A dryopithecine talus from Abocador de Can Mata (Vallès-Penedès Basin, NE Iberian Peninsula): Morphometric affinities and implications for hominoid locomotor behavior

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Abstract

Objectives. The functional interpretation of postcranial remains of Middle Miocene great apes from Europe (dryopithecines) suggests a combination of quadrupedalism and orthograde behaviors without modern analogs. We provide further insights based on an isolated dryopithecine talus (IPS85037) from the Middle Miocene (11.7 Ma) Abocador de Can Mata locality ACM/C8-B* (Vallès-Penedès Basin, NE Iberian Peninsula), which represents the most complete one known to date.

Material and Methods. We compare the specimen with an extant anthropoid sample (*n* = 68) and the stem hominoid *Ekembo heseloni* (KMN RU 2036, ~18 Ma, Kenya) using 3D geometric morphometrics. For the two fossil tali, we assess their phenetic affinities using a between-group principal components analysis (bgPCA), estimate body mass based on centroid size, and make locomotor inferences using a partial least-squares regression (PLSR) between talar shape and locomotor repertoire.

Results. Its large inferred body mass (~38 kg) and the possession of several hominoid-like features (albeit combined with more plesiomorphic traits) support the attribution of IPS85037 to a male dryopithecine. The bgPCA indicates that IPS85037 falls close to the extant hominoid variation and is less cercopithecoid-like than that of *Ekembo*, whose inferred locomotor repertoire is vastly dominated by quadrupedalism (81%). In contrast, the locomotor repertoire inferred from IPS85037 combines important quadrupedal (32%) and vertical climbing/clambering (50%) components with only moderate suspension (10%).

Discussion. Our results align with previous inferences derived from other postcranial elements of Middle Miocene dryopithecines and, given their classification as crown hominoids, support the hypothesis that certain suspensory adaptations shared by extant hylobatids and hominids likely evolved independently.

Keywords

Functional morphology; Miocene apes; Talus; Geometric morphometrics; Locomotion.

1. Introduction

1.1. The talus of Miocene apes

The talus plays an important role in primate posture and locomotion, being involved in body weight transmission and stability/mobility at the ankle joint—including foot flexion-extension and abduction–adduction at the talocrural joint, pronation-supination at the subtalar joint, and flexion-extension at the midtarsal joint (Lewis, 1980ab). Accordingly, talar morphology is tightly linked to foot function and substrate preference (Turley & Frost, 2013; Parr et al., 2014), and these differences can even be characterized among closely related taxa (Dunn, Tocheri, Orr, & Jungers, 2014; Knigge, Tocheri, Orr, & McNulty, 2015; Friesen et al., 2024). Hence, the talus is of great value for making locomotor inferences in extinct primates (e.g., Day & Wood, 1968, 1969; Lisowski, Albrecht, & Oxnard, 1974, 1976; Alba et al., 2014; Marigó, Roig, Seiffert, Moyà-Solà, & Boyer, 2016; Püschel, Gladman, Bobe, & Sellers, 2017; Püschel, Marcé-Nogué, Gladman, Bobe, & Sellers, 2018, Püschel et al., 2020;).

Among hominoids (the ape and human clade), much emphasis has been devoted to the interpretation of talar morphology in fossil hominins in relation to bipedal adaptations (e.g., Day & Wood, 1968; Latimer, Ohman, & Lovejoy, 1987; Parr et al., 2014; Sorrentino et al., 2020). For Miocene apes, talar morphology has been mostly related to different types of arboreal behaviors, including the distinction between plesiomorphic (i.e., 'monkey-like') quadrupedalism and more apomorphic (i.e., modern 'ape-like') behaviors such as vertical climbing, suspension, and knuckle-walking (Day and Wood, 1969; Lisowski et al., 1974, 1976; Langdon, 1986). However, further insight into the evolution of talar morphology in extant hominoid lineages is hampered by the scarcity of fossil tali attributable to crown members of this group. On the other hand, there is a relatively good record of fossil tali of both putative stem catarrhines (Le Gros Clark & Thomas, 1951; Harrison, 1982; Morbeck, 1983; Begun, 1987; Leakey & Leakey, 1987; Rose, Leakey, Leakey, & Walker, 1992; Kordos & Begun, 2001) and hominoids (Le Gros Clark & Leakey, 1951; Le Gros Clark, 1952; Harrison, 1982; Walker & Pickford, 1983; Hill & Ward, 1988; Leakey, Leakey, & Walker, 1988; Ward, Walker, Teaford, & Odhiambo, 1993; McCrossin, 1994; Rose, Nakano, & Ishida, 1996; Ward, 1998; Ishida, Kunimatsu, Takano, Nakano, & Nakatsukasa, 2004; Dunsworth, 2006; Nakatsukasa et al., 2012; Russo et al., 2024) from the Early to Middle Miocene of Africa. In the Miocene of Eurasia, ape tali are more scarce, being restricted to the great apes (hominids) from the Late Miocene—one talus attributed to *Sivapithecus* (Pilbeam et al., 1977; Pilbeam, Rose, Badgley, & Lipschutz, 1980; Morbeck, 1983; Madar, 1996) and an undescribed talus attributed to *Rudapithecus* (Kordos & Begun, 2001; Begun, 2002, 2009)—as well as *Oreopithecus* (Straus, 1963; Szalay & Langdon, 1986)—of controversial systematic affinities but currently interpreted as a likely stem hominoid (Pugh, 2022; Urciuoli & Alba, 2023; Alba et al. 2024a).

To inform the evolution of ape locomotion, here we describe an unpublished talus (IPS85037) from the latest Middle Miocene of Abocador de Can Mata local stratigraphic sequence, previously attributed (without being described or figured) by Alba, Casanovas-Vilar, Garcés, & Robles (2017: Table 2; Alba et al., 2022: SOM Table S6) to Dryopithecinae indet. The subfamily Dryopithecinae sensu Alba (2012) is an extinct group of Middle to Late Miocene great apes from Europe that is sometimes distinguished at the tribe rank (i.e., Dryopithecini) by some other authors (e.g., Begun, 2009). Although they are generally considered extinct great apes (i.e., Hominidae; Alba, 2012; Begun, 2015; Urciuoli et al., 2021; Urciuoli & Alba, 2023), as supported by cladistic analyses (Alba et al., 2015; Pugh, 2022), it is still uncertain whether they constitute a clade or a paraphyletic assemblage (Alba, 2012; Almécija et al., 2021). A consensus has yet to be reached as to whether dryopithecines are stem hominids (Andrews, 1992; Casanovas-Vilar, Alba, Garcés, Robes, & Moyà-Solà, 2011; Alba, 2012; Alba et al., 2015) or crown hominids more closely related to either pongines (Moyà-Solà & Köhler, 1993, 1995, 1996; Agustí et al., 1996) or hominines (Begun, 2002, 2009, 2015, 2018; Begun, Nargolwalla, & Kordos, 2012). However, most recent cladistic analyses support the view that dryopithecines are stem hominids, with Late Miocene hispanopithecins (*Hispanopithecus* and *Rudapithecus*) occupying a more derived position toward crown hominids than the Middle Miocene dryopithecines (Pugh, 2022). The dryopithecine talus described here was found isolated in a locality that has yielded no further primate remains (Alba et al., 2017). The size of the specimen discounts an attribution to the small-bodied catarrhines that have been recovered from ACM (Alba et al., 2010a, 2015; Alba, Moyà-Solà, Robles, & Galindo, 2012a; Bouchet et al., 2024), but does not enable a conclusive assignment to any of the large-bodied dryopithecines recorded from slightly older sediments from the ACM sequence (Moyà-Solà, Köhler, Alba, Casanovas-Vilar, & Galindo, 2004, Moyà-Solà et al., 2009ab; Alba, 2012; Alba & Moyà-Solà, 2012; Alba et al., 2013, 2020, 2024b), namely *Pierolapithecus catalaunicus*, *Anoiapithecus brevirostris*, or *Dryopithecus fontani*.

Based on comparisons with extant anthropoid primates by means of three-dimensional geometric morphometric (3DGM) techniques, we evaluate the closest morphological affinities of the ACM dryopithecine talus and make locomotor inferences based on the covariation between talar shape and locomotor behavior, as well as additional morphofunctional considerations. During the last decade, 3DGM has been increasingly applied to the study of catarrhine talar morphology (Turley & Frost, 2013), with emphasis on extant hominoids (Parr, Chatterjee, & Soligo, 2011; Parr et al., 2014; Knigge et al., 2015; Friesen et al., 2024) and extinct hominins (Rosas et al., 2017; Sorrentino et al., 2020). However, to our knowledge this is the first study where a Miocene ape talus is analyzed by means of 3DGM. All dryopithecines for which postcranial elements are available show a mosaic of plesiomorphic and apomorphic features that do not match the body plan found in any living ape—reflecting combinations of positional behaviors that have no modern analog (e.g., Alba, 2012; Ward, 2015; Almécija et al., 2021). Consequently, we predict that IPS85037 will not closely resemble the talar morphology of any extant ape lineage. Instead, we expect that it will exhibit a mosaic morphology combining plesiomorphic (‘monkey-like’) and apomorphic (modern hominoid-like) features. In addition, Middle Miocene dryopithecins are considered to be postcranially less derived than Late Miocene hispanopithecins, including *Danuvius* (Alba, 2012; Almécija et al., 2021; Urciuoli and Alba, 2023)—presumably lacking the suspensory specializations of the latter (Moyà-Solà et al., 2004; Moyà-Solà, Köhler, Alba, Casanovas-Vilar, & Galindo, 2005; Almécija, Alba, Moyà-Solà, & Köhler, 2007; Almécija, Alba, & Moyà-Solà, 2009; Alba, Almécija, & Moyà-Solà, 2010b; Böhme et al., 2019; Pina, Alba, Moyà-Solà, & Almécija, 2019; but see Begun & Ward, 2005; Deane & Begun, 2008, 2010). Thus, we also predict that IPS85037 will lack adaptations for suspensory locomotion, contrary to later hispanopithecins. Therefore, despite not being attributable to genus rank, the ACM dryopithecine talus not only provides new insight into the locomotor adaptations of dryopithecines but also contributes to a better understanding of talar morphology evolution and its locomotor implications in crown hominoids.

