Dance of the Cave Bear: Honouring the Scientific Legacy of Björn Kurtén

# Bear feet with Björn: tarsal evolution in the origin of polar bears

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Polar bears (Ursus maritimus) diverged from brown bears (U. arctos) in the last one million years. Polar bears have a strikingly different external appearance because of their white pelts and large size, but osteological differences are thought to be limited to flatter crania and altered dentition, with little difference in the postcrania despite swimming frequently and living almost entirely on icy substrates. This paper shows that polar bears have substantial differences in their tarsal form and function from other bears, including their close relatives, the brown bears. Ankle gear ratio records the major functional transition from semi-cursorial hemicyonines to the more plantigrade locomotion of crown ursines. Analysis of tarsal morphology among seven extant ursines show that the arboreal species *Helarctos malayanus*, *Melursus ursinus*, Tremarctos ornatus, U. thibetanus, and U. americanus have morphologies that permit greater movement at the transverse tarsal and lower ankle joints, especially broader and more gently curved astragalocalcaneal and sustentacular facets on the calcaneum and their articular equivalents on the astragalus, as well as broader and more gently curved navicular facets on the astragalar head. U. arctos and U. maritimus, which are strongly terrestrial, have smaller sustentacular facets and pronounced interlocking between astragalus and calcaneum at the sustentaculum. Polar bears, however, differ from brown bears in that this interlocking is less tight and thus permits more movement at the lower ankle joint. The phylogenetic comparative analysis of shape shows that the divergence in ankle morphology of the polar bear from the brown is one the most rapid bursts of tarsal evolution in ursines.

# Introduction

Just remember that's a bear there in the bunch with you,

And they just don't come no better than a bear. (Steven Fromholz 1975)

As a recently, strikingly, and perhaps incom-

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pletely diverged species, the origin and fate of the polar bear, *Ursus maritimus*, is of interest from both evolutionary and ecological perspectives. Closely related to the brown bear *Ursus arctos*, polar bears are members of the tribe Ursini that includes all extant bears except the spectacled bear *Tremarctos ornatus* and the giant panda *Ailuropoda melanoleuca* (Fig. 1). Polar bears are the



**Fig. 1**. Time-calibrated phylogeny of the bear species included in this study. Species with 3D morphometric data are indicated in bold type. Oxygen isotope proxy for global paleotemperature is from Zachos *et al.* (2001). Bear images are copyright-free clipart: *Tremarctos ornatus* from Bertuch (1824), *Helarctos malayanus* from Simons (1875), and the rest from *Wild Animals CD-ROM and Book* (Dover Electronic Clip Art 2012).

only large terrestrial predator to inhabit offshore ice shelves (Dayton et al. 1994) and their white coloration is an adaptation to that unique habitat that visibly differentiates them from their closest relative the brown or grizzly bear, U. arctos. They are the largest and most carnivorous of living bears, specializing primarily on the ringed seal, Pusa hispida, which they attack while the seals are hauled out on ice floes or by pursuit into the water (DeMaster & Stirling 1981). Polar bears hunt throughout the year except when ice is absent or during pregnancy, feeding almost exclusively on blubber, which they store in fat reserves to sustain them when prey is scarce (Rode & Stirling 2017). Polar bears have been known to swim for distances greater than 65 km and for durations longer than 48 hours using "dog-paddle" strokes of their large forearms and paws (DeMaster & Stirling

1981, Fish 1992, Chester 2016, Rode & Stirling 2017). The divergence between *U. maritimus* and *U. arctos* occurred sometime after the onset of Arctic ice, which began appearing as early as 44–41 Ma but became extensive only after 14 Ma and was persistent throughout the year only since about 4 Ma (St. John 2008, Stein 2019). Today the polar bear is confined to the high Arctic, but extralimital fossil occurrences demonstrate that its range expanded southward during Quaternary glacial advances (Erdbrink 1953, Kurtén 1964). In the past three decades anthropogenic climate change has already reduced summer sea ice and is likely to produce ice-free polar seas as early as 2030 (Stein 2019).

Kurtén was among the first to quantify how polar bears differ morphologically from their close relatives the brown bears and to confirm the recent timing of their divergence (Kurtén 1958, 1964, 1968, Kurtén & Anderson 1980). Although long recognized as a distinctively large white bear, it was not until the 20th century that serious consideration of the polar bear's relationships to other bears began (see review in Erdbrink 1953). Some authors argued early on that polar bears are very closely related to brown bears because of their propensity to hybridize (e.g., Trouessart 1916, Thenius 1953), whereas other authors argued given dental characteristics and fossil evidence that polar bears diverged as early as the Pliocene as a parallel lineage descended from Ursus etruscus (e.g., Airaghi 1922). Kurtén, one of the early paleontological contributors to the modern evolutionary synthesis, based his studies on population-thinking, statistical analysis, and consideration of ontogenetic development, growth allometry, and the fossil record (e.g., Kurtén 1953, 1955, 1967). He showed that, while extant polar bears have proportionally smaller carnassials and narrower skulls for their size, the proportions of these structures in Late Quaternary specimens approach the allometric trend of U. arctos (Kurtén 1964). In the same study he also showed that the only demonstrable polar bear fossils are Holocene in age except for a massive ulna found in the Thames terraces at Kew Bridge in London, from deposits which are now known to be about 86-72 ka (Current & Jacobi 2011, Stevens & Reade 2021). Based on these observations, Kurtén concluded that polar bears originated in the last 120 ka, since the end of the last interglacial (Kurtén 1964).

Subsequent paleontological finds have supported the interpretation that polar bears originated since the last interglacial, the oldest putative fossil now being a 130-110 ka mandible from Svalbard (Ingólfsson & Wiig 2009). Genomic analyses have complicated the picture, however, because molecular clock estimates suggest a much older divergence between 920-620 ka (Kutschera et al. 2014, Kumar et al. 2017). Genomic studies show that hybridization between bear species is not just common in captive settings, but that natural gene flow between lineages has occurred at several times and places during the phylogenetic history of Ursidae, including between brown and polar bears. Extant polar bear populations have shallow intraspecific divergences of only about 100 ka, similar to paleontological estimates for the species' origin, and are most closely related to brown bear populations in northern Europe (Kumar *et al.* 2017). These two lines of evidence suggest that polar bears have a complicated history of divergence from brown bears in which episodes of differentiation have been interspersed with hybridization as sea ice waxed and waned over the last 1 Ma.

