Palmar, Patellar, and Pedal Human Remains from Pavlov

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ABSTRACT

Excavations in the 1960s in the central area of the Pavlov I site (southern Moravia, Czech Republic) produced a rich early (Pavlovian) Mid Upper Paleolithic (MUP) archeological record, abundant faunal remains, and thirty-nine human remains. The last, recently identified from the faunal collections, consist of two patellae (Pavlov 34 and 35), a partial second metacarpal (Pavlov 36), and two pairs of partial pedal skeletons (Pavlov 37 and 38). As such, they join the isolated and associated human remains from Pavlov I Northwest and Southeast, as well as those from the neighboring sites of Dolní Věstonice I and II. Pavlov 36 is an unremarkable and average sized metacarpal. Pavlov 34 and 35, which may be a pair, are among the largest known for the Upper Paleolithic and are relatively thick; Pavlov 34 has strongly asymmetrical femoral facets. The Pavlov 37 paired tarsometatarsal skeletons (22 elements) are from the longest known Paleolithic feet, indicating a stature among the tallest MUP individuals; Pavlov 38 (14 elements) is of average MUP size. The pedal remains are notable for their relatively long talar necks, gracile metatarsals, and (for Pavlov 37) large naviculocuboid facets. Together these remains provide additional data on Mid Upper Paleolithic human appendicular variation.

INTRODUCTION

The past decade has seen a renewed interest in the appendicular remains of Early and Mid Upper Paleolithic humans in the contexts of the paleobiology of these early modern humans, the preceding transition from late archaic to early modern humans across Eurasia, and trends in human biology through the Upper Paleolithic (Holt and Formicola 2008; Trinkaus 2013). These assessments have been associated with reanalyses and/or primary paleontological descriptions of Mid Upper Paleolithic limb bones (e.g., Trinkaus and Svoboda 2006; Trinkaus et al. 2014; Vacca et al. 2012; Villotte et al. 2015, 2017), with the large sample of human remains from the Pavlovian sites of Dolní Věstonice I and II and Pavlov I playing a prominent role. In particular, the sites of Dolní Věstonice II and Pavlov I have contributed both associated skeletal remains and isolated elements identified from the excavated faunal remains (Sládek et al. 2000; Trinkaus et al. 2000, 2010). It is in this context that we present here additional human remains, excavated by the late Bohuslav Klíma and recently identified by PW and JW from the Pavlov I faunal remains. They consist of a probable pair of patellae (Pavlov 34 and 35), a partial metacarpal 2 (Pavlov 36), and two pairs of variably complete tarsometatarsal skeletons (Pavlov 37 and 38).

THE PAVLOV I ARCHAEOLOGICAL CONTEXT

These human remains were originally identified only as mammalian remains, and consequently curated with the

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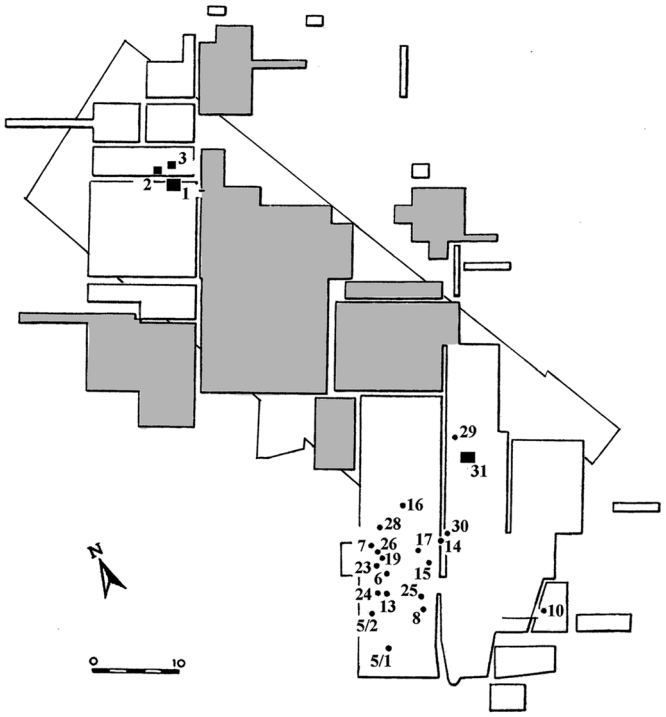

Figure 1. Plan of the Pavlov I site. The gray area is Pavlov-Centre, Pavlov-Northwest is to the upper left with the locations of Pavlov 1 to 3 indicated, and Pavlov-Southeast is in the lower right with the positions of the other Pavlov I human remains provided (all isolated elements except for the Pavlov 1 partial skeleton and the Pavlov 31 partial hands). The outline of the 2013–2015 salvage excavations, done prior to the building of the modern site museum, is indicated by the oblique rectangle (scale: 10 meters).