1.2. Age and geological background

The ACM local stratigraphic sequence is located at els Hostalets de Pierola (Catalonia, Spain), in the Penedès sector of the Vallès-Penedès Basin (NE Iberian Peninsula). This basin is a Neogene half-graben limited by Pre-Littoral and Littoral Catalan Coastal Ranges, close to Barcelona, that has yielded a rich fossil vertebrate record from the Early to the Late Miocene (Casanovas-Vilar et al., 2016a). The sedimentary deposits of the basin are broadly structured in two complexes of continental units, with intercalated marine and transitional units (Casanovas-Vilar et al., 2016a). The ACM stratigraphic sequence belongs to the upper continental complexes, which are Middle to Late Miocene in age (Alba et al., 2006, 2017; Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2016ab; Casanovas-Vilar, Jovells-Vaqué, & Alba, 2022). The sediments from ACM predominantly consist of mudstones, which were deposited in the distal-to-marginal, inter-fan zones of the coalescing alluvial fan systems of Olesa and els Hostalets de Pierola (Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2016b; Alba et al., 2017).

Based on litho-, bio-, and magnetostratigraphic correlation, the ACM sequence spans from 12.6 to 11.1 Ma (Middle to Late Miocene) and covers the Mammal Neogene (MN) zones MN6 (late portion), MN7+8, and MN9 (earliest portion), being correlated to the late Aragonian and earliest Vallesian (Casanovas-Vilar et al., 2016b; Alba et al., 2017, 2022). The primate fossil talus described here was found isolated in the framework of paleontological surveillance performed during the construction of Sector B of Cell 8 of the Can Mata landfill in 2014. Its exact stratigraphic position (locality ACM/C8-B*) relative to the ACM composite sequence (Alba et al., 2017, 2022) was recorded, enabling a correlation with the base of normal polarity subchron C5r.2n, with an interpolated age of 11.65 Ma (Alba et al., 2022) that coincides with the Middle/Late Miocene (Serravallian/Tortonian) boundary (Raffi et al., 2020). Isotopic and mesowear data from the ACM fauna suggest that the time span comprised between 11.7 and 11.6 Ma at ACM was characterized by greater habitat heterogeneity than previous periods (DeMiguel et al., 2021), which might explain the coexistence between large-bodied dryopithecines and the small-bodied crouzeliid *Pliobates* around this time (Alba et al., 2017; DeMiguel et al., 2021).

2. Materials and methods

2.1. Studied material and comparative sample

IPS85037 (Fig. 1a-e) is housed at the Institut Català de Paleontologia Miquel Crusafont (ICP) in Sabadell, Spain. The fossil was compared with a broad sample of extant anthropoids using 3DGM techniques. The extant comparative sample comprises 68 tali from 22 primate species across 14 genera, providing good phylogenetic coverage (Table 1; see Fig. 2 for a representation of the main groups and Supplementary Information [SI] Table S1 for further details). A talus of the Early Miocene hominoid *Ekembo heseloni* (KMN-RU 2036) was also included in the comparative sample (Walker & Pickford, 1983) to gain insight about the stem hominoid condition. Additionally, the morphological affinities between IPS85037 and other relevant tali from Miocene apes and extinct catarrhines are assessed to better understand the evolution of hominoid talar morphology and its locomotor implications.

2.2. Surface scanning

3D virtual models of the specimens from the comparative sample were derived from surface scans obtained using a Geomagic Capture scanner (3D Systems, Rock Hill, USA) and subsequently cleaned using Geomagic Wrap 2019 (3D Systems, Rock Hill, USA). In turn, IPS85037 was scanned using a NextEngineTM 3D scanner HD (NextEngine, Inc., Santa Monica, USA) using high definition (HD) settings following the protocol detailed by Hammond et al. (2016). The scanner's range was adjusted to Macro settings and the highest possible resolution (160 points per square inch). The three final scans obtained—one 360°

scan and two bracket scans (top and bottom)—were fused in Scan Studio PRO v. 1.7.3 (NextEngine, Inc., Santa Monica, USA) to obtain the final surface mesh, which underwent postprocessing following standard protocols (Tocheri et al., 2011; Hammond, Plavcan, & Ward, 2016) using Geomagic Studio 12 (3D Systems, Rock Hill, USA). Since the talus virtual models included in the comparative sample were from the left side (or had been mirrored to appear as such), the 3D model of IPS85037 was mirrored to perform the analyses. The virtual model from the described specimen is available from MorphoSource (SI File S1). Similarly, the talus belonging to *E. heseloni* (KMN RU 2036) was scanned from the original specimen using the same procedure than for IPS85037.

2.3. Geometric morphometrics

Landmark protocol To perform the 3DGM analyses, 36 landmarks were placed following a protocol devised to capture the overall talar shape (Fig. 3; Table 2). The 3D models were landmarked using Landmark Editor v. 3.0.0.6 (Wiley et al., 2005). All analyses were performed in the statistical software R v. 4.4.0 (R Core Team, 2024), using the visual interface RStudio desktop v. 2023.3.0.386 (RStudio, Inc, Boston, USA). In addition, a table with a list of 11 talar measurements using linear metrics (following Youlatos, 1999) is provided for comparative purposes (Table 3). A generalized Procrustes analysis (GPA) was performed to obtain the Procrustes-aligned coordinates using ‘gpagen’ function of ‘geomorph’ package v. 4.0.7 (Adams & Otarola-Castillo, 2013).

Intra– and inter–observer repeatability tests were performed to confirm the repeatability of the landmark coordinate digitization used for geometric morphometric analyses (Shearer et al., 2017). Landmark coordinates were placed by four different researchers (SI Fig. S1a) and four times by the same researcher (SI Fig. S1b) to test for the inter– and intra–observer repeatability, respectively. Procrustes distances (SI Tables S2 and S3) and per-landmark variance (SI Fig. S2; SI Table S4) were calculated. No significant differences were found between the intra- and inter-observer conditions (t = 1.4035, p = 0.1651), indicating that the landmark configuration is repeatable by different researchers.

Principal components analysis A between-group principal components analysis (bgPCA; Culhane, Perriere, Considine, Cotter, & Higgins, 2002) was performed on the Procustes-aligned coordinates using ‘groupPCA’ function of ‘Morpho’ package v. 2.12 (Schlager, 2017). Four groups were defined a priori: platyrrhines, cercopithecoids, hylobatids, and hominids. Unlike a standard PCA, a bgPCA maximizes variance along the axes based on the centroids of the groups defined a priori, with the scores of individual specimens being subsequently plotted post hoc onto the morphospace, thereby enhancing group distinction. The data from the fossil 3D models (IPS85037 and KMN-RU 2036) were projected a posteriori on each analysis. Bivariate plots among between-group principal components (bgPCs) were plotted using the ‘ggplot2’ package v. 3.5.1 (Wickham, 2016). For visualization purposes, a thin-plate spline deformation of the 3D model of a reference talus was carried out using the functions ‘shape.predictor’ and ‘tps3d’ of the ‘geomorph’ and ‘Morpho’ packages, respectively, and ‘shade3d’ of the ‘rgl’ package1.1.3 (Adler & Murdoch, 2020). The ‘mshape’ and ‘findMeanSpec’ functions of the package ‘geomorph’ were used to find the closest specimen to the sample mean to use as reference. The specimen selected was a talus of *Pan paniscus* (RMCA 27698).

To assess the presence of allometric effects, the three resulting bgPCs were regressed using the ordinary least-squares method (OLS) against natural log-transformed (ln) centroid size of the talus for each specimen using the ‘procD.lm’ function in ‘geomorph’ and plotted using the package ‘ggplot2’.To address the concerns about potentially spurious grouping when bgPCA is applied to highly multidimensional datasets (Bookstein, 2019; Cardini, O’Higgins, & Rohlf, 2019)—such as those coming from 3DGM analyses—we designed the sample to include groups with a large number of individuals (Rohlf, 2021). We also followed Cardini & Polly's (2020) recommendation to perform a cross-validated bgPCA on the raw data using the 'groupPCA' function of the package 'Morpho.' With the same aim in mind, we also computed group mean differences for the raw shape data, regular bgPCA scores, and cross-validated bgPCA scores using the 'lm.rrpp' function of the R package 'RRPP' v. 2.0.0 (Collyer & Adams, 2018). In addition, a standard PCA was performed to evaluate the differences between the bgPCA and a standard PCA using 'prcompfast' function of 'Morpho'. In this second case, 3D data of IPS85037 and KMN-RU 2036 were projected a posteriori as well.

