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Astragalus ecomorphology in Quaternary elephantids

DARÍO FIDALGO,[1]* PALMIRA SALADIÉ,[2,3,4] JOSEP VALVERDÚ,[2,3,4] ANTONIO PINEDA,[2,3] ROSA HUGUET,[2,3,4] JOAN MADURELL-MALAPEIRA[5] and ANTONIO ROSAS[6]

[1]Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity, Berlin, Germany
[2]Institut Català de Paleoecologia Humana i Evolució Social, Tarragona, Spain
[3]Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, Tarragona, Spain
[4]Unit Associated to CSIC, Department of Palaeobiology, Museo Nacional de Ciencias Naturales, Madrid, Spain
[5]Earth Science Department, University of Florence, Florence, Italy
[6]Department of Palaeobiology, Museo Nacional de Ciencias Naturales, Madrid, Spain

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ABSTRACT: The astragalus plays a fundamental role in the graviportal locomotion of proboscideans, reflecting the biomechanical constraints imposed by large body masses. This study analyses the morphological variability of the astragalus in Quaternary elephantids using linear biometry and 3D geometric morphometrics, incorporating an unpublished astragalus of *Mammuthus meridionalis* from the Calabrian (ca. 0.9 Ma) of Barranc de la Boella (eastern Iberian Peninsula) within a broad comparative framework of fossil and extant forms. The results reveal a marked allometric relationship, whereby larger individuals have relatively flatter astragali, regardless of their taxonomic affinity. The Barranc de la Boella specimen fits this pattern perfectly, showing dimensions comparable to those of the largest elephantids of the Gelasian, Calabrian and Chibanian. No clear phylogenetic signal is detected in the morphology of the astragalus, suggesting that body size dominates the observed variation and limits its usefulness in discriminating specific taxonomic affinities or ecological adaptations.
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KEYWORDS: 3D geometric morphometrics; allometry; ankle bones; body mass; proboscideans

Introduction

Elephants (Elephantidae, Gray 1821) constitute a family of animals extant today only in South and Southeast Asia, and sub-Saharan Africa. They are the last survivors of a highly successful group of animals (order Proboscidea Illiger 1811), which included colossal forms present from the Miocene onwards across virtually all continents, except for Australia. Their current distribution is largely constrained by human activity, with populations in the temperate zones of Eurasia and America (represented by the genus *Mammuthus* Brookes 1828) having become extinct between the Late Pleistocene and Early Holocene (Smith et al., 2023). This group shares some unique characteristics, the most notable of which is that its members are the largest and heaviest land animals in existence today (Cantalapiedra et al., 2021).

Proboscideans have graviportal locomotion, that is, they show specific adaptations linked to heavy weight-bearing (Bader et al., 2024). The bones of the foot (tarsals, metatarsals and phalanxes) form a rigid structure adapted to optimise the weight distribution, enabling a slow but efficient gait (Hutchinson et al., 2011). As part of the tarsals, the astragalus of the proboscideans is robust and massive, reflecting their need to support a large body weight (exceeding 10 tonnes). This bone has a wide and deep trochlea for the tibia, which confers important joint stability to support weight and allow limited but powerful movements (Smuts and Bezuidenhout, 1994). At the same time, this broad and flat articular surface helps to distribute the weight evenly (Bonnan et al., 2005; Paul, 2008). In proboscideans, it has been proposed that variations in astragalus morphology may indicate both a relationship in response to differences in body size and a phenotypic response of their adaptations to different habitats (Scarborough et al., 2015; Chen and Tong, 2016).

It is clear that the astragalus plays a key role in supporting the weight of the hind leg in proboscideans. Given the importance of this structure in the locomotor strategies of such iconic taxa, and following the methodological advances used in recent studies such as that by Tetaert *et al.* (2026), in this work, we analyse the morphological variability of the Quaternary elephantids astragalus using a combined approach of linear biometry and three-dimensional geometric morphometrics (3DGM). We focus on an unpublished astragalus of *Mammuthus meridionalis* from the Calabrian (ca. 0.9 Ma) site of Barranc de la Boella (El Forn locality, East Iberia), integrating it into a broad comparative framework including extant and extinct elephantids. Our main objectives are (i) to assess the relationship between astragalus size and shape across Quaternary elephantids; (ii) to discuss whether astragalus morphology reflects phylogenetic affinities or is primarily driven by body mass and locomotor constraints; and (iii) to discuss the palaeoecological implications of the astragalus morphology of the Barranc de la Boella specimen within the context of Quaternary elephantid diversity.

