (*Euryzygomatomys*, *Clyomys*), and the semiaquatic (*Myocastor*) taxa are characterized by a more robust tarsus. In turn, arboreal and semifossorial forms are characterized by short and robust metatarsals, whereas those of terrestrial and semiaquatic taxa are more elongated. Some of the differences observed between arboreal and terrestrial echimyids (e.g., robustness of the tarsus, the interlocking of the bones, the metatarsal length, and the relative size of the cuboid) are comparable, although to a lesser degree, to those observed between the highly arboreal erethizontoids and the most specialized cursorial cavioids (Figures 7 and 8A). The morphological variation observed within echimyids may be interpreted as functional, with their dissimilar tarsal-metatarsal complex reflecting their different locomotor habits. Beyond this variation, the anatomy of the echimyid foot does not deviate noticeably from the TMPI; so that it can be interpreted as constrained by phylogeny. The tarsal-metatarsal complex of the subterranean Ctenomyidae shares several features with that of echimyids,

possessing essentially a TMPI (Figure 7), but with some specializations (such as relatively more robust metatarsals and mesaxony), that are interpreted as adaptations to dig. Octodontids mainly differ from echimyids and *Ctenomys* by having a more elongated and narrow tarsal-metatarsal complex, displaying a gracile TMP II (Figure 7 and 8A). In turn, within octodontids, the fossorial *Tympanoctomys* has shorter metatarsals than the surface dwelling *Octodontomys* and the saxicolous *Octomys*. In sum, Octodontoids show a broad range of tarsal-metatarsal morphologies in agreement with their diverse locomotor habits. This morphological variation could be explained both as a product of different locomotor adaptations as well as a result of the phylogenetic effect at the family level (Figure 8A).

Cavioids share a robust TMP II (Figure 7 and 8A), characterized by features that are compatible with cursorial habits. Nevertheless, as noted above, a gradient of morphological variation is detected between the semiaquatic *Hydrochoerus*, the ambulatory *Cuniculus*, and the remaining cavioids (Figure 8A). The cursorial *Dolichotis*, *Pediologus*, *Dasyprocta* and *Myoprocta* have a typical TMP II, with features that are interpreted as adaptations to run. This morphology departs further from that of the generalized *Cuniculus paca*, an ambulatory species without specializations to run, which displays a configuration that “anticipates” the specialized tarsal-metatarsal pattern of the typical cursorial species. On the other hand, *Hydrochoerus* is the cavioid with the most robust tarsus and relatively shortest metatarsals; features that are interpreted as adaptations to swim (García-Esponda & Candela, 2016). The anatomical variation observed within Cavoidea facilitates different locomotor behaviors, but maintains a distinctive cavioid tarsal-metatarsal complex. The phylogenetic signal evident here may point to cavioids being ancestrally cursorial with later divergence in the semiaquatic *Hydrochoerus*.

Chinchilloids exhibit a marked variation when comparing the saltatorial *Lagidium* and *Chinchilla* to *Lagostomus*. The latter genus shows a typical TMP II, while the former have a rather intermediate morphology between TMPI and TMP II (Figures 7 and 8A). This variation can be interpreted as the result of different adaptations to jump and dig, respectively, but also it could be explained by phylogenetic effects.

Therefore, the diverse tarsal-metatarsal morphologies detected between the main clades of caviomorphs reflect their diverse locomotor habits regardless of their different evolutionary histories (Figure 8B). Furthermore, our study indicated similar morphological trends of the tarsal-metatarsal complex in distantly related species that display similar locomotor habits. For example, all cursorial taxa, including *Dasyprocta* and *Myoprocta* (Dasyproctidae), *Dolichotis* and *Pediologus* (Caviidae), and even the ambulatory *Trinomys* and *Proechimys* (Echimyidae), display elongation of the metatarsals (Figure 2B). Similarly, fossorial octodontoids, belonging to three different families (Echimyidae, Ctenomyidae and Octodontidae) have short and robust metatarsals. So, as noted in other mammals (e.g., Muñoz, Cassini, Candela, & Vizcaino, 2017; Samuels et al., 2013), within and between different superfamilies of caviomorphs, species with similar locomotor habits display similar tarsal-metatarsal features as a result of convergent evolution, despite their distinct evolutionary histories.