Finally, we computed the typicality probabilities of group membership for the fossil specimens using the 'typprobClass' function of the 'Morpho' package. Unlike posterior probabilities, which are customarily calculated in discriminant analyses and assume that classified individuals belong to one of the a priori defined groups, typicality probabilities evaluate the similarity of a specimen to each group separately. Although the classification of each specimen is similarly based on the highest probability, the typicality probabilities also represent the p-value to test the null hypothesis of group membership (separately for each group). Thus, even if the highest typicality probability denotes the highest morphometric affinities, it might still indicate that the specimen does not fit within the variation of the group if $p < 0.05$.

2.4. Body mass estimation

Talus size, as captured using either linear measurements (Tsubamoto, Egi, Thaung-Htike, & Zin-Maung-Maung-Thein, 2016), articular areas (Yapuncich, Gladman, & Boyer, 2015), or centroid size in 3DGM analyses (Parr et al., 2014), has been established as a suitable proxy of body mass (BM). We followed the latter approach to estimate BM for the described dryopithecine talus. As the comparative sample does not include individuals of known BM, mean data (SI Table S5) for both males and females of each species were taken from the literature (Smith & Jungers, 1997). In the case of polytypic species, the average of subspecies BM means was computed for each sex. To estimate BM, allometric regressions of ln BM vs. ln centroid size were performed using an OLS regression with the ‘lm’ function of the ‘stats’ package. Body mass estimates for IPS85037 and KMN-RU 2036 were derived from the best-fit regression line by further applying the quasi-maximum likelihood estimator (QMLE) to account for the logarithmic transformation bias (Smith, 1993). The latter was computed as $\mathrm{QMLE} = \exp(\mathrm{SEE}^2/2)$, where SEE is the standard error of estimate of the regression. 50% and 95% confidence intervals (CIs) were computed for each BM estimate of the fossil specimen.

2.5 Partial least-squares regression

Previous studies (e.g., Püschel et al., 2018, 2020; Llera Martin et al., 2022) have shown that it is possible to distinguish between main locomotor modes and substrate preferences using tarsal shape, as well as to infer the locomotor behavior of fossil primates on its basis. These studies discretized locomotor categories or substrate preferences into a limited number of categories to enable the application of different classification algorithms. Although certainly valuable, these approaches have limitations that arise from the fact that any classification scheme is a simplification of the actual locomotor repertoire displayed by any primate species, which includes a variety of locomotor behaviors. Other studies have overcome such limitations using two-block partial least-squares analysis (2B-PLS; Rohlf & Corti, 2000), which enables the assessment of major patterns of covariation between a shape data matrix (e.g., talar shape) and a locomotor behavior data matrix (e.g., Almécija, Orr, Tocheri, Patel, & Jungers, 2015; Fabre, Marigó, Granatosky, & Schmitt, 2017; Fabre, Granatosky, Hanna, &

Schmitt, 2018; Fabre, Peckre, Pouydebat, & Wall, 2019; Püschel et al., 2017). These studies have shown that it is possible to find strong covariation patterns between behavioral data (e.g., locomotion) and the shape of certain skeletal elements, which may be used to make paleobiological inferences. However, the aforementioned works only focused on extant species and did not try to infer the locomotor behavior of extinct taxa. In addition, the standard version of 2B-PLS in the morphometric literature is a symmetric analysis that, in its classic formulation, does not allow predictions (Zelditch, Swiderski, & Sheets, 2012). However, there is a type of partial least-squares analysis more comparable to regression, known as partial least-squares regression (PLSR), that allows the generation of predictive models (Wold, Sjöström, & Eriksson, 2001). This method has been previously applied in geometric morphometrics to predict one block of shape variables from another one (e.g., Schlager, 2013; Archer et al., 2018; Bastir et al., 2019; Torres-Tamayo et al., 2020), and recently has been used to estimate the locomotor behavior of early primate species, yielding a good predictive performance (Monclús-Gonzalo, Alba, Duhamel, Fabre, & Marigó, 2023, Monclús-Gonzalo et al., under review). Therefore, we applied a PLSR approach to infer the locomotor behavior of the two Miocene apes included in the studied and comparative samples based on their talar shape.

The two blocks of data consisted of (1) talar shape (Procrustes-aligned coordinates) averaged by species and (2) locomotor mode percentages (LMPs)—i.e., the percentage time a species spends performing a certain locomotor behavior—for the 21 extant species included in the extant comparative sample. *Homo sapiens* was excluded from the comparative sample due to its highly specialized locomotor repertoire, which consists almost exclusively of terrestrial bipedalism. Locomotor data were taken from the literature (see references in SI Table S6). Five locomotor modes were distinguished: (1) quadrupedal walking, bounding, and running; (2) clambering and vertical climbing; (3) leaping, dropping, and hopping; (4)

bridging, brachiation, and suspensory locomotion; and (5) bipedal walking. Because the locomotor data came from different sources, and not all behaviors reported in the original studies were considered, we rounded the LMPs to percentages for those species that included small amounts of locomotor modes not considered in this study, ensuring that they add up to 100%. In addition, to ensure that our locomotor predictions were between 0 and 100%, we first converted the percentages to proportions by dividing them by 100 and then we applied a logit transformation, which can be defined as ln [P/(1–P)], where P is a proportion (Cramer, 2003). This transformation was done prior to carrying out the PLSR to avoid nonsensical results (e.g., LMPs higher than 100% or lower than 0%). Given that ln (0) is undefined, we added 1% to any LMP equal to 0 and then we rounded up again the LMPs to ensure that they added up to 100% before carrying out the logit transformation.

The PLSR is based on the same basic machinery as the standard 2B-PLS, which means that it finds the principal components of covariation between the blocks of variables by means of decomposing the covariance matrix of the two blocks into two sets of eigenvectors (one for each set of variables) and eigenvalues, using a singular value decomposition to generate a matrix of singular values (the square roots of the eigenvalues), a matrix of eigenvectors for the first set of variables and the transpose of the matrix of eigenvectors for the second set of variables (Rohlf & Corti, 2000). We carried out this step by using the ‘two.b.pls’ function of the ‘geomorph’ package, and we run 9,999 iterations for significance testing. The PLSR works by regressing the first block of variables on the vector obtained from the scores for the second block of variables (i.e., the LMPs were regressed on the talar shape values that were projected onto the obtained singular vectors). This step was done using the ‘procD.lm’ function of the same package (9,999 iterations were used). To obtain LMP predictions, the talar shape values were projected onto the obtained singular vectors and then multiplied by a matrix consisting of the linear model coefficients. This process was done with the talar shape (Procrustes-aligned coordinates) averaged for extinct species to derive locomotor inferences (i.e., estimated percentages for the various locomotor modes). Given that, prior to the PLSR, the LMPs were subjected to a logit transformation, the obtained predictions were transformed back into percentages by applying an inverse logit transformation, defined as exp(X) / [1 + exp(X)], where X corresponds to a logit transformed value. The obtained predictions were then rounded up again to ensure that they added to 100%. To assess the PLSR predictive performance, we performed a 'leave-one-out cross-validation' (LOOCV), which means that separate analyses were carried out for each one of the predictions, excluding the particular individual for which the prediction was being calculated (Kuhn & Johnson, 2013). Using these cross-validated results, we computed the mean absolute error (MAE; i.e., the arithmetic average of the absolute errors) to assess our prediction results using the extant sample (Willmott & Matsuura, 2004).

Additionally, the talus specimen closest to the multivariate mean of the talar shape dataset (*Pan paniscus*, RMCA 27698) was warped to represent the covariation between shape and LMPs along the first singular vectors (following the same procedure as that explained above to visualize the shapes associated to the negative and positive extremes of each axis of the bgPCA). A principal component analysis (PCA) was carried out with the LMPs using the 'prcomp' function of the R package 'stats'. The PCA scores and the loadings of each locomotor variable were assembled in the same scatterplot (as a biplot). The estimated locomotor repertoires of IPS85037 and KMN RU 2036 were projected onto the latent space to visualize their placement within the 'ecospace' defined by extant species' locomotor behavior. The direction and length of each vector indicate the region of the scatterplot in which the locomotor variable is more represented. As a result, those specimens projected the furthest in the direction of a given vector are those whose locomotor repertoire possesses the highest percentage in the direction of the corresponding locomotor variable.

3. Results

3.1. Description

The right talus IPS85037 (Fig. 1a-e) is well preserved except for minor damage on the lateral edge of the trochlea, the medial tubercle, the posterior calcaneal facet, and the medial edge of the talar head, as well as a crack at the level of the neck. The talar body is dorsoplantarly taller than mediolaterally wide. The trochlea is wedge-shaped (broader anteriorly than posteriorly), displays a moderately deep central groove and has a slightly dorsoplantarly higher lateral trochlear rim compared to the medial one. The groove for the flexor hallucis longus tendon is placed in a mid-trochlear position, flanked by a well-developed posterior lateral tubercle and a similarly developed (but somewhat damaged) posterior medial tubercle. The articular facet with the fibula is relatively dorsoplantarly tall and moderately expanded laterally. The medial tibial facet is moderately steep and does not reach the plantar side of the bone. The neck is relatively long and slender, medially angled, has a subsquare cross-section almost as wide as high, and displays a strong medial orientation. The posterior calcaneal facet is relatively shallow, subsquare (except for its proximal edge, which tapers toward the medial tubercle), slightly concave, and obliquely oriented. The sulcus tali is relatively broad and shallow. The anterior calcaneal facet is continuous and mediolaterally narrow, extending up to the anterior end of the sulcus tali. The talar head, relatively small and ovoid, bears a markedly convex articular surface that extends more laterally than medially and shows a slight medial torsion.