Material and methods

Material

Among the specimens analysed in this study is an unpublished astragalus of *Mammuthus meridionalis* from the El Forn locality (Barranc de la Boella archaeo-palaeontological site, East Iberia,

*Correspondence: D. Fidalgo, as above.
Email: dfidal01@ucm.es

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ca. 0.9 Ma; Fig. 1). This specimen (BB12_EF_4_K12_6), despite having been excavated in 2012, was only recently identified after a necessary restoration process was completed. For more information on *M. meridionalis* in Barranc de la Boella, see Fidalgo *et al.* (2025).

For the linear biometric analysis, data newly obtained by the authors were used alongside open data from previous publications (Table S1). In total, one specimen of *Palaeoloxodon recki*, two specimens of *Elephas maximus*, four of *Mammuthus meridionalis*, nine specimens of *Mammuthus trogontherii*, 21 specimens of *Mammuthus primigenius*, eight specimens of *Palaeoloxodon antiquus* and three specimens of *Loxodonta africana* were included. Of these data, 28 specimens of all species included have been measured specifically for this work: 11 specimens from Chen and Tong (2016) of *M. meridionalis, M. trogontherii* and *M. primigenius*; eight specimens from Scarborough *et al.* (2015) of *E. maximus, L. africana* and *P. antiquus*; and one specimen of *M. meridionalis* from Fuente Nueva 3 from Ros-Montoya (2010). For further information, see Table S1.

The 3DGM analysis included a sample of 26 specimens of *P. recki* ($n = 1$), *E. maximus* ($n = 1$), *M. meridionalis* ($n = 1$), *M. trogontherii* ($n = 1$), *M. primigenius* ($i = 18$) and *P. antiquus* ($n = 3$, two of which are possibly from the same individual: MB_1999_a and b) and *L. africana* ($n = 1$) (Table S2). The sample was mainly digitised at the Museum für Naturkunde (Berlin, Germany) for this work, with the exception of the specimen of *E. maximus* (IMNH_1486; MorphoSource id: 000168770) from the Idaho Virtualisation Lab (Idaho Museum of Natural History) and the specimen of *L. africana* (MSCC_020) from the Turner Geospatial Centre at The Mammoth Site of Hot Springs. For more details on the provenance of the specimens, see Table S1. The specimens were scanned in three dimensions using the 3DMAKERPRO Mole multispectral scanner, with 0.005 mm precision and 0.1 mm resolution, which includes its own standard software (JMStudio).

For the anatomical nomenclature of the specimens, that used by Smuts and Bezuidenhout (1994) and Chen and Tong (2016) was used (Fig. 1(A)). For phylogenetic and/or taxonomic considerations, the combined proposals from Baleka *et al.* (2021), Todd (2009) and Konidaris *et al.* (2020) were used.

Linear biometry

In order to quantitatively compare the biometric characteristics of the quaternary elephantid astragalus, a linear biometric analysis was performed using the maximal width of the astragalus and the maximal length of the navicular facet (Fig. 2(C)). The comparative data were taken from the 3D model database digitised by one of the authors (D.F.) together with other specimens from online 3D model databases and previously published scientific literature (see Table S1; Scarborough et al., 2015; Chen and Tong, 2016; Ros-Montoya, 2010). The astragalus biometric data were plotted in a scatter plot using Past 4.03 software (Hammer et al., 2001; Fig. 2(C)).