We also observed species with different locomotor habits, but sharing a similar morphology of some features. For example, the cursorial *Dolichotis* (Caviidae), the semiaquatic *Myocastor* (Echimyidae), and the saltatorial *Chinchilla* (Chinchillidae) are all characterized by an elongated pes (Figure 2B). This suggests, at least for this feature, the existence of morphological convergence of different locomotor behaviors. This can be an example of multiple selective advantages of a single trait (e.g., Losos, 2011), as the same morphological adaptation can be functionally important for different ecologies. While elongation of the pes increases stride length and length of the out lever in cursorial and jumping taxa, it functions to increase the size of the paddling limb in semiaquatic taxa (Emerson, 1985; Hildebrand, 1985a; Samuels & Van Valkenburgh, 2008). Nevertheless, other tarsal-metatarsal characters of these same taxa are very different between them (for example the width of tarsus, the type of TTJ, and the relative size of cuboid), which could be indicative of a phylogenetic effect or that different functional requirements are acting on the morphological traits.

Finally, we observed different morphologies of the tarsal-metatarsal complex in species with similar locomotor habits, as seen in the semiaquatic *Hydrochoerus* and *Myocastor*. As most semiaquatic rodents (Howell, 1930), *Myocastor* has elongated metatarsals and uses pelvic paddling as the main mode of swimming (Samuels & Van Valkenburgh, 2008). In contrast, the capybara is characterized by a quadrupedal paddling mode of swimming, displaying relatively robust and short metatarsals. In agreement with these different modes of swimming, *Myocastor* and *Hydrochoerus* show dissimilar tarsal-metatarsal morphologies that are interpreted as different adaptations for a similar style of life (another example of many-to-one mapping of form to function, see Wainwright, 2007; Losos, 2011). Semiaquatic caviomorphs add to those mammalian species that show different structural solutions to similar environmental challenges (Hildebrand, 1985a,b; Samuels et al., 2013; Stein, 2000).

Likewise, among those caviomorphs with digging abilities, different tarsal-metatarsal patterns were identified: *Euryzgomatomys*, *Clyomys*, and *Ctenomys* show different versions of TMPI, whereas *Tympanoctomys* and *Lagostomus* have different configurations of TMP II. These differences can be interpreted as reflecting different adaptations to dig as well as the presence of phylogenetic signal at different taxonomic levels.

We conclude that the variation observed in the tarsal-metatarsal patterns of caviomorphs can be explained by function-based hypotheses expressing specific adaptations, but within its particular phylogenetic context.

5.2 | The Usefulness of Tarsal Characters in Cladistic Analyses

An essential aspect that arises from our study is the lack of independence of certain tarsal-metatarsal characters. Because the tarsus is a complex multi-bone system, constituted by coadapted bones, it is expected that a change in some of their elements involves a modification of the tarsal-metatarsal complex as a whole, within the coupled system (Salton & Szalay, 2004; Szalay, 1994; Szalay & Sargis, 2001). So,

for example, the position of the sustentaculum of the calcaneus in relation to the calcaneo-cuboid facet is detected as a nonindependent feature with respect to the relative position of the CCJ and ANJ. Other nonindependent tarsal characters are: orientation of the astragalus head, which is related to relative size of the medial tarsal bone and with a degree of plantar contact with that bone; the relative robustness of the ectocuneiform, which is related to relative size of the cuboid; relative size of the entocuneiform, which is related to the degree of contact with the medial tarsal bone, as well as with the degree of development of Mt I and digit I; the degree of close-packing of the metatarsals, which is related to the degree of development of Mt I and Mt V, as well as with the degree of elongation of Mt II-IV.

However, the tarsus is not necessarily considered as the sum of numerous characters or only as one complex trait (Szalay, 1994). As was indicated by Szalay (1994, pp. 112), the system "...changes in such ways that while the elements making them up are coadapted, the components are capable of somewhat independent evolutionary change within the complex." We identified that the plantar structures, the reduction and close-packing of metatarsals and the robustness of specific tarsal bones change in different ways according to the taxonomic group and the locomotor specializations. Thus, the tarsal-metatarsal complex can be recognized as a functional-adaptive system of interrelated characters, but in which some elements are able to change individually. Under this perspective the foot structures will be useful as reliable independent characters for cladistic analyses of caviomorphs.

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APPENDIX: LIST OF CAVIOMORPH SPECIMENS EXAMINED (WITH TARSUS OR PART OF TARSUS PRESERVED) (NUMBER OF SPECIMENS IN BRACKETS)

Specimens examined are housed in the following collections: MLP, Museo de La Plata (La Plata, Argentina); CNP, Colección de Mamíferos del Centro Nacional Patagónico (Puerto Madryn, Argentina); IADIZA CM, Colección Mastozoológica del Instituto Argentino de Investigaciones de Zonas Áridas (Mendoza, Argentina); CML, Colección Mamíferos Lillo (San Miguel de Tucumán, Argentina); MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina); MMPMa, Museo Municipal de Ciencias Naturales “Lorenzo Scaglia” (Mar del Plata, Argentina); MPS-Z, Museo de Ciencias Naturales “P. Antonio Scasso” (San Nicolás, Argentina); MN; Museu Nacional (Rio de Janeiro, Brazil); AMNH, American Museum of Natural History (New York, USA), FMNH, Field Museum (Chicago, USA); YPM, Yale Peabody Museum of Natural History (New Haven, USA); Zoological Museum University of Copenhagen (ZMUC).