Despite their impressive ability to swim and navigate icy substrates, Kurtén (1964) suggested that polar bears were not distinctive from terrestrial brown bears in their locomotor morphology. His assertion was not based on detailed comparisons of postcrania, however, and the present paper will test his hypothesis using ankle morphology.

Most living bears are scansorial or semi-arboreal, including the giant panda *Ailuropoda melanoleuca*, the spectacled bear *Tremarctos ornatus*, the sun bear *Helarctos malayanus*, the Asian black bear *Ursus thibetanus*, sloth bear *Melursus ursinus*, and the American black bear *U. americanus* (Herrero 1972, Laurie & Seidensticker 1977, Chorn & Hoffmann 1978, Fitzgerald & Krausman 2002). Bears that climb regularly tend to have longer claws, larger angles of rotation in pronation and supination in the forelimb, fleshier extensor muscles in the hindlimb, and greater ability to evert the hindfoot (Davis 1964, Herrero 1972, Sasaki *et al.* 2005, Amaike *et al.* 2021).

In contrast, brown bears and polar bears are more terrestrial. Most adult brown bears lose the ability to climb trees as they reach adult size (Herrero 1972). Like brown bears, polar bears do not climb, but the two species have distinctively different locomotor repertoires. Polar bears walk on their icy substrate with swaying hips and fully extended limbs. They run with a transverse gallop that maintains a midline center of gravity, their feet have extensive hair-covered areas between the fleshy pads that increase the area of contact with the ice, and they have minimal ability to pronate and supinate their forelimbs compared to other ursids (Renous et al. 1998, Amaike et al. 2021). Polar bears also have proportionally flatter heads, larger forefeet, and denser limb bones than other bears (DeMaster & Stirling 1981, Pagono et al. 2019).

For convenience, I refer in this paper to the extant *T. ornatus*, *H. malayanaus*, *M. ursinus*,

*U. americanus*, and *U. thibetanus* as being more "arboreal" because they spend appreciable time in trees throughout their life and often sleep and feed there, and I refer to *U. arctos* and *U. maritimus* as being more "terrestrial" because they rarely or never ascend trees as adults but these differences are one of degree and all bears are probably capable of climbing, at least when they are small.

Crown-group bears are likely to have had terrestrial, possibly cursorial ancestors. Despite the widespread tree-use among living bears, this locomotor specialization is likely independently derived in most of their lineages because early ailuropodines like *Agriotherium* and *Huracan*, tremarctines like *Arctodus*, and outgroup Hemicyoninae had long-distance walking or cursorial specializations (Hunt 1998, Matheus 2003, Figueirido *et al.* 2010, Meloro & de Oliveira 2019, Jiangzuo *et al.* 2023).

In this paper, I analyze the form and function of the bear tarsus to determine whether polar bears are substantially diverged in locomotor morphology from brown bears. To do that I first compare morphologies to identify similarities and differences associated with locomotor function and put those changes into an evolutionary phylogenetic context in which to assess the divergence of the polar bear. Davis (1964) argued that comparative anatomy must play a substantial role in the study of evolution because it is the only line of evidence to study phenotypic adaptations to new environments. This study uses comparative morphology to evaluate whether polar bears have diverged in tarsal morphology from brown bears, and if so whether those differences are related to specializations for locomotion in their unique Arctic environment. Linear measurements of the calcaneum of extant and extinct ursids, including the hemicyonines, are used to evaluate broad phylogenetic patterns of body size and hindfoot locomotor mechanics. Three-dimensional (3D) scans of the calcaneum and astragalus of seven extant species — Helarctos malayanus, Melursus ursinus, Tremarctos ornatus, Ursus thibetanus, U. americanus, U. arctos, and U. maritimus - are used for a more detailed phylogenetic assessment of the form and function of the tarsus, including its shape and mobility. Comparative morphology and geometric morphometric analysis are assessed in a phylogenetic context to determine the extent to which *U. maritimus* and *U. arctos* are differentiated in tarsal form and function given their relatively recent common ancestry and iterative history of hybridization.

### Material and methods

Institutional abbreviations: AMNH = American Museum of Natural History (vertebrate paleontology collection), FMNH = Field Museum of Natural History (mammalogy collection), INSM = Indiana State Museum (vertebrate paleontology collection), MU = University of Missouri Zooarchaeology Collection, OMNH = Oklahoma Museum of Natural History (vertebrate paleontology collection), UCMP = University of California Museum of Paleontology (vertebrate paleontology collection), UF = University of Florida Natural History Museum (vertebrate paleontology collection), UT = University of Texas (vertebrate paleontology collection), WRAZL = Indiana University William R. Adams Zooarchaeology Collection.

Calcaneal measurements were collected from 40 bears representing 8 extant and 4 extinct species with Mitutoyo digital calipers (Appendix). The maximum length and the length of the distance between the anterior margin of the sustentacular process at its base and the proximal end of the calcaneal tuber were measured and the calcaneal gear ratio (max length/sustentacular length) was calculated following Polly (2010) (Fig. 2A). For each species, these variables were averaged across the individuals in the sample and care was taken to include both males and females in the samples where possible to minimize intraspecific variation and sexual dimorphism (see Appendix for sample sizes and sex information). Calcaneal length, as with any uncorrected osteological measurement, is generally correlated with body size and readers should note that evolution of this variable is essentially tracking size and is shown simply to provide a context for interpreting the gear ratio (see analysis below). The gear ratio, on the other hand, is a dimensionless index of the mechanical efficiency of hind foot extension. It is functionally linked to

body size (larger species tend to have lower gear ratios), scansoriality and fossoriality (lower gear ratios provide more strength for lifting the body or scratch digging with the hind foot), and with the degree of digitigrady when compared across Carnivora as a whole (plantigrade ursids tend to have lower gear ratios than digitigrade canids and felids, *see* for example Polly 2010, Polly & Sarwar 2014).