3D geometric morphometrics

Following the general ideas of Tetaert *et al.* (2026), another approach to quantifying the shape and size of the digitised proboscidean astragalus has been carried out from a study protocol based on 3D geometric morphometrics (Lawing and Polly, 2010). For this purpose, landmark configuration has been developed (Fig. 1(B); Table S3). The anatomical characterisation, together with details of each landmark, are described in Fig. 1(B) and Table S3. The sample considered in this analysis has been digitised by one of the authors (D.F.), and specimens from online databases of 3D models have been included (Table S2).

Measurement of each specimen was carried out in Viewbox version 4.0 software (dHAL, Kiffisia, Greece), following the

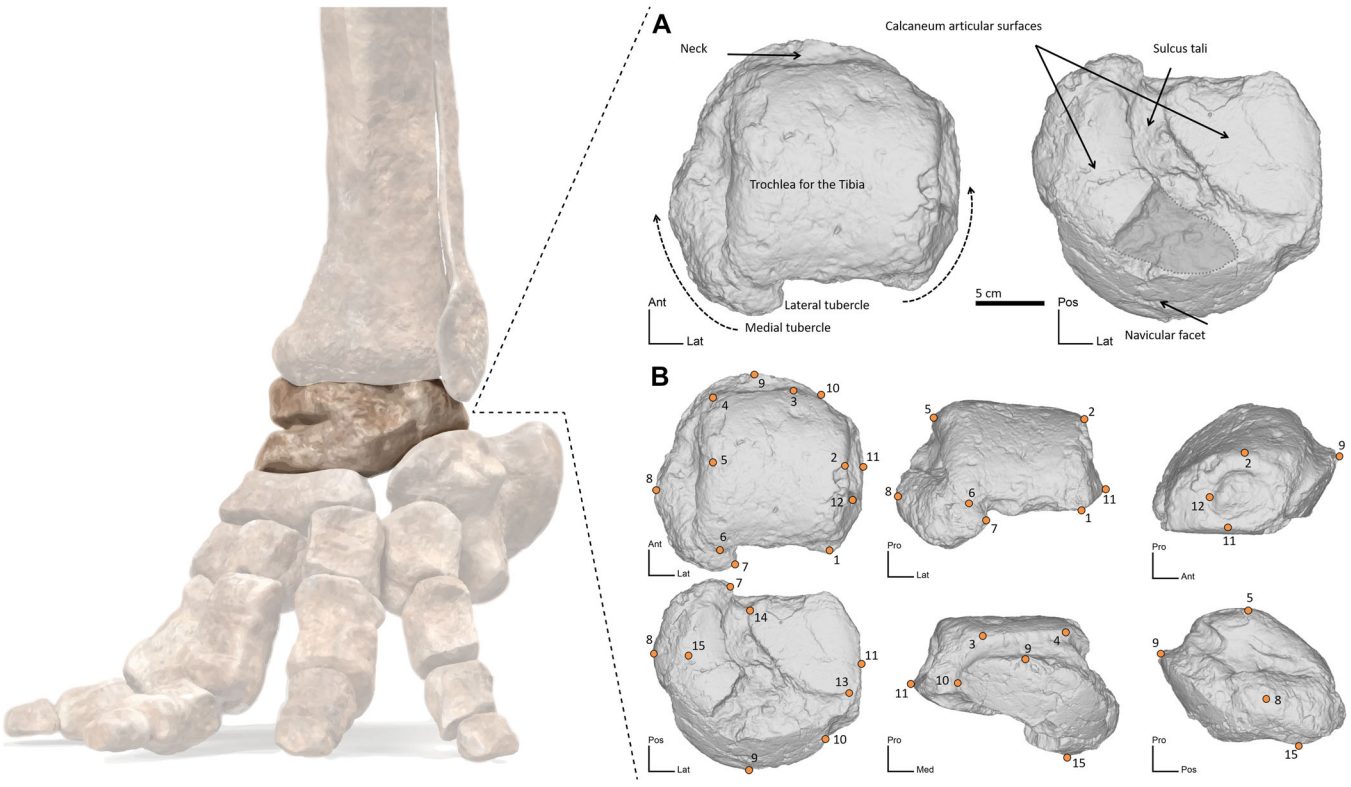


Figure 1. Anatomical location of the astragalus in a mammoth's foot, together with (A) Anatomical nomenclature of the elephantid astragalus, modified from Smuts and Bezuidenhout (1994) and Chen and Tong (2017). (B) 3D Geometric morphometrics landmark template for the measurement of elephantid astragalus (for a description of the landmarks, see Table S3). Orientations: Ant, anterior; Pos, posterior; Lat, lateral; Med, medial; and Pro, proximal. [Color figure can be viewed at wileyonlinelibrary.com]