3.2. Comparison with stem catarrhine and other Miocene ape tali

The trochlear morphology of IPS85037, like that of stem catarrhines and other Miocene apes, exhibits an anteriorly broad articular facet and a relatively deep trochlear depth comparable to the dendropithecid *Simiolus enjiessi* (Leakey & Leakey, 1987; Rose et al., 1992), the pliopithecoid *Pliopithecus antiquus* (Senut, 2012), and most Miocene hominoids (*Ekembo heseloni*, *E. nyanzae*, *Equatorius africanus*, *Nacholapithecus kerioi*, and *Sivapithecus sivalensis*; MacInnes, 1943; Le Gros Clark & Leakey, 1951; Pilbeam et al., 1980; Harrison, 1982; Walker & Pickford, 1983; Leakey & Leakey, 1987; Rose et al., 1992, 1996; McCrossin, 1994; Madar, 1996; Ishida et al., 2004; Nakatsukasa et al., 2012). It differs from the dendropithecid *Dendropithecus maccinesi* (Le Gros Clark & Thomas, 1951) and the nyanzapithecid *Rangwapithecus gordoni* (De Silva, 2008) in displaying a deeper trochlear groove. The lateral trochlear rim of IPS85037 is only slightly higher than the medial rim, as in extant hominoids (particularly orangutans and hylobatids; Turley & Frost, 2013), dendropithecids (*D. maccinesi* and *S. enjiessi*; Le Gros Clark & Thomas, 1951; Leakey & Leakey, 1987; Rose et al., 1992), *Oreopithecus* (Szalay & Langdon, 1986), and the stem pongine *Si. sivalensis* (Pilbeam et al., 1980; Madar, 1996). Conversely, the lateral trochlear rim of IPS85037 is less prominent than that of extant cercopithecoids (Strasser, 1988), pliopithecoids (*P. antiquus* and *Anapithecus hernyaki*; Begun, 1987; Senut, 2012), and several stem hominoids (*Turkanapithecus kalakolensis*, *E. heseloni*, *E. nyanzae*, *Eq. africanus*, and *N. kerioi*; Harrison, 1982; Walter & Pickford, 1983; Leakey & Leakey, 1987; Ward et al., 1993; McCrossin, 1994; Ishida et al., 2004; Nakatsukasa et al., 2012).

Posteriorly, IPS85037 displays a deep and well-defined groove for the tendon of the m. flexor hallucis longus, and a rather well-developed posterior lateral tubercle. This condition is also met by the stem hominoid *Proconsul major* and *Orepithecus* (Harrison, 1982; Szalay & Langdon, 1986; De Silva, 2008). IPS85037 further resembles the afropithecid *N. kerioi* in the well-developed lateral posterior tubercle (Ishida et al., 2004; Nakatsukasa et al., 2012). Conversely, the condition of IPS85037 is markedly distinct from the shallow groove displayed by pliopithecoids (Begun, 1987; Senut, 2012) and the afropithecid *Eq. africanus*

(McCrossin, 1994). Moreover, IPS85037 resembles extant hominoids in the less concave facet for the medial tibial malleolus and the lack of a dorsal ridge on the talar neck (Conroy & Rose, 1983). In the latter feature, IPS85037 is similar to *R. gordoni*, *Pr. Major*, and *O. bambolii* (Harrison, 1982; Szalay & Langdon, 1986; De Silva, 2008) but different from the deeply cupped facet and the pronounced dorsal ridge exhibited by pliopithecoids (*P. antiquus* and *Epipliopithecus vindobonensis*; Zapfe, 1958; Senut, 2012), dendropithecids (*Micropithecus songhorensis* and *S. enjiessi*; Le Gros Clark & Thomas, 1951; Leakey & Leakey, 1987; Rose et al., 1992) and several stem hominoids (*E. heseloni*, *E. nyanzae*, *Eq. africanus*, and *N kerioi*; MacInnes, 1943; Le Gros Clark & Leakey, 1951; Harrison, 1982; Walker & Pickford, 1983; Leakey & Leakey, 1987; Rose et al., 1992, 1996; McCrossin, 1994; Ishida et al., 2004; Nakatsukasa, et al., 2012), which resemble instead the extant cercopithecoids (Le Gros Clark & Leakey, 1951; Harrison, 1982).

IPS85037 resembles most stem catarrhines and Miocene apes in the gracile and moderately elongate neck (Harrison, 1982), with the exception of *O. bambolii*, which resembles extant hominoids (excluding orangutans) in the extremely abbreviated neck (Szalay & Langdon, 1986). In contrast, IPS85037 resembles *O. bambolii* and differs from other Miocene apes and stem catarrhines in the medially angled neck, albeit less markedly so than in *O. bambolii* (Szalay & Langdon, 1986). IPS85037 resembles the pliopithecoid *P. antiquus* (Senut, 2012), as well as the stem hominoids *T. kalakolensis* (Leakey & Leakey, 1987) and *Pr. major* (Harrison, 1982; De Silva, 2008) in the small and spherical head. In contrast, IPS85037 differs in this regard from dendropithecids (*D. maccinesi* and *S. enjiessi*; Le Gros Clark & Thomas, 1951; Leakey & Leakey, 1987; Rose et al., 1992) and several Miocene apes (*E. heseloni*, *E. nyanzae*, *Eq. africanus*, *N. kerioi*, and *O. bambolii*; MacInnes, 1943; Le Gros Clark & Leakey, 1951; Harrison, 1982; Walker & Pickford, 1983; Szalay & Langdon, 1986; Rose et al., 1996; Ward et al., 1993; McCrossin, 1994; Ishida et al., 2004;

Nakatsukasa et al., 2012), which exhibit mediolaterally broad and large heads like those of extant cercopithecoids and African apes.

IPS85037 has a relatively flat and proximodistally elongated posterior calcaneal facet, comparable to that of orangutans (Langdon, 1986). In this regard, IPS85037 differs from stem catarrhines and Miocene apes except *O. bambolii* (Harrison, 1982; Conroy & Rose, 1983; Langdon, 1986), which, like IPS85037, possesses a shallow and elongated facet (Szalay & Langdon, 1986). Moreover, IPS85037 displays a small divergence between the posterior calcaneal facet and the long axis of the trochlea, matching extant hominoids, the pliopithecoid *An. hernyaki* (Begun, 1987), *N. kerioi* (Ishida et al., 2004; Nakatsukasa et al., 2012), and *Si. sivalensis* (Pilbeam et al., 1980; Madar, 1996). The sulcus tali of IPS85037, separating the anterior calcaneal facet from the posterior, is intermediate between the condition of extant great apes (deep and narrow) and gibbons and non-hominoid anthropoids (shallow and broad; Harrison, 1982). Finally, IPS85037 resembles stem catarrhines and most other Miocene apes in the anteromedially L-shaped anterior calcaneal facet (Harrison, 1982), except for *O. bambolii*, which differs from IPS85037 and resembles extant hominoids in possessing a crescent-shaped facet (Szalay & Langdon, 1986).

3.3. Morphometric comparisons

The bgPCA (Fig. 4) correctly classifies 100% of cases in the four extant groups defined a priori (platyrrhines, cercopithecoids, hylobatids, and hominids), whereas the bgPCA with cross-validation (SI Fig. S3a and b) correctly classifies 94% of cases (SI Tables S7 and S8). The similarities between standard PC scores (SI Fig. S4a and b), and standard and cross-validated bgPC scores suggest that discrimination is not spurious. In addition, significant group differences in the raw shape data indicate the presence of group structure in our sample ($R^2 = 0.23$, $p < 0.001$). Even if the amount of variance increases considerably when group differences are computed for bgPC ($R^2 = 0.77$, $p < 0.001$) and cross-validated bgPC scores ($R^2 = 0.71$, $p < 0.001$), the overall similarities between the Z-scores computed for the raw data (Z = 6.49), bgPC scores (Z = 13.79), and cross-validated bgPC scores (Z = 12.01) allow us to reject the presence of spurious grouping in the analysis.

The bgPC1 (62% of total variance; Fig. 4a and b) reflects differences in talar body shape (broader and stouter toward positive scores vs. slenderer toward negative scores), wedging of the trochlea (broader anteriorly than posteriorly toward positive scores vs. subparallel rims toward negative scores), the shape of the posterior calcaneal facet (slenderer and medially tapered toward negative scores and broader and more squared toward positive scores), the anterior calcaneal facet (proximodistally longer and mediolaterally narrow toward positive scores and broader and more proximodistally restricted toward negative scores), proximodistal elongation and robusticity of the talar neck (shorter and more robust toward positive scores and proximodistally longer and slenderer toward negative scores), and the relative size of the talar head (smaller and more spherical toward negative scores). This axis separates platyrrhines (negative end of the axis) from cercopithecoids (moderately negative scores) as well as hylobatids (moderately negative or positive scores) and hominids (mostly positive scores), with hylobatids partly overlapping with both cercopithecoids and hominids. A significant allometric relationship is found between bgPC1 and talus size, indicating a strong positive correlation that accounts for 78% of the variance (SI Fig. S5a, Table 4). This result parallels the rough gradient of decreasing body size observed along bgPC1, although hylobatids exhibit comparably more positive scores (overlapping with the lower end of great apes) than expected given their body size, while monkeys (especially platyrrhines), in contrast, display lower bgPC1 values than that expected on this basis.