faunal remains from Pavlov I in the Budišov Castle osteological storage of the Moravian Museum, Brno. Of the human remains, only the Pavlov 34 patella bears a label, which refers to the excavation year as 1961, Squares 1 and 2. However, the location of the whole assemblage in the Budišov osteological storage and their curation together suggests that the Pavlov 34 to 38 human fossils all originate from the later stages of Klíma´s excavation during the 1960s, which were undertaken in Pavlov-Centre (Figure 1). If so, the new finds complement the previously known human remains, documented and published, from Pavlov-Southeast and –Northwest (Sládek et al. 2000; Trinkaus and Svoboda 2006; Trinkaus et al. 2010; Vlček 1991, 1997), excavated by Klíma during the 1950s (Svoboda 1994, 1997, 2005).

Pavlov-Centre is the least well-known part of the site. In contrast to the other sectors, we lack the original field documentation for these excavation seasons. Klíma (1977) published a circular pit feature, K14 excavated in 1961, now interpreted as a storage pit. In 2014, during a new excavation for the Archaeopark Museum building, we reopened the whole Pavlov I excavation area and documented the remaining features on the original surface, namely a shallow pit S3 with faunal remains, a network of charcoal concentrations (hearths?) and additional faunal and lithic material (Svoboda et al. 2016: Figures 2, 3, 7). These new observations confirm that the typical settlement units ("huts") were concentrated primarily in the Southeast and Northwest sectors (see Svoboda et al. 2016: Figure 3).

Concerning the associated materials from Pavlov-Centre, Klíma (1987) mentioned an antler industry, and Verpoorte (2005) studied the lithics from the 1963 and 1964 seasons, without noting a significant difference with other parts of the site. Also, one ^{14}C date on charcoal from the 1961 excavation (GIN 104: 26,000±350 ^{14}C BP; 30,960±412 cal BP) fits in with the larger series of dates for the dominant (Evolved Pavlovian) occupation stage at this site (Svoboda et al. 2016: Figure 11).

MATERIALS AND METHODS

The new Pavlov I human remains consist, as noted, of a partial metacarpal 2 (Pavlov 36), right and left patellae (Pavlov 34 and 35), a pair of largely complete tarsometatarsal skeletons, lacking only the right cuboid and metatarsal 5 (Pavlov 37), and a less complete right tarsometatarsal skeleton lacking only the lateral cuneiform plus the left talus, calcaneus and metatarsal 4 (Pavlov 38) (Appendix I). All of them sustained some degree of surface erosion and etching, especially the Pavlov 38 anterior tarsals and metatarsals. Yet, a substantial number of standard osteometrics and discrete traits are recordable with minimal estimation (Appendix II). From the Pavlov I site, they join the Pavlov 1 associated skeleton, the Pavlov 2 to 4 masticatory remains, the Pavlov 5 to 29 plus 32 isolated teeth, the Pavlov 30 and 33 phalanges, and the Pavlov 31 partial hand remains (Sládek et al. 2000; Trinkaus et al. 2010), as well as the associated and isolated remains from Dolní Věstonice I and II (Sládek et al. 2000; Trinkaus et al. 2000, 2010).

To evaluate size and proportions, the Pavlov 34 to 38 remains are compared principally to other Mid Upper Paleolithic (MUP) remains from western Eurasia, with the inclusion of limited data from the Early Upper Paleolithic (EUP) sites of Mladeč, Nazlet Khater, and Tianyuan (collectively E/MUP) (Appendix III). To place them in a broader temporal context, data are included for Middle Paleolithic late archaic (Neandertal) and modern human remains (Nean and MPMH respectively), as well as more limited data for Late Upper Paleolithic (LUP) western Eurasian humans. The data derive from personal measurement of the original remains, primary paleontological descriptions of the specimens, M. Samsel and S. Villotte. In several comparisons, for which Late Pleistocene data are limited (see Table 1 and Figure 12 below) and/or recent human variation is functionally relevant (see Figures 17, 19, and 23 below), pooled recent human (sedentary but non-industrial) data are included: from the Woodland Amerindian site of Libben, Ohio (collections: Kent State University), the predynastic Egyptian site of Keneh (collections: Harvard Peabody Museum), and the Serbian Mistihalj medieval site (collections: Harvard Peabody Museum). Given decreases in post-Pleistocene skeletal hypertrophy (Chirchir et al. 2015; Ruff et al. 2015), comparisons reflecting robustness are limited to Late Pleistocene humans.