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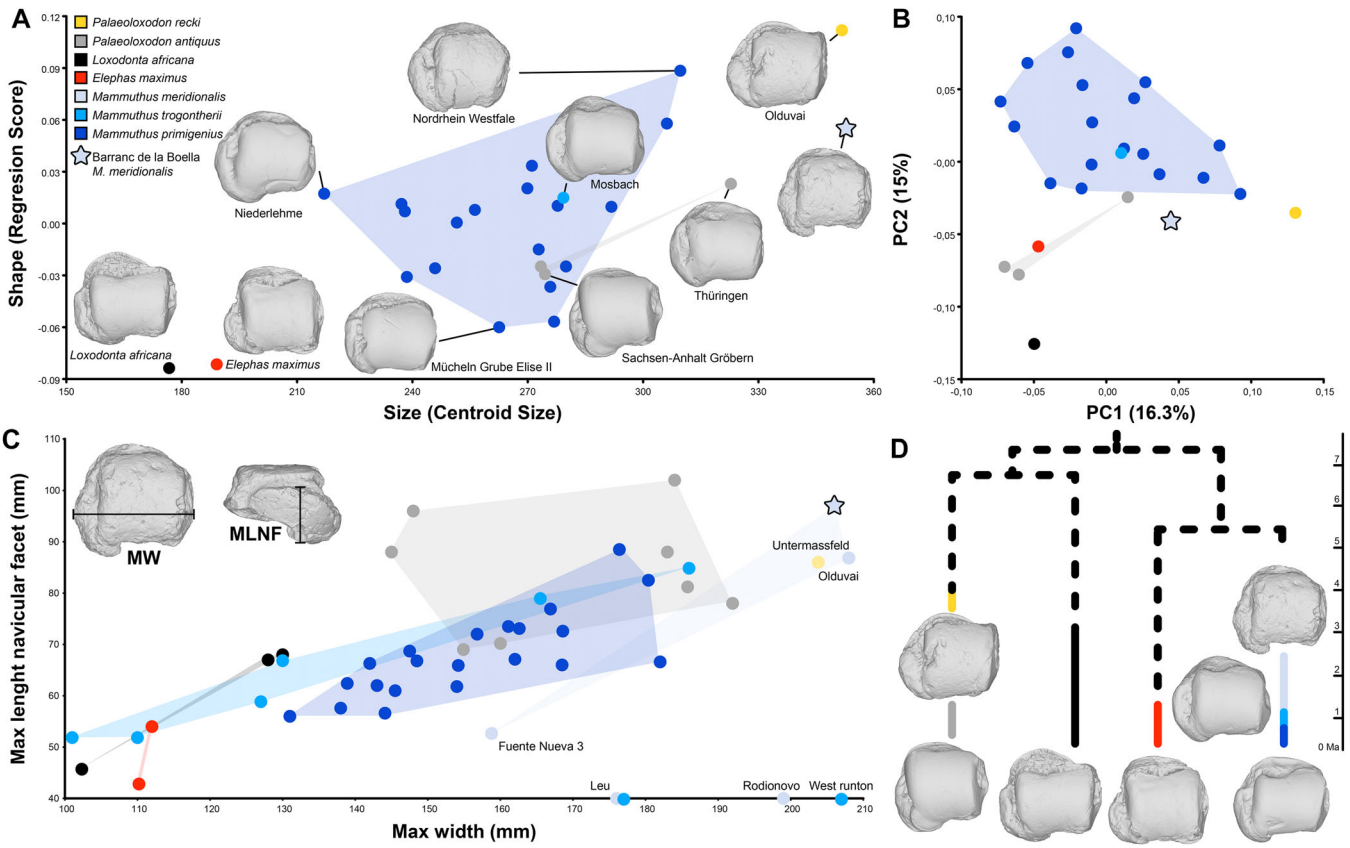