Three-dimensional (3D) surface scans of the calcaneum and astragalus were assembled for the eight extant ursini. Five species were scanned de novo for this study, four using a Medit i600 structured light scanner (Ursus maritimus, WRAZL 9710081; U. arctos, WRAZL 1710009; U. thibetanus, WRAZL 0110011) a fifth with a NextEngine laser scanner (Tremarctos ornatus, FMNH 142010). Scans of the other three species were provided by Alexa Wimberly and Graham Slater of University of Chicago from one of their ongoing projects (U. americanus, FMNH 18865; Helarctos malayanus; Melursus ursinus, FMNH 27441). The resolution of the meshes was standardized by downsampling them to approximately 100 000 vertices while retaining their original size using Slicer3D ver. 5.6.1 (Fedorov et al. 2012).

To study allometry and relationships between the sizes of tarsal facets, the volume (mm<sup>3</sup>) and surface area (mm<sup>2</sup>) of each bone were calculated from the 3D meshes using MeshLab ver. 2023.12 (Cignoni *et al.* 2008). Surface areas (mm<sup>2</sup>) of the following joint facets were also calculated using MeshLab (Fig. 2B–H): the cuboid facet, sustentacular facet, and astragalocalcaneal facet (calcaneum) and the navicular facet, trochlear facet, calcaneoastragalar facet, sustentagular facet, and cuboid facet (astragalus).

The allometric relationship of body size to tarsal size and gear ratio was assessed with linear regression. Body mass data were assembled from the literature and the mid-point between the largest and smallest reported sizes, which should approximate a median body mass, was used to represent each of the seven extant species. Data were linearized for regression by applying ln-transformation and by cubing calcaneum length to have equal dimensionality as the other variables (LaBarbera 1989). Because gear ratio is dimensionless it was not transformed. Sig-



Fig. 2. Tarsal morphology and terminology. (A) Overview of the location and function of the astragalus (blue) and calcaneum (orange) in a diagrammatic left bear foot in medial view. Maximum length and sustentacular (sust.) length are the two linear caliper measurements used to calculate gear ratio. Calcaneum of *Ursus maritimus* (WRAZL 9710081) in (B) dorsal, (C) distal, and (D) proximal views. Astragalus of the same specimens in (E) dorsal, (F) plantar, (G) distal, and (H) proximal views. Blue dots and codes show the endpoint locations of semilandmark curves. Abbreviations: acf = astragalocalcaneal facet, caf = calcaneoastragalar facet, cf = cuboid facet, nf = navicular facet, sf = sustentacular facet, tf = trochlear facet.

nificance of the relationship between the tarsal variables and body size was assessed with ordinary least-squares linear regression and a Pearson product-moment correlation (*R*). These calculations were performed with *Mathematica* ver. 13.3 (Wolfram Research, Inc.).

Tarsal facet sizes are expected to covary based on the types of joint movement (Szalay 1977, 1994, Jenkins & McClearn 1984, Lewis 1989, Polly 2006). To assess the pattern in bears, a matrix of Pearson product-moment correlations (R) was calculated between facets in the calcaneum (cuboid facet, sustentacular facet, and astragalocalcaneal facet) and astragalus (navicular facet, sustentacular facet, calcaneoastragalar facet, cuboid facet, and troclear facet). To remove the effect of body size from these correlations, the proportional size of each facet was calculated by dividing its surface area by the entire surface area of its bone. The sample size for all these correlations is seven. Because the purpose is simply to see which relationships are positive and which are negative, no statistical analysis was performed to determine whether they are different from 0 or from 1. The pattern of correlation is presented graphically in the contoured fashion of Kurtén's developmental field diagrams (Kurtén 1967). These calculations were also performed with Mathematica ver. 13.3 (Wolfram Research, Inc.).

For shape analysis, equally spaced semilandmarks (Bookstein 1997) were placed around the perimeters of the same 8 joint facets as well as the muscle attachment scar of the gastrocnemius at the proximal end of the calcaneal tuber using Slicer3D and SlicerMorph (Rolfe et al. 2021). Each outline consisted of equally spaced semilandmarks tied at homologous points after MacLeod (1999) as follows. The outline of the calcaneal cuboid facet was broken into two segments of 10 equally spaced semilandmarks each at its most lateral and most medial points (landmarks c1 and c2; Fig 2C). The calcaneal sustentacular facet curve was broken into three segments of 10 equally spaced semilandmarks each, the first running from the distomedial-most point to the proximal-most point (landmarks s1 and s2; Fig. 2B) and then from the proximal-most point to the distolateral-most point (landmarks s2 and s3). The astragalocalcaneal facet outline was broken at the proximal-most and distolateral-most points with 10 equally spaced semilandmarks in each segment (landmarks ac1 and ac2; Fig. 2B). The outline of the gastrocnemius scar was comprised of 20 equally spaced semilandmarks pinned at the dorsal midline. The calcaneum thus had a total of 80 equally spaced 3D semilandmarks. The outline of the navicular facet on the astragalus was pinned at the most lateral and most medial points with 10 equally spaced landmarks in each segment (landmarks n1 and n2; Fig. 2G). The astragalar sustentacular facet outline was broken at the distomedial-most and proximal-most points with 10 semilandmarks in each segment (landmarks sf1 and sf2; Fig. 2F). The calcaneoastragalar facet outline was broken and the distal-most and proximal-most points with 10 semilandmarks in each section (landmarks ca1 and ca2; Fig. 2F). The astragalar cuboid facet outline was bounded with 10 semilandmarks pinned at the medial-most point (landmark c1; Fig. 2F). Finally, the trochlear facet was outlined following the crests of the trochlear ridges and the proximal and distal synovial capsule margins pinned at the end of each ridge with 10 equally spaced semilandmarks along each ridge, 8 along the proximal margin, and 6 along the distal margin (landmarks t1-t4; Fig. 2E). The astragalus was thus given a total of 108 semilandmarks. Spacing of semilandmarks was done with Morphometrics for Mathematica ver. 13 (https:// doi.org/10.5281/zenodo.11288554).