The comparisons employ linear and angular measurements detailed in Bräuer (1988) and ones previously employed for Late Pleistocene human patellar and pedal remains (see Trinkaus 1975a, b, 2000; Trinkaus et al. 2014). Additional measurements as permitted by the preservation of the Pavlov remains are described in Appendix II. Linear measurements were taken with Mitutoyo plastic digital sliding calipers, provided to the nearest 0.1mm and generally accurate to the nearest 0.5mm; angles were obtained with a moveable arm steel protractor or derived trigonometrically from linear measurements. Metatarsal 1 diaphyseal hypertrophy is assessed using the midshaft subperiosteal polar moment of area, computed from external diameters using standard ellipse formulae (O'Neill and Ruff 2004), and modeling the diaphysis as a solid beam given non-significant differences across Late Pleistocene human samples in lower limb relative cortical thicknesses (Trinkaus 2015; Trinkaus and Ruff 2012).

The metric comparisons are principally graphical, and antimeric values, as available for Pavlov 37 and 38 (and comparative sample specimens), are averaged to provide a single line or data point per individual. The reference samples are compared using Kruskal-Wallis non-parametric tests for the individual measurements presented in box-plots. The box plots provide the median, the interquartile range (IQR) for the box, 1.5 × IQR + box up to maximum/minimum values for the whiskers, plus any outliers (Hintze 2016). For the assessments employing bivariate distributions, the samples are compared using the vertical deviations of the individual values from the reduced major axis (RMA) lines of the pooled comparative samples. It is recognized that these comparisons to RMA lines are dependent on the compositions of the comparative samples, as are most such assessments; alternative approaches (such as comparisons of slopes and intercepts) are limited by small paleontological sample sizes, especially for the MPMH. Ratios (or indices) are employed (even though they involve fitting data to a line constrained to an intercept of zero) for bivariate comparisons with little correlation between the variables.

To further evaluate the proportions of the Pavlov remains, their dimensions, ratios or deviations from the RMA lines are assessed using a one-sample t-test versus the E/MUP sample. The p-values across the comparative samples are evaluated using a sequentially reductive Bonferroni multiple comparison correction (Rice 1989), adjusted by the number of comparisons per bone (Proschan and Waclawiw 2000). These adjustments, plus the modest fossil sample sizes, result in a number of statistically non-significant p-values, even when the differences are substantial (i.e., as with the Pavlov 34, 35 and 37 size comparisons; see Figures 4, 10, and 11 below). All calculations were done using NCSS 11.0.6 (Hintze 2016).

THE PAVLOV I HUMAN REMAINS

THE PAVLOV 36 METACARPAL 2

The surface of the Pavlov 36 metacarpal 2 is mildly eroded and has fine encrustations, but its morphology is evident (Figure 2; see Table A2 below). It presents a modestly beveled dorsoradial head (hence its identification as a left metacarpal 2), a smooth dorsal diaphysis, and a palmar diaphysis with a muscular (second palmar interosseus) line extending proximally from the ulnar palmar head. The ulnar side is smooth, but the radial side has a pronounced sulcus beginning near midshaft and becoming deeper to the mid-proximal diaphyseal break. The distal epiphysis is fully fused and the fusion line obliterated, indicating fully adult status.

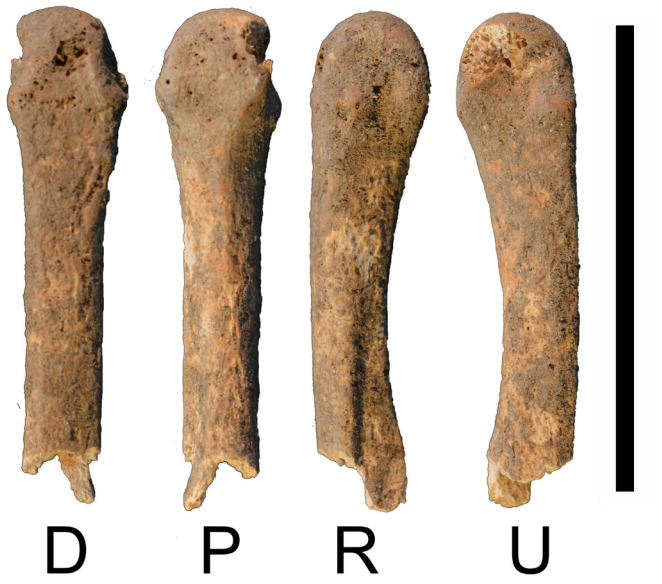

Figure 2. The Pavlov 36 left metacarpal 2 in dorsal (D), palmar (P), radial (R), and ulnar (U) views (scale bar: 5cm).