Figure 2. (A) Scatter plot of the regression score (Procrustes coordinates against logarithm of the centroid size [LogCS]) versus CS of the 3D geometric morphometrics (3DGM) data from the Quaternary elephantids astragalus. (B) Scatter plot of the 3DGM data principal component analysis (PCA) dimensionality reduction analysis, with the variability picked up by the first two PCs (principal components) in brackets in the title of the axes. (C) Scatter plot of the linear biometric data from the Quaternary elephantids astragalus. (D) Phylogenetic proposal used, combined phylogenetic data from Baleka *et al.* (2022), Todd (2009) and Konidaris *et al.* (2020). The analyses include the graphical expression of the shape change associated with their axes. All the astragalus figured are in proximal view. [Color figure can be viewed at wileyonlinelibrary.com]

methodology described in Bastir *et al.* (2019). The coordinates of the landmarks measured for this study can be viewed in Table S2. In order to include the largest possible sample of individuals, the few landmarks of missing structures of specimens with missing parts have been estimated mathematically. The protocol used for the estimation of missing landmarks is based on TPS interpolation (Gunz et al., 2009). This protocol has been carried out in RStudio (v. 2023.03.0 + 386) using the function *estimate.missing* from package geomorph v. 4.0.5 (Baken et al., 2021; Adams et al., 2024).

To quantify the intraobserver measurement error associated with landmark digitisation, the Barranc de la Boella specimen (designated as the 'problem specimen') was digitised six times on 6 different days by the same researcher. Then, these six measurements from the problem specimen were compared with the other digitised astragalus from our sample. The shape differences were assessed through Procrustes distances, defined as the square root of the summed squared distances between Procrustes registered landmark configurations and their shape coordinates (O'Higgins, 2000; Gunz et al., 2009; Mitteroecker and Gunz, 2009). An acceptable intraobserver error requires that the largest Procrustes distance between the repetitions of the problem specimen has to be smaller than the smallest Procrustes distances between the compared specimens (Morecroft et al., 2010). The highest Procrustes distance between the repetitions of the same specimen was much lower than the smallest Procrustes distance between specimens. Therefore, the intraobserver error is acceptable.

Whole 3D GM data processing and analysis, and the production of graphical results were implemented in the software MorphoJ 1.07a (Klingenberg, 2011), Past 4.03 (Hammer et al., 2001), R and RStudio (v. 2023.03.0 + 386). For each data set, landmark configurations were subjected to a generalised Procrustes analysis: they were rotated, translated into a common centroid and scaled to unit centroid size (CS) to remove any variation unrelated to shape (Gower, 1975; Bookstein, 1991). To assess variability in the astragalus morphology, independent principal component analysis (PCA) dimensionality reduction analysis was performed, detailing the variability picked up by the first two PCs (Principal Components) in brackets in the title of the axes (Fig. 2(B)). The analyses include the graphical expression of the shape change associated with their principal axes of variance. For the evaluation of the size of each specimen, the CS and the LogCS of those 3D models that were correctly scaled were used. This relationship has been expressed graphically by means of a scatter plot of the regression score (Procrustes coordinates against LogCS) versus Cs (Fig. 2(A)).

Results

Principal component analysis (PCA) performed on the 3D geometric morphometry data of the astragalus shows a distribution of data in the first principal component (PC1; 16.3% of variability; Fig. 2(B)), which highlights differences in the relative height of the trochlea for the tibia versus the total extent of this articular facet (relative height of the astragals body). In its more positive values, PC1 includes more relatively flattened specimens, while in its more negative values, it includes relatively taller astragali. In this sense, the Barranc de la Boella specimen is within the variability collected for

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M. primigenius, moving away from the current proboscidean species, *P. antiquus* from Sachsen-Anhalt Gröbern and *P. recki* from Olduvai. The second principal component (PC2; 15% of the variability; Fig. 2(B)), on the other hand, mainly highlights the relative position of the trochlea with respect to the articular facet for the navicular and the medial tubercle. In the more negative values, we find less developed medial tubercles and a greater projection of this structure in values that are more positive. In this aspect, the specimen from Barranc de la boella is found in mean values that negatively exceed the variability recorded for *M. primigenius* and the specimen of *M. trogontherii* included (from Mosbach), but close to the minimum values of the first species, of the specimen of *P. antiquus* from Thüringen or of the specimen of *P. recki* (Fig. 2(B)).