For each bone, semilandmarks were Procrustes superimposed (Rohlf & Slice 1990) and then projected into a morphospace using a covariance-based principal component analysis (PCA), the scores of which serve as shape variables for downstream quantitative analyses (Dryden & Mardia 1998). A phylogenetic tree was projected into the shape space to create a "phylomorphospace" that shows trajectories in shape evolution for each branch based on Brownian-motion reconstructions of the ancestral shapes lying at each node (Rohlf 2002). All morphometric analyses and visualizations were done in *Mathematica* ver. 13.3 (Wolfram Research, Inc.) and the *Morphometrics for Mathematica* package.

Phylogenetic comparative methods were used to create the phylomorphospace described above and to visualize evolution of calcaneal traits and shape. A phylogenetic tree was compiled from Trajano and Ferrarezzi (1995), Ginsburg and Morales (1998), Hailer *et al.* (2012), Kutschera et al. (2014), Mitchell et al. (2016), Kumar et al. (2017), Wang et al. (2017), and Jiangzuo et al. (2023) and time calibrated using the same sources. Traits were mapped onto the phylogenetic tree using a Brownian motion model of evolution (Martins & Hansen 1997). Univariate versions of Pagel's lambda ( $\lambda$ ) and Blomberg's kappa (K) were estimated for the calcaneal measurement traits (Pagel 1993, Blomberg et al. 2003) and the multivariate extension  $K_{multi}$  was used for the geometric morphometric data (Adams 2014). K is an index of the proportion of covariance structure in the trait explained by the covariance structure of the phylogenetic tree and it ranges from 0 when there is no phylogenetic structure to 1 or higher when the structure is fully consistent with a Brownian motion model of evolution (Blomberg *et al.* 2003).  $\lambda$  is a scaling index for how much the internal branches of the tree need to be proportionally reduced for the data to fit a Brownian motion model, and like K it can range from 0 when there is no phylogenetic structure to 1 or higher when the data are fully consistent with the phylogenetic topology (Pagel 1993). All phylogenetic comparative analyses were conducted with the package Phylogenetics for Morphometrics ver. 6.9 (https:// doi.org/10.5281/zenodo.10447177).

# Results

# Evolution of locomotor proportions in Ursidae

Tarsal size has a strong relationship to body size in bears. The relationship between calca-

neum length, calcaneum volume, and astragalar volume is statistically significant and the variables all have strong correlations with body size (Table 1 and Fig. 3). *Tremarctos ornatus* has proportionally small tarsals relative to body size and *Melursus ursinus* has large ones, but overall, the size of the tarsal scales with body size at the intraspecific scale of this study.

Calcaneum length, which serves as the numerator of the calcaneum gear ratio, and which changes as a function of body size, has been quite variable in the phylogenetic diversification of ursids (Fig. 4A). Tremarctos ornatus, the Andean bear, is one of the smallest species in the analysis, but its close relative Arctodus simus, an extinct short-faced tremarctine bear from North America, is the largest bear that ever lived. While it is the largest extant bear, the polar bear Ursus maritimus is notably smaller than either Arctodus or the extinct North American ailuropodine Huracan schneideri. Ursus arctos and U. maritimus are both large compared to other crown ursines, and the latter shows another burst of enlargement relative to its sibling species. Because of the widespread homoplasy in size, the phylogenetic structure of calcaneum length is poor (Pagel's  $\lambda = 0$  and Blomberg's K =0.15).

In contrast, the gear ratio of foot extension has strong phylogenetic structure (Fig. 4B). The gear ratio describes the lever moment of extension around the center of rotation of tibio-tarsal joint, represented by the position of the sustentacular facet relative to the total length of the calcaneum (Polly 2008, 2010). The gear ratio index is normally high when the lever

Table 1. Tarsal sizes and mid-point body masses for seven extant bear species.

Species	Mean calcaneum length (mm)	Gear ratio	Calcaneum volume (mm <sup>3</sup> )	Astragalus volume (mm³)	Mid body mass (kg)	Body mass source
Helarctos malayanus	53.8	1.11	11268	7477	46	Fitzgerald & Krausman (2002)
Melursus ursinus	71.0	1.08	22767	15880	58	Garshelis et al. (1999)
Tremarctos ornatus	56.0	1.19	9825	8011	118	Garcia-Rangel (2012)
Ursus americanus	70.0	1.14	18549	11071	68	Larivière (2001)
Ursus arctos	83.7	1.09	55703	31264	222	Pasitschniak-Arts (1993)
Ursus maritimus	97.0	1.11	79713	47547	400	Rode & Sterling (2017)
Ursus thibetanus	67.2	1.13	23674	14663	107	Than <i>et al.</i> (1998)



**Fig. 3.** Correlation of (**A**) calcaneum length, (**B**) calcaneum volume, (**C**) astragalus volume, and (**D**) calcaneum gear ratio with midpoint body mass; R and p are the correlation coefficent and probability, respectively, for the regression.

mechanics of this joint have high efficiency, such as in digitigrade cursors where the ratio is usually greater than 1.20. The ratio is low when extension has mechanical advantage, such as in plantigrade walkers, climbers, or scratch diggers where it is often less than 1.15 (Polly 2010,

2020, Polly et al. 2017). Gear ratio is highest in the stem hemicyonine bears Phoberocyon johnhenryi (ratio = 1.24) and Hemicyon barbouri (ratio = 1.19), which were generally mobile, digitigrade canid-like carnivores (Hunt 1998). Crown ursines have lower gear ratios in keeping with their plantigrade locomotor morphology, among the lowest of any carnivoran (Polly et al. 2017). Interestingly, Tremarctos ornatus has what in this analysis looks like a secondarily high gear ratio (ratio = 1.19) compared to its sibling taxon Arctodus simus, which has the lowest gear ratio of any of the bears (ratio = 1.08). The higher gear ratio of Tremarctos is not related to having a more digitigrade stance, however. Unlike in the hemicyonines and Huracan whose high ratio comes from the sustentacular process being positioned relatively proximally along the length of the calcaneum, the high ratio in Tremarctos is a by-product of having a distally positioned but proximodistally narrow sustentacular process that is linked to its more mobile mid-tarsal joint and associated with a specialized tree-climbing morphology. The narrowness of the sustentacular process gives Tremarctos a proportionally smaller denominator in the gear ratio, thus making the ratio higher than in other bears, even the more terrestrial ones like Ursus arctos and U. maritimus, but not because it is particularly fleet footed.