The bgPC2 (23% of the variance; Fig. 4a) is driven by the shape of the talar body (negative scores are associated with a shallower and more dorsoplantarly compressed trochlea and positive scores with a deeper and dorsoplantarly higher trochlea), the relative height of the lateral rim (more symmetrical rims toward negative scores and distinctly dorsoplantarly higher lateral rim, compared to the medial rim, associated with positive scores), the size of the posterior lateral tubercle and the development of the groove for the flexor hallucis longus tendon (smaller tubercle and less well-developed groove toward positive scores), the shape of the posterior calcaneal facet (mediolaterally broader facet more extended medially than laterally toward positive scores), and the anterior calcaneal facet (more concave toward negative scores). This axis separates the more arboreal and/or suspensory species (platyrrhines, hylobatids, and orangutans), which display negative scores, from the more cursorial cercopithecoids (positive scores). African apes and humans display intermediate scores and overlap slightly with cercopithecoids and only minimally (especially in the case of chimpanzees) with other platyrrhines, hylobatids, and orangutans. Unlike bgPC1, bgPC2 is not significantly correlated with talar centroid size (SI Fig. S5b; Table 4), indicating that shape changes along this axis are not affected by size-scaling effects. The bgPC2 seemingly reflects differences in locomotor behavior, with the most arboreal and suspensory hominoids (hylobatids and orangutans) overlapping with the suspensory platyrrhines (*Ateles* and, to a lesser extent, *Alouatta*). Non-suspensory platyrrhines (*Cebus*) also overlap with hylobatids and orangutans, but remarkably exhibit less negative scores than either *Ateles* or *Alouatta*. The bgPC2 shows a locomotor gradient, with terrestrial and semiterrestrial species displaying more positive scores than arboreal ones—except for committed arboreal cercopithecoids such as *Colobus* or *Nasalis*, which cluster with (semi)terrestrial cercopithecoids instead of other arboreal species.

The bgPC3 (15% of total variance; Fig. 4b) reflects differences in the shape of the trochlea (increased wedging toward positive scores), the size of the lateral posterior tubercle and depth of the groove for the flexor hallucis longus tendon (larger tubercle and deeper groove toward positive scores), and the shape of the anterior calcaneal facet (proximodistally more elongated toward positive values). This axis clearly discriminates hylobatids (very negative scores) from the rest of the comparative sample (which extensively overlaps from intermediate to moderately positive scores). The bgPC3 is significantly correlated with talus size (SI Fig. S5c; Table 4). However, allometric effects can be excluded as the main driver of variation along this axis, as they only explain 8% of shape variance—as further illustrated by the overlap between humans and great apes with the much smaller monkeys and the segregation of hylobatids from all monkeys irrespective of size.

Along bgPC1, both IPS85037 and KMN-RU 2036, characterized by a mediolaterally narrow and dorsoplantarly high astragalar body and a proximodistally elongated neck, overlap with hylobatids and cercopithecoids (Fig. 4). Regarding bgPC2 (Fig. 4a), IPS85037 closely approaches the variation of hylobatids and overlaps with that of the suspensory orangutans and atelids, as well as cebids. In contrast, KMN-RU 2036 displays a more positive score that approaches the cercopithecoid condition and overlaps with the knuckle-walking African apes and bipedal humans. The different scores along bgPC2 can be explained by differences in talar shape between the two fossil specimens. IPS85037 shows some remarkable similarities with the tali of pongines and hylobatids, such as a slightly prominent lateral rim, a well-developed groove for the flexor hallucis longus tendon and medial and lateral tubercles), a shallow and slightly angled (relative to the long axis of the bone) posterior calcaneal facet, a proximodistally elongated and medially angled neck and a spherical and convex talar head. In contrast, KMN-RU 2036 more closely approaches the cercopithecoid condition in these regards. Finally, both IPS85037 and KMN-RU 2036 are distinguished from hylobatids along bgPC3 (Fig. 4b), as both tali display a relatively wedged and dorsoplantarly deeper trochlea, as well as a more developed groove for the flexor hallucis longus tendon, similarly to the remaining taxa. The differences between the two fossil tali are further confirmed by the typicality probabilities (Table 5), with IPS85037 showing greatest affinities with platyrrhines but further matching the hominid variation, whereas KMN-RU 2036 is classified as a cercopithecoid despite not being incompatible either with the platyrrhine variation.

3.4. Body mass estimation

The allometric equation derived to estimate body size is reported in Table 6. The BM estimate for IPS85037 is 38 kg (95% CI = 35–42 kg), thus being roughly the average size of a female orangutan (Smith and Jungers, 1997). Conversely, the BM estimate for KMN RU 2036 is 13 kg (95% CI = 12–14 kg), comparable to male siamangs and slightly larger than most atelids, and similar to male macaques as well as female baboons (Smith and Jungers, 1997).

3.5. Partial least-squares regression

The covariation between talar shape and locomotor behavior is significant and explains a considerable amount (92%) of covariance in the first two PLS axes (Table 7). The PLSR predictive performance is presented in SI Figure S6a-e and SI Tables S9 and S10.

The first axis (PLS1; Fig. 5a; 77% of covariance) discriminates between most suspensory species (*Pongo*, hylobatids), in the most positive scores of the shape axis, and the most quadrupedal ones (African apes, cercopithecoids), located at the negative side of the axis. Platyrrhines, which engage in a more generalized locomotor behavior—including moderate amounts of arboreal quadrupedalism, climbing, and clambering, as well as some leaping (although some species, particularly atelids, also display tail-assisted suspensory behaviors)—are located in intermediate scores of the shape axis. Suspensory species are associated with a proximodistally longer trochlea, more symmetrical rims, a more laterally flaring fibular facet with a more gently inclined slope, a deeper groove for the flexor fibularis tendon and more developed posterior lateral tubercle, a shallower, narrower, and more elongated posterior calcaneal facet, a shallower sulcus talus, and a smaller and more spherical talar head. Conversely, most quadrupedal species exhibit a mediolaterally wider (and proximodistally shorter) trochlea, a higher lateral rim, a steeper fibular facet (in which only the base is laterally protruding), a shallower groove for the flexor fibularis and a less developed posterior lateral tubercle, a more concave and shorter posterior calcaneal facet, a deeper sulcus tali, and a larger talar head. IPS85037 is projected onto intermediate scores, overlapping with platyrrhines, which indicates that its locomotor behavior likely included moderate amounts of quadrupedalism and climbing/clambering, and only a moderate proportion of suspensory behaviors. In contrast, KMN-RU 2036 displays very negative scores, close to the negative end of the axis, suggesting that its locomotor repertoire was dominated by quadrupedalism.

The second axis (PLS2; Fig. 5b) discriminates the larger-bodied great apes on positive scores, thus being associated with slower-paced locomotion involving climbing, clambering, and suspensory movements, but completely lacking leaping from the lightly built platyrrhines, cercopithecoids, and gibbons. These latter habitually engage in swifter movements —such as fast quadrupedal progressions, brachiation, and leaping. Siamangs, despite their relatively small body size—comparable to many male macaques, female baboons, and the larger platyrrhine species—exhibit more positive scores than other hylobatids, in agreement with their generally slower and less acrobatic locomotor behavior . Positive scores are associated with a stouter talar shape, a more marked wedging of the anterior part of the trochlea, a shorter (and semilunar-shaped) anterior calcaneal facet, and a shorter and more medially angled neck. Contrarily, negative scores are associated with a slenderer and more gracile talar shape, parallel trochlear rims, a proximodistally longer anterior calcaneal facet, and a longer and less medially angled neck. IPS85037 falls closer to siamangs and great apes, suggesting that it similarly engaged in slower and more cautious locomotion without leaping (not surprisingly, given its large BM) and with high amounts of climbing and clambering. In contrast, KMN-RU 2036 (in accordance with its smaller BM) is located in more negative scores, overlapping with some of the lager-sized platyrrhines and cercopithecoids, which suggests a more agile locomotion (compatible with some degree of leaping) with less climbing/clambering than IPS85037 as well as extant great apes and siamangs.

The estimated locomotor repertoire for the hominoid to which IPS85037 belonged (Fig. 6, Table 8) includes large percentages of vertical climbing/clambering (CL = 50%) and quadrupedalism (QWR = 32%), and a comparatively restricted suspensory component (S = 11%). This locomotor profile, characterized by higher amounts of vertical climbing/clambering and quadrupedalism but lacking substantial suspensory behaviors, approaches the condition of two extant species: *Alouatta seniculus* (QWR = 46%; CL = 41%; S = 10%) and *Pan paniscus* (QWR = 36%; CL = 51%; S = 9%). In contrast, KMN RU 2036 is reconstructed as possessing a remarkably different locomotor repertoire, dominated by quadrupedalism (QWR = 81%), and with much lower percentages of vertical climbing/clambering (CL = 9%) and suspension (S = 2%).