The analysis including overall astragalus size (understood as centroid size = CS) against astragalus shape (understood as the regression score of Procrustes distances against LogCS) shows a remarkably linear relationship between astragalus shape and size (Fig. 2(A)). Those specimens that stand out for their large size show a generally more dorso-plantarly flattened morphology with respect to their articular facet extension. This phenomenon is also noticeable in the linear biometry analyses, which highlight the large size of the Barranc de la Boella specimen, comparable only to *P. recki*, *M. trogontherii* from West runton or *M. meridionalis* from Untermassfeld and Rodicnovo (Fig. 2(C)). These analyses distinguish the Barranc de la Boella specimen from the morphologies and sizes recorded for *P. antiquus*, highlighting a greater relative dorso-plantar height in the latter species. Also striking is the biometric similarity of the BB specimen with that of *P. reckii* from Olduvai and its biometric differences with the specimen from Fuente Nueva 3.

Taking into account the combined phylogenetic data from Baleka *et al*. (2021), Todd (2009) and Konidaris *et al*. (2020), no clear phylogenetic clustering is observed (Fig. 2(D)) in the morphospace defined by either linear (Fig. 2(C)) or geometric morphometrics analyses (Fig. 2(A), (B)). Instead, species overlap extensively, and the main source of variation appears to be size-related, although some tendency towards separation between *Palaeoloxodon antiquus* and *Mammuthus* specimens from the Gelasian, Calabrian and Chibanian can be observed. These results should be interpreted with caution, given the uneven taxonomic representation.

Discussion

The majority of results point to a primary relationship between the quantified anatomy of the astragalus and its size in our sample of Quaternary elephantids. This observation is fully consistent with the findings recently published by Tetaert *et al*. (2026) regarding proboscideans in general. In extant proboscideans (*Loxodonta africana* and *Elephas maximus*), maximum sizes in adult males have been documented as reaching 6.000–7.000 kg (Osborn, 1936; Christiansen, 2004). In contrast, representatives of the genus *Mammuthus* from the Gelasian, Calabrian and Chibanian attained significantly larger body sizes. Specifically, maximum sizes have been estimated in individuals of *Mammuthus trogontherii* and large individuals of *Mammuthus meridionalis*, reaching and exceeding 10.000 kg (Lister and Stuart, 2010; Romano et al., 2022). Sizes close to these values have been estimated for individuals of the species *Palaeoloxodon antiquus* (Larramendi et al., 2017; Estráviz López and Mateus, 2018; Biswas et al., 2024). Some specimens of the African species *Palaeoloxodon recki* have been found with similar or even higher estimated masses (Christiansen, 2004; Larramendi, 2015). This information would reinforce the idea of a direct relationship between the size and shape of the astragalus and the mass of individuals and would highlight the large size that the individual of *M. meridionalis* from Barranc de la Boella would have reached, close to that estimated for *P. recki*.

Caution is warranted, given the nature of the fossil sample included in this study. The taphonomic context of the materials included has not preserved dental elements or long bones associated with the astragali, preventing an estimation of the individuals' age based on dental stage or appendicular epiphyseal fusion stages (e.g., Laws, 1966; Herridge, 2010). Since proboscideans are very long-lived and demonstrate considerable ontogenetic allometry in many skeletal elements (e.g., Miller et al., 2007), this issue would need to be addressed more carefully in the future, especially because taphonomic bias can drastically skew sample representation (Lister and Agenbroad, 1994). A similar situation arises in the case of estimating the sex of the individuals. Given the degree of sexual dimorphism found in some skeletal elements of proboscideans (e.g., Kongtueng et al., 2025), this factor presents another clear limitation on the ability to generalise the observations presented here.