#### Morphological comparisons

Morphological differences are readily apparent among the seven extant species (Fig. 5). To understand the features described here and their functional interpretation, readers may wish to refer to general descriptions of tarsal joints and their movements provided by Szalay (1977, 1994), Jenkins and McClearn (1984), Sarrafian (1989, 1993), Lewis (1989), Huson (1991), Hall and Shereff (1993), Polly (2007), and Dorn-Lange *et al.* (2008).

#### Upper ankle joint

The axis of rotation at the upper ankle joint between astragalus and tibia (represented by



Fig. 4. Phylogenetic patterns in the evolution of (A) calcaneum length and (B) calcaneum gear ratio. Scale bar is color coded with yellow representing the reconstructed ancestral value of each trait, red the maximum value, and blue the minimum value.

the line and circle on the astragalus) is almost perfectly perpendicular to the long axis of the calcaneum (represented by the line through the calcaneum) in the terrestrial U. arctos (Fig. 5J), whereas the angle is oblique in the more arboreal species (Fig. 5P, V, Bb, Hh, Nn), which is likely related to partial eversion and inversion of the foot with extreme flexion and extension (Sasaki et al. 2005). Note the obliquity of rotation is least in U. americanus among the more arboreal taxa. The axis of rotation is also somewhat oblique in the polar U. maritimus (Fig. 5D), which may be related to the implied eversion and inversion of the foot necessary to maintain the swaying hip walking gait in which the feet are placed in front of one another described by Renous et al. (1998).

Movement at the upper ankle joint is more strongly constrained to a plane by tall trochlear ridges in terrestrial *Ursus arctos* (Fig. 5I) compared to the lower ridges in the highly arboreal *U. thibetanus* (Fig. 5U), *Tremarctos ornatus* (Fig. 5Aa), and *Melursus ursinus* (Fig. 5Mm), and to a lesser degree in *U. americanus* (Fig. 5O). Low ridges on the trochlea are often associated with increased ability to invert and evert the foot. The polar bear has ridges that are intermediate in their height between *U*. *arctos* and the more arboreal taxa (Fig. 5C) that may also be related to its peculiar walking gait, but it also has a proportionally broader trochlea and upper ankle joint that may be associated with the increased stability on ice. Interestingly, the trochlear ridges are very high in *Helarctos malayanus* even though it has arboreal habits (Fig. 5Gg).

#### Lower ankle joint

The structure of the tarsal bones suggests considerable variety among these seven species in the degree of movement possible at the lower ankle joint (equivalent to the subtalar joint in human medical literature). Movement at this joint takes the form of a complex rotation in which the calcaneoastragalar facet of the astragalus slides across the astragalocalcaneal facet of the calcaneum and the sustentacular facet of the astragalus slides across and rotates around the sustentacular facet of the calcaneum (see general ankle references cited above).

The calcaneoastragalar facet of the astragalus wraps tightly around its counterpart on the calcaneum in the two terrestrial species *Ursus arctos* (Fig. 5G) and *U. maritimus* (Fig. 5A),



Fig. 5. Comparisons of the calcaneum (orange) and astragalus (blue) of (A–F) Ursus maritimus, (G–L) U. arctos, (M–R) U. americanus, (S–X) U. thibetanus, (Y–Dd) Tremarctos ornatus, (Ee–Jj) Helarctos malayanus, and (Kk–Pp) Melursus ursinus. The diameter of the circle is 56 mm in all panels as scale.

with a nearly 90° angle between the proximal and dorso-distal parts of the articulation. By comparison, the articulation is much broader and gently curved in the more arboreal *U. americanus* (Fig. 5M), *U. thibetanus* (Fig. 5S), *Tremarctos ornatus* (Fig. 5Y), and *Melursus ursinus* (Fig. 5Kk), although the relationship is more tightly curved in *Helarctos malayanus*, similar to the more terrestrial species (Fig. 5Ee). The tight fit in *U. arctos* and *U. maritimus* leaves little room for movement of the astragalus at this joint (Fig 5B, H) but ample room in the arboreal species (Fig. 5N, T, Z). This relationship can also be seen in the shape and size of the sustentacular facet on the calcaneum in dorsal view, which is small, circular, and strongly constricted

in *U. arctos* (Fig. 5K), but larger and more longitudinal in the other species. In this latter aspect, *H. malayanus* is like the other arboreal species (Fig. 5Ff) suggesting that even though the sustentacular facets have an angled occlusion, there is still more intertarsal movement in this species than in the two terrestrial ones.

The relative size and curvature of the astragalocalcaneal facet on the calcaneus also differs among the species. This facet is short and tightly curved in both *Ursus maritimus* and *U. arctos* (Fig. 5E, K) and less so in the arboreal species, especially *Tremarctos ornatus, Helarctos malayanus*, and *Melursus ursinus* where it forms a very large gently curved surface (Fig. 5Cc, Ii, Oo).

Collectively these features suggest considerable mobility in the lower ankle joint in Tremarctos ornatus and Melursus ursinus, intermediate mobility in Ursus americanus and U. thibetanus, and a quite constrained condition in U. arctos. The condition of U. maritimus is different than the rest in that it appears to be somewhat constrained by the highly angular articulation at the sustentacular process, but with some flexibility as indicated by the elongate sustentacular facet. Interestingly, the configuration in Helarctos malayanus is quite unique in containing a combination of features shared with both the more arboreal and terrestrial taxa. Future study of the functional morphology of the ankle in this species would be of interest.