The PCA carried out on the locomotor percentages of the extant primate species distributes taxa according to their locomotor repertoire (Fig. 7; SI Table S11). The first axis (PC1), which accounts for 41% of the total variance, discriminates quadrupedal species (platyrrhines, cercopithecoids, and African apes; most negative scores) from suspensory ones (orangutans and hylobatids; most positive scores). The second axis (PC2), which accounts for 26% of the total variance, separates those species with some leaping capabilities (including several platyrrhines, cercopithecoids and hylobatids, except for the larger-bodied siamangs;

most positive scores) from those taxa with more proclivity for climbing/clambering locomotion and lacking leaping behaviors (*Alouatta*, siamangs, and great apes; most negative scores). IPS85037 is projected closer to *Pan paniscus* and *Alouatta seniculus*, whereas the mainly quadrupedal locomotor repertoire estimated for KMN-RU 2036 overlaps with the more quadrupedal extant species.

4. Discussion

4.1. Body size, sex assignment, and taxonomic attribution

The talus IPS85037 displays several modern hominoid-like features (such as a wedge-shaped trochlea, broader anteriorly than posteriorly, well-developed posterior tubercles, an only slightly concave depression for the medial malleolus, a relatively flat, elongate and obliquely oriented posterior calcaneal facet and a medially angled talar neck) despite an overall ‘monkey-like’ appearance (Harrison, 1982; Langdon, 1986; Gebo, 1989; Drapeau, 2022). This fact, coupled with its large body size, supports its attribution to a dryopithecine instead of any of the small-bodied catarrhines (*Pliopithecus* and *Pliobates*) recorded at ACM (Alba et al., 2010a, 2012a, 2015; Bouchet et al., 2024). The estimated BM IPS85037 (~38 kg) is close to the average BM of female orangutans (Smith & Jungers, 1997) and only slightly lower than estimates previously derived for other Vallès-Penedès dryopithecines: ~43 kg for *P. catalaunicus* from ACM/BCV1 (~12.0 Ma; Alba et al., 2022), based on a lumbar vertebra of the male holotype individual (Susanna, Alba, Almécija, & Moyà-Solà, 2014); ~44 kg for *D. fontani* from ACM/C3-Az (~11.9 Ma; Alba et al., 2022), based on an isolated femur (Moyà-Solà et al., 2009a); and ~39–40 kg for the male skeleton of *Hispanopithecus laietanus* from Can Llobateres 2 (~9.6 Ma; Casanovas-Vilar et al., 2016b), based on vertebral and femoral measurements (Moyà-Solà et al., 2004, 2009a; Susanna et al., 2014). These estimates indicate that Vallès-Penedès male dryopithecines were generally slightly smaller on average than extant male chimpanzees. Thus, although IPS85037 more closely resembles the average female body mass of orangutans, given the usually marked sexual size dimorphism of Miocene apes (Schrein, 2006; Scott, Schrein, & Kelley, 2009), roughly comparable to that of extant orangutans (with males about twice the size of females), attributing IPS85037 to a female individual would imply a BM of ~75 kg, much larger than previously recorded for any Vallès-Penedès hominoid. Therefore, based on the estimated BM, we conclude that IPS85037 most probably belonged to a male specimen.

With an estimated age of ~11.7 Ma, IPS85037 represents one of the two latest occurrences of dryopithecins at ACM, postdating the latest record of the small-bodied pliopithecid *Pliopithecus canmatensis*, and minimally predating that of the crouzeliid *Pliobates cataloniae* (Alba et al., 2017, 2022; DeMiguel et al., 2021). The lack of associated craniodental material, together with the fact that the talus is not recorded for any of the ACM dryopithecins, make it impossible to attempt a taxonomic assignment to genus rank. However, based on both body size (see above) and chronology, IPS85037 might belong to any of the dryopithecins recorded from slightly older deposits along the ACM stratigraphic sequence—*P. catalaunicus, A. brevirostris*, and *D. fontani* (Moyà-Solà et al., 2004, 2009ab; Alba et al., 2013, 2020, 2024b) —which overall range from ~12.4 to 11.9 Ma (Alba et al., 2017, 2022). To our knowledge, IPS85037 is the first complete dryopithecine talus described in detail—the talus originally attributed to *Rudapithecus hungaricus* by Morbek (1983) was subsequently reassigned to the pliopithecoid *Anapithecus* by Kordos & Begun (2001), while only an undescribed partial talus (RUD 135) is seemingly attributable to *R. hungaricus* (Begun 2002, 2009). For this reason, even if no genus attribution is warranted, the quantitative comparisons between IPS85037 and the tali of extant anthropoids and the stem hominoid *Ekembo heseloni* (KMN-RU 2036), as well as the morphological comparisons with other recovered Miocene ape and stem catarrhine tali, provide invaluable insight into the locomotor repertoire of Miocene dryopithecines as well as for the evolution of crown-hominoid locomotion.

4.2 Morphofunctional inferences and quantitative comparisons with extant anthropoids

The morphology of IPS85037, as it is frequently the case of Miocene ape morphology (e.g., Moyà-Solà et al., 2004; Pugh et al., 2023), displays a mosaic of features that is unknown among extant anthropoids, combining an overall plesiomorphic appearance as compared with extant apes with some traits that more closely resemble the derived talar morphology of modern hominoids (Harrison, 1982; Conroy & Rose, 1983; Drapeau, 2022). Among plesiomorphic traits, the possession of a dorsoplantarly high talar body along with a relatively deep trochlea suggests less conjunct rotation (adduction and abduction) at the talocrural joint during dorsi- and plantarflexion, indicating that the movement occurring at the upper ankle joint is mostly limited at the parasagittal plane (Langdon, 1986; Ward, 1998). Likewise, having an anteromedially L-shaped anterior calcaneal facet (resembling non-hominoid primates) has been associated with more limited inversion capabilities at the subtalar joint (Lewis, 1980b)—contrasting with the crescent-shaped facet of extant hominoids, which has been related to increased inversion capabilities (Szalay and Langdon, 1986).

Other features of IPS85037 that appear derived towards the crown hominoid condition are functionally related to high ranges of foot mobility and more powerful hallucal grasping (Langdon, 1986; Drapeau, 2022). For instance, IPS85037 resembles extant hominoids (particularly orangutans and hylobatids) in the possession of a more symmetrical trochlea, with a lateral rim that is only slightly dorsoplantarly higher than the medial one (Langdon, 1986). The functional significance of this character is unclear, although it has been suggested that the presence of a prominent lateral rim might increase the amount of abduction accompanying the dorsiflexion of the foot (Strasser, 1988). This, in turn, may be related to effective weight transfer during inversion and favor arboreal behavior, as concluded from studies performed in extant catarrhines (Turley & Frost, 2013; Dunn et al., 2014; Knigge et al., 2015). However, it is noteworthy that this feature is more marked in terrestrial cercopithecines and African apes than in more arboreal cercopithecines, colobines, and Asian apes, suggesting a possible relationship with the use of terrestrial and/or larger horizontal substrates—as an adaptation for foot stabilization during walking and running, by limiting foot abduction and maintaining the foot in the parasagittal plane (Langdon, 1986). The anterior widening of the trochlea in IPS85037 may be related to dorsiflexion during vertical climbing by facilitating the close packing of the talocrural joint as in extant great apes (Conroy & Rose, 1983; Langdon, 1986; DeSilva, 2008, 2009). Posteriorly, the groove for the flexor hallucis longus tendon and the moderate development of the lateral (which serves as the attachment of the posterior talofibular ligament) and medial (which increases the load of the m. flexor hallucis longus) posterior tubercles are variably present among Miocene apes and stem catarrhine tali (Harrison, 1982; Drapeau, 2022). Judging by the depth of the groove and the moderate development of the lateral posterior tubercle, which acts as the insertion of the posterior talofibular ligament (an important ankle stabilizer during dorsiflexion; Leardini, O’Connor, Catani, & Giannini, 2000), IPS85037 is inferred to have possessed a powerful hallucal grasping, resembling extant African apes and suggesting frequent use of vertical climbing (De Silva, 2008). A strong hallucal grasp is inferred in other Miocene apes as well (Harrison, 1982; Langdon, 1986; Ward et al., 1993; Dunsworth, 2006). On the medial side, IPS85037 displays only a slightly concave facet for articulation with the medial malleolus of the tibia that does not project medially, contrary to the close-packed configuration during dorsiflexion found in cercopithecoids (Le Gros Clark & Leakey, 1951; Conroy & Rose, 1983, Harrison, 1986). This suggests an ankle adapted for withstanding large loadings during extreme dorsiflexion (De Silva, 2008). Similarly, the lack of a dorsal ridge on the talar neck, which is inferred to act as a locking mechanism for stopping the tibia during dorsiflexion, further indicates an ankle with a mobile talocrural joint (Le Gros Clark and Leakey, 1951; Harrison, 1982).