Erethizontoidea

Erethizontidae

- *Erethizon dorsatum* (1) MLP1086
- *Coendou prehensilis* (5) MN 4923, MN 4925, MN 4936, MN 34186, MLP 1084
- *C. spinosus* (1) MPS-Z 185
- *C. insidiosus* (2) MN 46936, MLP 18.VII.97.2
- *Chaetomys subspinosus* (2) MN 9680, MN 46250

Cavioidea

Cuniculidae

- *Cuniculus paca* (6) MN 60557, MN 1682, MN 4878, MN 4871, MN 8476, MACN 49.396

Dasyproctidae

- *Dasyprocta azarae* (8) CNP 896, CNP 790, MN 4848, MN 4852, MN 1854, MN 4859, MN 4961, MN 134185.
- *Myoprocta acouchi* (2) YPM 1360, AMNH 130148

Caviidae

Caviinae

- *Cavia aperea* (10) MLP 15-II-96-49, MLP 29.XII.00.15, MLP 585.3, MLP 585.4, MLP 5.VI.00.8, MLP 30.V.02.7, MLP 15.II.96.49, MLP 2.IV.02.9, MLP 11.VIII.99.54, MPS-Z 203-206.
- *Microcavia australis* (7) MLP 26.VII.01.21, MLP 26.VII.01.22, MLP 7.IV.99.7, MACN 34.7, MACN 40.53, CNP 1033, CNP 276,
- *Microcavia* sp. (2) MACN 36.36, MPS-Z 2014
- *Galea leucoblephara* (= *G. musteloides*) (4) MACN 28-141, MLP 1928, MLP 1929, CNP 1470

Dolichotinae

- *Dolichotis patagonum* (8) MLP 208, MLP 252, MLP 250, MLP 642, MLP 236, MLP 249, MLP 275, MPS-Z 186
- *Pediolagus salinicola* (4) MACN 30.388, MLP 1081, MPS-Z 197, MPS-Z 198

Hydrochoerinae

- *Hydrochoerus hydrochaeris* (7) MACN 43.43, MACN 31.18, MACN 14.038, MPS-Z 141, MPS-Z 142, MPS-Z 143, MPS-Z 188

Chinchilloidea

Chinchillidae

Chinchillinae.

- *Chinchilla* sp. (5) MACN 13037, MACN 26116, MACN 39390, MACN 45.11, MLP 31.XII.02.37
- *Lagidium viscacia* (3) MPS-Z 199, MLP 20.21, MACN 44.25

Lagostominae

- *Lagostomus maximus* (7) MACN 48.85, MLP 1083, MLP 27.IV.95.1, MPS-Z 200, MLP 15.V.96.3, MACN 23.14, MACN 21983

Octodontoidea

Octodontidae

- *Octomys mimax* (1) IADIZA CM 03785
- *Octodontomys gliroides* (2) CNP 651, MACN 25.197
- *Tympanoctomys kirchnerorum* (1) CNP 1819
- *T. aureus* (1) CML 4136

Ctenomyidae

- *Ctenomys* sp. (2) MPS-Z 201, CNP UP 3609
- *C. talarum* (1) MLP 2507
- *C. australis* (1) MLP 7.XI.95.7
- *C. magellanicus* (1) CNP UP 3599

Echimyidae

- *Myocastor coypus* (5) MLP 1172, MPS-Z 202, MPS-Z 213, MACN, MMPMa 28
- *Phyllomys pattoni* (1) MN 33515

- *Makalata didelphoides* (2) AMNH 97324, FMNH 62051
- *Proechimys guairae* (= *Proechimys poliopus*) (1) MLP 22.II.00.7
- *P. steerei* (1) FMNH 55403
- *Trinomys dimidiatus* (3) MN 48010, MN 31370, MN 31426
- *Euryzgomatomys spinosus* (2) MN 31351, MLP 16.VII.02.11
- *Clyomys laticeps* (1) ZMUC L77
- *Lonchothrix emiliae* (1) AMNH 94866
- *Dactylomys dactylinus* (1) YPM 1391
- *Kannabateomys amblyonyx* (2) FMNH 94340, MN 1961
- *Olallamys albicaudus* (1) FMNH 71130