#### The transverse tarsal joint

The transverse tarsal joint between the distal facets of the astragalus and calcaneum and the proximal facets of the cuboid and navicular is also important for hindfoot inversion movements. In bears, the cuboid facet on the astragalar head and the shape of the navicular facet are likely indicators of mobility at this joint. In *Ursus arctos*, the cuboid facet only barely projects past the distal calcaneum when the astragalus is in locked articulation (Fig. 5L) and the distal face of the navicular facet is much flatter than in the other species (Fig. 5J) suggesting that the transverse tarsal joint has less ability to slide than in the other taxa. By comparison, the more arboreal taxa have a large, curved cuboid

facet that projects well beyond the distal end of the calcaneum (Fig. 5R, X, Dd, Pp) and their navicular facets are broad and curved (Fig. 5P, V, Bb, Hh, Nn). The polar bear also has a comparatively large, curved cuboid facet (Fig. 5F) and somewhat curved navicular facet (Fig. 5D), suggesting more movement at the transverse tarsal joint than its close relative the brown bear, perhaps facilitating its peculiar gait or swimming locomotion.

# Correlation and relative size of joint facets

The facets of the astragalus and calcaneum guide and constrain movements at the upper and lower ankle joints and at the transverse tarsal joint. The movements at these joints constrain movements of the hindfoot and limb and therefore relative performance in different parts of an animal's locomotor repertoire. Because the components of the ankle interact together, we expect them to covary in ways that are directly related to patterns of joint mobility. Generally, joints with greater mobility have asymmetrically sized surfaces between their occluding facets, the difference in size between the ball of the humerus and the glenoid facet in the human shoulder joint being an extreme example (MacConaill 1946a, 1946b, 1946c, Szalay 1994).

The surface areas of the facets of the calcaneum and astragalus (mm<sup>2</sup>) in the seven bears are reported in Tables 2 and 3 along with the total surface area (mm<sup>2</sup>) and volume (mm<sup>3</sup>) of each bone. In general, the areas of the facets correlate with overall size of the bones and of the animals. Their relative sizes, however, differ in systematic ways, as do the correlations among them. To analyze these patterns, the area of each facet was divided by the total area of the corresponding bone to give a proportional size. Figure 6A shows a correlation matrix of the standardized facet sizes between the calcaneum and astragalus drawn in the contoured fashion of Kurtén's developmental field diagrams (Kurtén 1967).

The sizes of the cuboid facet of the calcaneum and the navicular facet of the astragalus, both of which contribute to the transverse tarsal joint, are inversely correlated (R = -0.22). The sustentacular facets of both bones have a negative correlation with the cuboid facet of the calcaneum (R = -0.41) and the navicular facet of the astragalus (R = -0.39), indicating that as the sustentacular facet gets larger, the transverse tarsal facets get smaller. The cuboid facet of the astragalus is negatively correlated with the cuboid and sustentacular facets of the calcaneum (R = -0.66 and -0.60, respectively) but positively correlated with the astragalocalcaneal facet (R = 0.18), which is likely related to movement at the lower ankle joint along the sustentacular facets on inversion and eversion movements at the navicular and cuboid facets of the transverse tarsal joint (Jenkins & McLearn 1984). The two sustentacular facets articulate but the tendency is for them to be different size in mobile joints, like those of the more arboreal bears, and more similar in size in stable joints like those of the more terrestrial bears so this correlation is near zero (R = 0.09).

Interestingly, the astragalocalcaneal facet on the calcaneum, which is also involved in movement at the lower ankle joint, is inversely correlated with size to the navicular facet on the astragalus at the transverse tarsal joint (R =-0.46). The contrast between terrestrial Ursus *maritimus* and arboreal *Tremarctos ornatus* drive this relationship. While broad, the navicular head in Tremarctos is shallow resulting in a smaller facet surface (Fig. 5Aa) whereas the form of the navicular facet in the polar bear is deeper (Fig. 5C). Conversely, the astragalocalcaneal facet in Tremarctos is proportionally larger than in any of the bears (Fig. 5Cc) whereas the polar bear's is the smallest (Fig. 5E). The functional significance of these morphologies requires further study, but it seems likely that the lower ankle joint of Tremarctos experiences considerable movement that interacts with substantial inversion and eversion at the transverse tarsal joint (Jenkins & McLean 1984), whereas the ankles of all four Ursus species are probably more rigidly constrained, even the two arboreal species.

The ternary plots in Fig. 6 show the sizes on each bone of the three major facets of the lower

	Cuboid facet	Sustentacular facet	Astragalocalcaneal facet	Total surface area (mm²)	Total volume (mm <sup>3</sup> )
Helarctos malayanus	145.6	153.0	194.5	3723	11268
Melursus ursinus	398.1	302.3	294.4	6020	22767
Tremarctos ornatus	126.6	145.9	253.2	3524	9825
Ursus americanus	261.5	206.4	239.5	5054	18549
Ursus arctos	470.4	464.1	426.6	11134	55703
Ursus maritimus	553.7	618.6	629.4	14073	79713
Ursus thibetanus	215.0	224.5	335.5	6149	23674

Table 2. Surface areas (mm<sup>2</sup>) of facets, and total surface area (mm<sup>2</sup>) and volume (mm<sup>3</sup>) of the calcaneum.

Table 3. Surface areas (mm<sup>2</sup>) of facets and total surface area (mm<sup>2</sup>) and volume (mm<sup>3</sup>) of the astragalus.