The possession of an elongated talar neck, normally considered the plesiomorphic condition for anthropoids, has been hypothesized to be driven by allometric effects (Harrison, 1982). However, this explanation does not apply to IPS85037, given its great ape-like BM. Orangutans also display a considerably elongated talar neck so that the talar head is projected further than the calcaneus, increasing the supination capability at the midtarsal joint during arboreal locomotion (Harrison, 1982; Gebo, 1989). The relatively deep grove for the flexor hallucis longus tendon in IPS85037 suggests that the calcaneus of the same individual, as in orangutans, was not distally elongated, implying a similarly high degree of midtarsal supination. In addition, the talar neck of IPS85037 also exhibits a very marked medial angulation, which is functionally related to the transmission of the compressive forces towards the medial side of the foot, occurring in arboreal animals with strong hallucal grasping (Barnett, 1955; Harrison, 1982). The spherical shape of the talar head in IPS85037 (similar to that of orangutans in size but somewhat smaller than that of cercopithecoids and African apes) and the great extent of the lateral side of the head (associated with better eversion capabilities of the forefoot) indicate that IPS85037 lacks the typical dorsal translation of the navicular observed in extant apes and would have been less capable to cope with large compressive forces than extant hominoids (Szalay & Langdon, 1986; Meldrum & Wunderlich, 1998). In turn, the posterior calcaneal facet, which is shallow and gently curved (resembling that of orangutans), indicates greater laxity and mobility at this joint, associated with better inversion capabilities at the subtalar joint (Gomberg, 1981; Langdon, 1986; Yapuncich & Granatosky, 2021). Finally, IPS85037 exhibits a small divergence between the posterior calcaneal facet and the long axis of the trochlea, facilitating the screw motion of the talus at the level of the subtalar joint and enhancing the inversion of the foot (Conroy & Rose, 1983).

The predicted LMPs for IPS85037 using the 2B-PLS regression models indicate a locomotor repertoire dominated by vertical climbing/clambering and quadrupedalism, with some degree of suspension. In contrast, the LMPs predicted for KMN RU 2036 indicate a very different locomotor repertoire, vastly dominated by quadrupedalism and with only small amounts of vertical climbing/clambering. These estimated percentages cannot be taken at face value because they are based on a single bone, although the errors computed for the extant species are not particularly large, indicating that the talus is a reliable predictor for locomotor behavior. Furthermore, the results for KMN RU 2036—which match the locomotor profile of some colobine monkeys and non-atelid platyrrhines (Youlatos & Meldrum, 2011; Hunt, 2016)—are consistent with previous locomotor inferences for *Ekembo* based on its postcranial morphology (Le Gros Clark, 1952; Conroy & Rose, 1983; Rose, 1983, 1988; Gebo et al., 1988; Gebo, Malit, & Nengo, 2009; Ward, 1993, 1997; Ward et al., 1995; Walker, 1997; Dunsworth, 2006; DaSilva, 2008). The combination of locomotor modes estimated for IPS85037 approaches that of two extant species: *Alouatta seniculus* and *Pan paniscus*. The former seems to be the species that exhibits the highest percentages of clambering/climbing among atelids (and platyrrhines in general; Youlatos & Meldrum, 2011), which has been related to the diversity of habitats exploited by this species (including gallery forests and different types of shrub woodlands; Schön Ybarra & Schön, 1987). In turn, bonobos are the most generalized great apes in terms of locomotion (Doran, 1993; Isler, 2002; Ramos, 2014). This is reflected by their pedal anatomy, which combines features related to high foot mobility (e.g., comparatively subequal lateral and medial talar rims, slightly concave posterior calcaneal facet, mediolaterally broad anterior calcaneal facet) and propulsion (such as relatively large heel to provide lever arm; Vereecke, D’Août, Payne, &

Aerts, 2005; Friesen et al., 2024). Compared to orangutans, which exhibit a slow and cautious locomotion dominated by orthograde clambering and forelimb-dominated suspension (Cant, 1987; Manduell, Morrogh-Bernard, & Thrope, 2011), bonobos engage much less frequently in suspensory behaviors and equally divide their time between the forest floor and the arboreal canopy (Ramos, 2014). Similarly to chimpanzees and gorillas, bonobos spend a great amount of their time on the ground, habitually moving quadrupedally using knuckle-walking, which is an unlikely behavior for IPS85037 based on the hand morphology of dryopithecines (Almécija et al., 2009; Alba et al., 2010b). However, bonobos also engage in more arboreal quadrupedalism than chimpanzees, being primarily palmigrade (Doran, 1993), a type of locomotor mode that was likely used by most Miocene apes to varying degrees (Rose, 1994; Almécija et al., 2007, 2009, 2021; Alba et al., 2010b, 2012; Alba, 2012; Ward, 2015). Moreover, the morphology of several pedal elements of bonobos (including the talus and the medial cuneiform) suggests that they possess a greater range of hallucal abduction compared to other African apes, offering an advantage for maintaining strong pedal grips while climbing more varied and smaller arboreal substrates (Friesen et al., 2024). Remarkably, some talar features of bonobos, providing them with greater versatility at the ankle and subtalar joints (such as the even lateral and medial trochlear rims and the slightly concave posterior calcaneal facet), are also present in IPS85037.

4.3. Implications for the evolution of crown hominoid positional behaviors

The feet of extant apes display increased mobility and prehensility as compared with those of other living anthropoids, in agreement with the more varied and non-stereotypical locomotor behaviors of the former, which may be interpreted as an adaption for navigating across precarious and unpredictably oriented arboreal substrates (Conroy & Rose, 1983; Hunt, 1991, 2016; DeSilva, 2008; Drapeau, 2022). In accordance with this, extant ape tali are distinguished by numerous adaptations related to enhanced stability during inversion and dorsiflexion, accommodating the foot into different positions and providing strong anchorage to the substrate (Conroy & Rose, 1983; Langdon, 1986; Strasser, 1988; Gebo, 1989; Parr et al., 2014; Drapeau, 2022). However, almost all recovered tali of different groups of Miocene apes and stem catarrhines (pliopithecoids and dendropithecids) lack evidence of a specialized modern hominoid-like derived morphology and, in most cases, exhibit remarkably morphological uniformity (Harrison, 1982; Conroy & Rose, 1983; Rose, 1994; Drapeau, 2022).

Talar morphology of stem catarrhines (e.g., pliopithecoids and dendropithecids) evinces a foot more adapted to stable dorsiflexion and inversion than earlier stem anthropoids (such as parapithecoids, oligopithecids and propliopithecoids; Fleagle, 1980; Fleagle & Simons, 1983, 1995; Gebo & Simons, 1987; Seiffert & Simons, 2001) and extant cercopithecoids and non-suspensory platyrrhines, as indicated by the possession of a mediolaterally broad talar head, although they still retain an overall plesiomorphic appearance, exemplified by their trochlear proportions, lack of lateral flaring of the fibular facet, and proximodistally elongated talar neck (Le Gros Clark & Thomas, 1951; Harrison, 1982; Rose et al., 1992). Consequently, they are reconstructed as arboreal quadrupeds with, in some cases, moderate climbing and suspensory capabilities, resembling extant atelids in some respects (Harrison, 1982; Sarmiento, 1983; Rose, 1988, 1994; Rose et al., 1992; Alba et al., 2015; Arias-Martorell, Alba, Potau, Bello-Hellegouarch, & Pérez-Pérez, 2015; Arias-Martorell et al., 2021). Stem hominoids overall still display a very plesiomorphic talar morphology, although they already exhibit some other derived hominoid-like features (e.g., fibular facet that flares more laterally) indicating a foot better adapted for grasping supports in a greater variety of positions than earlier stem catarrhines (Conroy & Rose, 1983; Walker, 1997; Dunsworth, 2006). For instance, proconsulids (*Proconsul* and *Ekembo*), despite their vastly disparate range of BM (from *Pr. africanus* and *E. heseloni*, estimated between 9 and 15 kg, to *Pr. major*, with a body mass around 60–90 kg, comparable to a female *Gorilla*; Harrison, 1982; Rafferty, Walker, Ruff, Rose, & Andrews, 1995), are reconstructed as primarily arboreal quadrupeds that engaged in some climbing and pronograde clambering, assisted by a strong hallux adapted to powerful grasping (Walker, 1997; Ward, 2015). Our estimated locomotor percentages for KMN RU 2036 (*E. heseloni*) are consistent with this view, obtaining a locomotor repertoire with a large quadrupedal component, little (but not insignificant) climbing and clambering, and a lack of suspensory behaviors. Only the largest species, *Pr. major*, exhibits some talar features (e.g., deep groove for the flexor hallucis longus, developed lateral and medial posterior tubercles), as well as other postcranial adaptations, suggesting higher proclivity for vertical climbing and other antipronograde behaviors (De Silva, 2008). Other stem hominoids, such as the afropithecids *Eq. africanus* and *N. kerioi*, provide further evidence that a broad plesiomorphic appearance, except for some derived hominoid-like features (e.g., fibular facet that flares more laterally, mediolaterally expanded talar head), characterized ape talar morphology during the Early/Middle Miocene (McCrossin, 1994; Rose et al., 1996; Ishida et al., 2004; Nakatsukasa et al., 2012).