At the phylogenetic level, no clear pattern can be observed in the morphology and size of the astragalus. Even so, it is true that it seems possible to distinguish between specimens of *Palaeoloxodon antiquus* and those of *Mammuthus* from the Gelasian, Calabrian and Chibanian, although some general shape convergences could be observed in the more derived forms of *Mammuthus trogontherii* or *Mammuthus primigenius*. Within the genus *Mammuthus*, only the morphological differences between the much larger forms of the Gelasian, Calabrian and Chibanian and those of the Late Pleistocene and Holocene seem evident, as has been highlighted on several occasions (Christiansen, 2004; Lister and Stuart, 2010; Larramendi et al., 2017). Based on a detailed study of the foot bones of the steppe mammoth (*M. trogontherii*), Chen and Tong (2016) highlight significant differences with the morphology observed in *M. primigenius* and *P. antiquus*, especially in the relatively quadrangled plantar surface of the astragalus, the surface occupied by the tubercle of the plantar surface and the extension of the neck. In turn, they indicate that the morphology of the astragalus seems to show transitional characteristics between that observed in *M. meridionalis* and that more derived from *M. primigenius*. Even so, they highlight that the morphology of the astragalus is very similar to that observed in *M. meridionalis* (Chen and Tong, 2016).

Extant proboscideans (genera *Loxodonta* and *Elephas*) inhabit diverse environments, such as savannahs, forests and deserts. Expanding on this diversity of substrates, woolly mammoths (*M. primigenius*) are known for their ability to move in snowy and cold terrain (Lister and Bahn, 2007). The posture of the feet in proboscideans has evolved to include both this ecological diversity and the graviportal variable, with the morphology of the astragalus playing a vital role in this process (Hutchinson et al., 2011). Even so, few studies have specifically evaluated the implication of the environment, or type of substrate, on the morphology of the astragalus in proboscideans. For example, Scarborough *et al*. (2015) highlight that the presence of a proportionally shorter and wider astragalus in dwarf elephants from Sicily and Malta (*Palaeoloxodon falconeri*) suggests a change in locomotion towards a slower and more efficient lifestyle in rough and mountainous terrain. Contrary to what Beden (1987) and Sanders (2011) highlighted, our results show a high degree of morphological similarity in the astragalus of *E. maximus* and *L. africana*, despite their phylogenetic distance (Thomas et al., 2000; Todd, 2009; Baleka et al., 2021). However, and due to the observed strong influence of body mass on the morphology of

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the astragalus in elephantids, the interpretations that can be made at this time are limited.

Conclusions

The results obtained in this study indicate that the morphology of the astragalus in Quaternary elephantids is strongly conditioned by body size, a signal that tends to outweigh phylogenetic and ecological differences between taxa. However, some general morphological trends are observed among certain groups, such as greater relative dorsoplantar height in *Palaeoloxodon antiquus* compared to more flattened morphologies in the large representatives of the genus *Mammuthus* from the Gelasian, Calabrian and Chibanian, differences that appear to be closely linked to variations in size. The astragalus of *Mammuthus meridionalis* from Barranc de la Boella fits fully within this general pattern, reflecting a large individual, with dimensions similar to those reported for *Palaeoloxodon recki* from Olduvai, and adapted to stable and efficient graviportal locomotion. Overall, the combination of linear biometric analysis and 3D geometric morphometrics shows that the astragalus in continental Quaternary elephantids is an informative element for inferring functional constraints related to load and joint stability, although its ability to discriminate fine taxonomic affinities or specific environmental preferences is limited when considered alone.

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Data availability statement

The data that support the findings of this study are available in the supplementary material of this article.

Supporting information

Additional supporting information can be found in the online version of this article.

Table S1. Database of specimens and measurements of Quaternary elephantid astragali used in linear biometric analyses.

Table S2. Database of specimens of Quaternary elephantid astragali used in 3D geometric morphometrics analyses.

Table S3. Description of the landmarks used in Quaternary elephantid astragali for the 3D geometric morphometrics analyses.

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