	Navicular facet	Sustentacular facet	Calcaneoastragalar facet	Cuboid facet	Trochlear facet	Total surface area (mm²)	Total volume (mm <sup>3</sup> )
Helarctos malayanus	264.6	166.1	232.6	26.2	574.2	2775	7477
Melursus ursinus	367.3	231.9	372.3	67.9	818.2	4380	15880
Tremarctos ornatus	281.5	177.3	232.7	74.2	607.4	2800	8011
Ursus americanus	449.5	182.5	265.3	46.8	748.3	3396	11071
Ursus arctos	914.2	399.3	562.3	162.0	1463.4	7281	31264
Ursus maritimus	1091.2	707.3	679.2	135.6	2131.4	9247	47547
Ursus thibetanus	415.6	214.5	372.9	70.7	884.4	4025	14663



**Fig. 6.** (**A**) Proportional size relationships among the facets of the calcaneum and astragalus. Correlations in proportional size (facet area/total surface area) between the three facets of the calcaneum in rows and the five facets of the astragalus in columns. Correlation coefficients (R) are on a contoured and colored background that shows the patterns of correlation. Ternary plots of the (**B**) calcaneum and (**C**) astragalus show the proportional sizes of the three major facets of each bone.

ankle joint and transverse tarsal joint for the seven species. The calcanea of the more arboreal species are similar in having proportionally smaller cuboid and sustentacular facets and larger astragalar facets than the two terrestrial species (Fig. 6A). Increased translation of the astragalus along an enlarged astragalocalcaneal facet and pivoting along a smaller sustentacular facet in the arboreal taxa is correlated with a smaller facet on the calcaneum for the cuboid bone to move at the transverse tarsal joint as is generally expected in more mobile joints (Mac-Conaill 1946a, 1946b, 1946c, Szalay 1994). The polar bear is similar to the brown bear in the calcaneal proportions but is slightly more like the arboreal taxa in having a larger astragalo-

calcaneal facet relative to cuboid. The arboreal taxa are also similar to each other in the proportions of the astragalar facets, with larger calcaneoastragalar facets and smaller sustentacular and navicular facets (Fig. 6B). Ursus maritimus departs substantially from U. arctos in its astragalar facet proportions with smaller navicular and calcaneoastragalar facets and a larger sustentacular facet which would allow for greater movement at the lower ankle joint, but not in the same way as the arboreal taxa where the lower ankle joint movement is a pivot that translates into rotation at the transverse tarsal joint.

# Shape analysis of the calcaneum and astragalus

Geometric morphometric shape of the two bones was analyzed based on semilandmark outlines of the facets and the insertion area of the gastrocnemius on the calcaneum (Fig. 7).

The more arboreal species are widely dispersed in shape space. This pattern is partly phylogenetic since the arboreal species shared their last common ancestor about 6 million years ago. Each of these three species has its own peculiar shape: the calcaneum of U. americanus is comparatively short relative to the length of the astragalus, which changes the positions of all of the facets relative to each other in both bones (Fig. 5M, P); the calcaneal tuber of U. thibetanus and the insertion of the gastrocnemius are relatively large (Fig. 5S, V); in Tremarctos the shapes of the cuboid facet and astragalocalcaneal facets on the calcaneum (Fig. 5Aa, Cc) and the trochlear and navicular facets on the astragalus (Fig. 5Aa) are quite distinctive. Helarctos malayanus has an unusual combination of sharply curved but slender and medially pointed sustentacular facet and a medially oriented astragalocalcaneal facet (Fig. 5Ii) and Melursus ursinus has a distinctively broad distal sustentacular facet and broadly curved astragalocalcaneal facet like T. ornatus (Fig. 5Oo).

The shapes of both calcaneum (Fig. 7A) and astragalus (Fig. 7B) in the two terrestrial species *Ursus arctos* and *U. maritimus* both lie at the same end of the first principal component of the morphospace, but they are also strongly diver-

gent from each other on PCs 2 & 3 given the recency of their common ancestry. Their differences are driven by the relative sizes and shapes of the astragalocalcaneal and sustentacular facets on the calcaneum (Fig. 5E, K) and the trochlear and navicular facets on the astragalus (Fig. 5C, D, I, J).

Because the phylogenetic time distances between these bears differs considerably, it is interesting to ask whether any of them stand out as being more different than expected for their divergence time. The phylogenetic trees in Fig. 4 show the amount of shape evolution along each branch scaled by branch length, with yellow being the most differentiated and blue being the least differentiated given the length of the subtending branch. For both calcaneum (Fig. 5C) and astragalus (Fig. 5D), the divergence between polar bear and brown bear stands out as high given the recency of their common ancestry. The shapes of Helarctos malayanus and Melursus ursinus also stand out as highly diverged from each other given their recency of common ancestry for the reasons discussed above.

# Discussion

Environmental transformations have caused major clade turnovers in bear evolution. Crown ursids began to diversify in the Late Miocene as global temperature began its downturn after the Miocene climatic optimum (Fig. 1). The ursines were generally largish, plantigrade or semi-digitigrade terrestrial to semi-arboreal animals. Earlier bears were very different. The hemicyonines were doglike, highly mobile, semi-cursorial animals that spread across Eurasia and North America by the mid-Miocene at the height of the climatic optimum (Hunt 1998, Van Valkenburgh 1999). Tarsal morphology records this functional turnover in which there is a sharp decrease in calcaneal gear ratio between hemicyonine and ursine taxa (Fig. 4).

Ursines took to the trees during their Late Cenozoic radiation seemingly independently in several lineages. The earliest pandas, for example, were more terrestrial and mobile than the living giant panda (Jiangzuo *et al.* 2023), which is also seen here in the higher ankle gear ratio in



**Fig. 7.** Geometric morphometric shape analysis of the calcaneum and astragalus. The phylomorphospaces show the differences in calcaneal (**A**) and astragalar (**B**) shape for the first three principal components of shape space. Relative rates of shape change along individual branches of the tree are shown for the calcaneum (**C**) and astragalus (**D**) with the fastest shape changes in yellow and the slowest in blue (units are squared Procrustes distances per million years).

Huracan relative to Ailuropoda. While decidedly plantigrade in their morphology, several lineages of ursines retained their ancestral terrestrial habits, including early tremarctines like Arctodus and extant brown bears. In keeping with independent evolution of climbing specializations among ursines, the functional morphology of the tarsals of extant arboreal bears differs substantially. The shapes of their calcaneal and astragali are strongly divergent from one another, as are the configurations of tarsal joints and their associated movements (Figs. 5-7). However, all of them differ in functionally consistent ways from the terrestrial brown and polar bears. The arboreal taxa all have more gently curved sustentacular facets that do not interlock tightly like the terrestrial species' do, and the surfaces of the astragalocalcaneal facet and its counterpart are also more gently curved and proportionally larger. While different in their detail, these arboreal morphologies all allow greater movement in the lower ankle and transverse tarsal joints than in the terrestrial taxa.