Compared to earlier Miocene ape and stem catarrhine tali, IPS85037 appears to be more derived towards the extant hominoid condition in features associated with greater mobility at the talocrural joint (a relatively wedged trochlea, subequal talar rims, the lack of a dorsal tubercle on the neck, a less concave articular basin for the medial tibial malleolus), subtalar joint (a slightly angled, proximodistally elongated and shallow posterior calcaneal facet), and greater prehensility (a deep groove for the m. flexor hallucis longus tendon, a developed and prominent lateral posterior tubercle, and a medially angled talar neck). However, the overall gracile appearance of IPS85037, emphasized by the relatively elongated neck and the small head, as well as for several plesiomorphic features (relatively deep trochlear groove, a L-shaped anteromedially located anterior calcaneal facet, a laterally extended articular facet for the navicular on the talar head) reveal that, independently on the acquisition of an orthograde body plan and a more forelimb-dominated locomotion, the structure of the foot remained relatively generalized during most of hominoid evolution, with only changes for increased mobility and stronger hallucal grasping but lacking clear-cut adaptations for suspensory behavior. A similar mosaic pattern is observed in the slightly younger stem pongine *Si. sivalensis*, revealing that the talocrural and subtalar joints had more limited inversion/eversion capabilities than in extant hominoids, but greater than in cercopithecoids (Pilbeam et al., 1980; Madar, 1996). In contrast, the Late Miocene stem hominoid *O. bambolii* exhibits a uniquely derived hominoid-like talar morphology among Miocene apes (Szalay & Langdon, 1986), which, together with other postcranial adaptations, has been associated with a wide array of antipronograde behaviors, including vertical climbing and suspension (Jungers, 1987; Russo & Shapiro 2013; Hammond, 2020).

The mosaic morphology of IPS85037 concurs with the pattern combining plesiomorphic and crown hominoid-like derived traits exhibited by other anatomical regions attributed to the Vallès-Penedès dryopithecines, particularly *Pierolapithecus* (Moyà-Solà et al., 2004, 2005; Almécija et al., 2009; Alba et al., 2010b; Hammond, Alba, Almécija, & Moyà-Solà, 2013; Pina, Almécija, Alba, O'Neil, & Moyà-Solà, 2014; Pina, DeMiguel, Puigvert, Marcé-Nogué, & Moyà-Solà, 2020) and *Dryopithecus* (Moyà-Solà et al., 2009a; Alba, Moyà-Solà, & Almécija, 2011; Almécija, Alba, & Moyà-Solà, 2012; Pina et al., 2019), but also to a lesser extent *Hispanopithecus* (Moyà-Solà & Köhler, 1996; Almécija et al., 2007; Alba, Almécija, Casanovas-Vilar, Méndez, & Moyà-Solà, 2012b; Tallman, Almécija, Reber, Alba, & Moyà-Solà, 2013; Susanna et al., 2014). Regardless of the exact phylogenetic position of dryopithecines, either as stem hominids (Andrews, 1992; Casanovas-Vilar et al, 2011; Alba, 2012; Alba et al., 2015; Pugh, 2022) or more closely related to pongines (Moyà-Solà &

Köhler, 1993, 1995, 1996; Agustí et al., 1996) or hominines (Begun, 2002, 2009, 2015, 2018; Begun et. al., 2012), the morphology and estimated locomotor repertoire of IPS85037 reinforce the numerous evidence (e.g., Tuttle, 1975; Larson, 1998; Alba, 2012; Almécija et al., 2021) that adaptations for suspensory locomotion and an orthograde body plan did not evolved at the same time, but rather were acquired independently in different lineages during hominoid evolution.

5. Conclusions

An isolated primate talus (IPS85037) from ACM dated to ~11.7 Ma (close to the Middle/Late Miocene boundary) is described and compared with a sample of extant anthropoids as well as the stem hominoid *Ekembo heseloni* (KMN RU 2036). Body mass estimates based on talar size (close to a female orangutan) and the possession of some derived modern hominoid features suggest that the specimen belongs to a male dryopithecine, but an attribution to genus rank is precluded by the lack of comparative material. Talar shape, quantified by means of 3DGM, indicates that IPS85037 displays a mosaic of plesiomorphic and apomorphic features relative to crown hominoids, unknown among modern anthropoids but resembling other Miocene ape tali. Compared to KMN RU 2036, IPS85037 presents several characters associated with a relatively more mobile talocrural and subtalar joints, as well as evidence of strong hallucal grasping. This is confirmed by the locomotor repertoire inferred from the covariation between talar shape and locomotor percentages, which indicate important quadrupedal and clambering/climbing components but much more restricted suspensory behaviors. Within extant species, *Alouatta seniculus* and *Pan paniscus* concur the most with this locomotor repertoire. In contrast, locomotor estimations based on KMN RU 2036 shape indicate a locomotor repertoire vastly dominated by quadrupedalism, resembling extant cercopithecoids. Both the morphology and locomotor repertoire inferred for IPS85037 are broadly consistent with previous inferences for the Middle Miocene dryopithecins *Pierolapithecus* and, to a lesser extent, *Dryopithecus* but differ from the greater emphasis on suspensory behaviors displayed by the younger hispanopithecins *Hispanopithecus*, *Danuvius*, and *Rudapithecus*.

Author contributions

Oriol Monclús-Gonzalo: Conceptualization (Equal); Formal analysis (Lead); Investigation (Lead); Methodology (Supporting); Writing - original draft (Lead); Writing - review & editing (Supporting). **Shubham Pal:** Formal analysis (Supporting); Investigation (Supporting); Writing - original draft (Supporting). **Thomas Puschel:** Methodology (Lead); Writing - review & editing (Supporting). **Alessandro Urciuoli:** Methodology (Supporting); Writing - review & editing (Supporting). **Victor Vinuesa:** Data curation (Supporting); Methodology (Supporting); **Josep Robles:** Data curation (Lead). **Sergio Almécija:** Conceptualization (Equal); Methodology (Supporting); Resources (Lead); Supervision (Supporting); Writing - review & editing (Supporting). **David M. Alba:** Conceptualization (Equal); Funding acquisition (Lead); Supervision (Lead); Writing - original draft (Supporting); Writing - review & editing (Lead).

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Data availability statement

The described original fossil is available for study from the ICP, which is a registered museums recognized by the Generalitat de Catalunya, while its digital 3D model is available from MorphoSouce with DOI pending. 3D landmark coordinates used in this study are openly available in figshare (https://figshare.com/s/fcc3e39fee03117ed06f).

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Figure captions

FIGURE 1 IPS85037, right talus of Dryopithecini indet. from ACM/C8-B*, in dorsal (A), plantar (B), lateral (C), medial (D), and distal (E) views.

FIGURE 2 Render images of the talus of Dryopithecini indet. from ACM/C8-B* (IPS85037) as compared to that of *Ekembol heseloni* (KMN RU 2036) and a selected sample of tali from extant anthropoids included in the comparative sample; from left to right, in dorsal, plantar, lateral, medial, and distal views. Scale bars equal 5 mm.

FIGURE 3 Landmark configuration utilized in this study (see Table 2 for landmark definitions). The specimen used as reference correspond to the talus of *Pan paniscus* (RMCA 27698).

FIGURE 4 Results of the between-group principal components analysis (bgPCA) as depicted by a bivariate plot of bgPC2 vs. bgPC1 (A) and bgPC3 vs. bgPC1 (B). The groups distinguished a priori are indicated by color-coded convex hulls, and each species is denoted by different symbols, as indicated in the legend. Fossil specimens (whose scores are projected a posteriori) are indicated by a cross (╳) sign (KMN RU 2036) and a plus (+)sign (IPS85037). The percentage of variance explained by each bgPC is reported within parentheses. Talar shapes associated with minimum (blue) and maximum (red) values of each bgPC axis are plotted below each scatterplot (dorsal, plantar, lateral, medial, proximal, and distal views are shown from left to right). Thin plate spline warps are based on a talus of *Pan paniscus* (RMCA 27698).

FIGURE 5 Results of the two-block partial least squares for the first (PLS1; A) and second (PLS2; B) set of linear combinations between the species-mean Procrustes-aligned coordinates quantified locomotor data. The vectors of the first (A) or second (B) PLS axis of the locomotor variables (LMPs) are plotted to the right of each scatterplot. The groups distinguished a priori are color-coded, and each species is denoted by different symbols, as indicated in the legend. Fossil specimens (whose scores are projected a posteriori) are indicated by an cross (╳) sign (KMN RU 2036) and a plus (+)sign (IPS85037). Talar shape associated and magnified 3 times with minimum (blue) and maximum (red) values of covariation are plotted below each scatterplot (dorsal, plantar, lateral, medial, proximal, and distal views are shown, from left to right). Thin plate splines warps are based on a talus of *Pan paniscus* (RMCA 27698). Abbreviations: QWR = quadrupedal walking, bounding, and running; CL = clambering, and vertical climbing; L = leaping, dropping, and hopping; S = bridging, brachiation, and suspensory locomotion; BI = bipedal walking.

FIGURE 6 Donut charts summarizing the estimated locomotor repertoires of the Dryopithecini indet (IPS85037) and *Ekembo heseloni* (KMN RU 2036), as well as representatives of the main anthropoid groups from the extant comparative sample (SI Table S6). Abbreviations: QWR = quadrupedal walking, bounding, and running; CL = clambering, and vertical climbing; L = leaping, dropping, and hopping; S = bridging, brachiation, and suspensory locomotion; BI = bipedal walking.

FIGURE 7 Results of the principal components analysis (PCA) based on locomotor variables (LMPs) estimated for the fossil specimens as summarized by a bivariate plot of the first two PCs. The groups distinguished a priori are color-coded, and each species is denoted by different symbols, as indicated in the legend. Fossil specimens (whose scores are projected a posteriori) are indicated by an ex (KMN RU 2036) and a plus sign (IPS85037). The vectors of each locomotor variable are projected as gray arrows. Abbreviations: QWR = quadrupedal walking, bounding, and running; CL = clambering and, vertical climbing; L = leaping, droppping, and hopping; S = bridging, brachiation, and suspensory locomotion; BI = bipedal walking.