In contrast to Kurtén's assertion that polar bears were not distinctive from their brown bear kin in their postcranial morphology, there are substantial differences in the form and function of the tarsus of *Ursus maritimus* that are associated with observations that have been made on their locomotion. These differences include a more rounded navicular facet, a more gently curved astragalocalcaneal facet, and a broader and more elongate sustentacular facet in the polar bear, which are directly contrasted in





Fig. 8. Comparison of the facet shapes of the tarsals of the brown bear Ursus arctos and polar bear U. maritimus. - A: Calcaneum in dorsal view. - B: Astragalus in dorsal view. - C: Astragalus in plantar view. The calcaneum and astragalus of the brown bear are rendered as a slightly transparent 3D mesh with the facet margins traced with a light gray line. The facets of the polar bear are superimposed in a black line with light gray lines tracing the equivalent semilandmark positions in the two taxa.

Fig. 8 with the morphology of the brown bear. The broad, gentle curves of the sustentacular and astragalocalcaneal facets on the calcaneum and their counterparts on the astragalus allow for considerably more movement at the lower ankle joint than in the brown bear, yet the comparatively small sizes of these facets and the tight interlocking of the bones at the sustentaculum differentiate the polar bear from its more distant arboreal relatives. The form and function of the polar bear tarsus is consistent with the unusual swaying walk and gallop that has been described by previous researchers, and probably also with sustained swimming abilities. The shape differentiation in the polar bear tarsus is among the largest in this study given its quite recent divergence time (Fig. 7). This study shows that the polar bear's uniqueness is not confined to its large size, white pelt, and carnivorous dentition.

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Appendix. Measurements of extant and fossil specimens used in this study; M = male, F = female.

Group	Species	Specimen	Sex	Calcaneum length (mm)	Sustentacular position (mm)	Gear ratio
Hemicyoninae	Hemicyon barbouri	AMNH 68165b	?	78.8	66.4	1.19
Hemicyoninae	Phoberocyon johnhenryi	UF 270997	?	58.6	47.4	1.24
Hemicyoninae	Phoberocyon johnhenryi	UF 1458	?	81.2	63.8	1.27
Hemicyoninae	Phoberocyon johnhenryi	UF 164791	?	70.1	58.3	1.20
Ailuropodinae	Ailuropoda melanoleuca	FMNH 36758	F	64.5	56.7	1.14
Ailuropodinae	Huracan schneideri	OMNH 13676	?	100.6	89.7	1.12
Ailuropodinae	Huracan schneideri	AMNH 181-3527	?	100.5	88.8	1.13
Ailuropodinae	Huracan schneideri	AMNH 103-586	?	94.5	80.7	1.17
Ailuropodinae	Huracan schneideri	FLMNH 24182	?	110.6	89.5	1.24
Tremarctini	Arctodus simus	UCMP 3719	?	100.5	96.8	1.04
Tremarctini	Arctodus simus	UCMP 10214	?	107.5	98.1	1.10
Tremarctini	Arctodus simus	UCMP 8324	?	95.6	88.6	1.08
Tremarctini	Arctodus simus	UCMP 3450	?	102.2	93.8	1.09
Tremarctini	Tremarctos ornatus	FMNH 41294	Μ	60.3	50.3	1.20
Tremarctini	Tremarctos ornatus	FMNH 142010	F	51.8	44.0	1.18
Ursini	Helarctos malayanus	FMNH 54201	F	54.4	48.8	1.11
Ursini	Helarctos malayanus	FMNH 54316	Μ	53.2	47.8	1.11
Ursini	Melursus ursinus	FMNH 27441	F	68.7	62.4	1.10
Ursini	Melursus ursinus	FMNH 27442	Μ	73.4	68.9	1.06
Ursini	Ursus americanus	INSM 71.09.0233	?	68.9	59.7	1.15
Ursini	Ursus americanus	FMNH 18864	?	59.4	52.1	1.14
Ursini	Ursus americanus	FMNH 57282	F	57.1	49.5	1.15
Ursini	Ursus americanus	WRAZL 0210076	?	67.2	58.1	1.16
Ursini	Ursus americanus	MU 755	?	65.4	59.8	1.09
Ursini	Ursus americanus	WRAZL 0210076	?	67.7	56.6	1.20
Ursini	Ursus americanus	INSM 71.981.14	?	78.3	71.5	1.09
Ursini	Ursus americanus	INSM 71.09.0233	?	68.9	59.7	1.15
Ursini	Ursus americanus	UT 933-726	?	74.5	66.8	1.12
Ursini	Ursus americanus	UCMP 27308	?	81.9	72.6	1.13
Ursini	Ursus americanus	UCMP 8423	?	81.3	71.3	1.14
					C	ontinued

Group	Species	Specimen	Sex	Calcaneum length (mm)	Sustentacular position (mm)	Gear ratio
Ursini	Ursus arctos	FMNH 63802	М	100.0	102.4	0.98
Ursini	Ursus arctos	FMNH 63803	F	84.9	74.5	1.14
Ursini	Ursus arctos	UM 197532	?	82.9	76.1	1.09
Ursini	Ursus arctos	UT M-3773	F	68.3	62.2	1.10
Ursini	Ursus arctos	WRAZL 1710009	?	82.5	70.6	1.17
Ursini	Ursus maritimus	FMNH 53989	?	94.1	79.9	1.18
Ursini	Ursus maritimus	FMNH 58827	Μ	100.0	100.8	0.99
Ursini	Ursus maritimus	WRAZL 9710081	?	96.9	84.7	1.14
Ursini	Ursus thibetanus	WRAZL 0110011	?	63.6	58.2	1.09
Ursini	Ursus thibetanus	FM 99349	Μ	70.8	60.8	1.16

### Appendix. Continued.