The original length of the bone is unknown, but it can be approximated if the distance from the distal head to the minimum diaphyseal diameters (especially the dorsopalmar one) of ≈35mm is regressed against articular length; a least squares regression based on recent human second metacarpals (r^2=0.669, n=40) provides an articular length of 68.6±3.0mm. The mean predicted value is close to an E/MUP mean (68.8±6.0mm, n=18, 59.3–79.5mm) and to those of the Dolní Věstonice 13, 15 and 16 males (69.7mm, 68.6mm, and 71.5mm respectively), but above that of the Dolní Věstonice 3 female (59.3mm).

THE PAVLOV 34 AND 35 PATELLAE

These two minimally damaged patellae (Figure 3; see Table A1 below) are very similar in overall size and substantially larger than the other available MUP patellae (Figure 4); the geometric means of their maximum dimensions (38.8mm and 38.3mm) are above the next largest MUP patella (Bausu da Ture 1: 37.1mm), 2.36 and 2.13 standard deviations above an MUP mean (33.7±2.2mm, n=11), and matched only by the Shanidar 1 Neandertal (38.3mm) and the LUP Chancelade 1 (38.8mm). Yet, the two bones differ in some of their morphological details. Pavlov 35 is modestly higher and narrower, and Pavlov 34 has a more medial articular crest and a deeper proximodistal sulcus on the lateral fac-

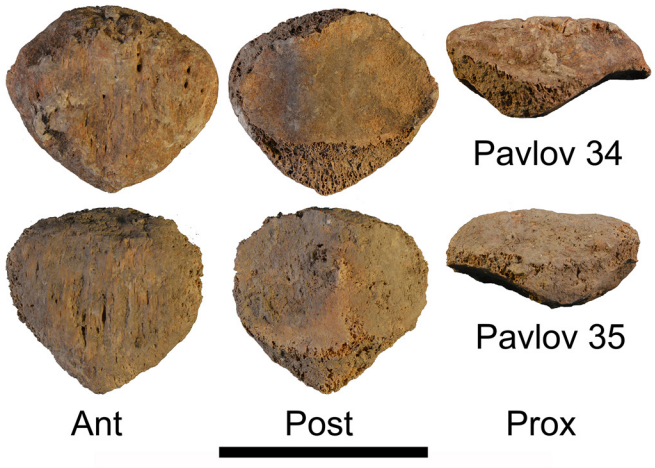

Figure 3. The Pavlov 34 and 35 right and left patellae in anterior (Ant), posterior (Post), and proximal (Prox) views (scale bar: 5cm).

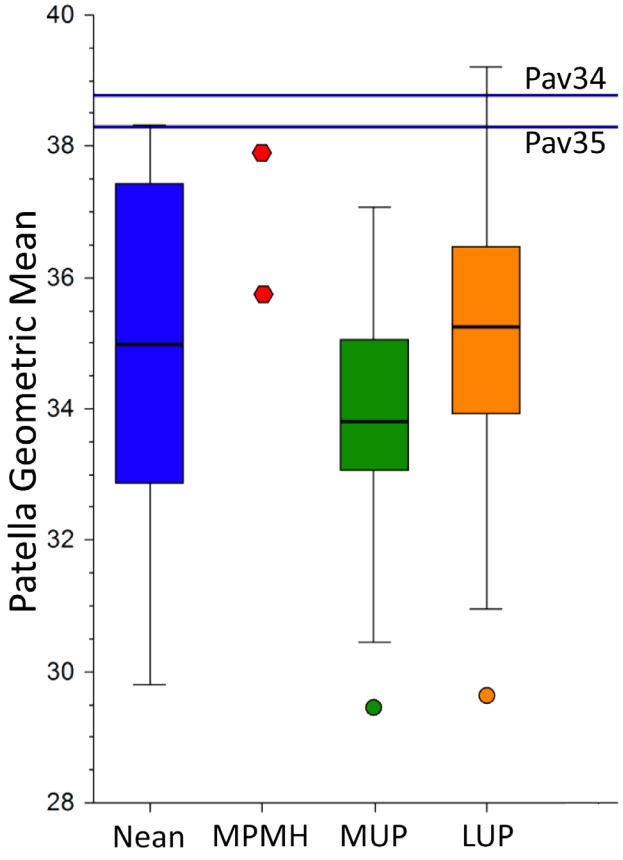

Figure 4. Boxplots of Pavlov (Pav) and Late Pleistocene patellar overall size, represented by the geometric mean of the maximum height, breadth and thickness (in mm). Nean: Neandertals (n=14); MPMH: Middle Paleolithic modern humans; MUP: Mid Upper Paleolithic humans (n=11); LUP: Late Upper Paleolithic humans (n=16). The comparative samples are not significantly different at p=0.193; Pavlov 34 and 35 are close to being significantly different from the MUP sample (p=0.049 and 0.070 respectively).

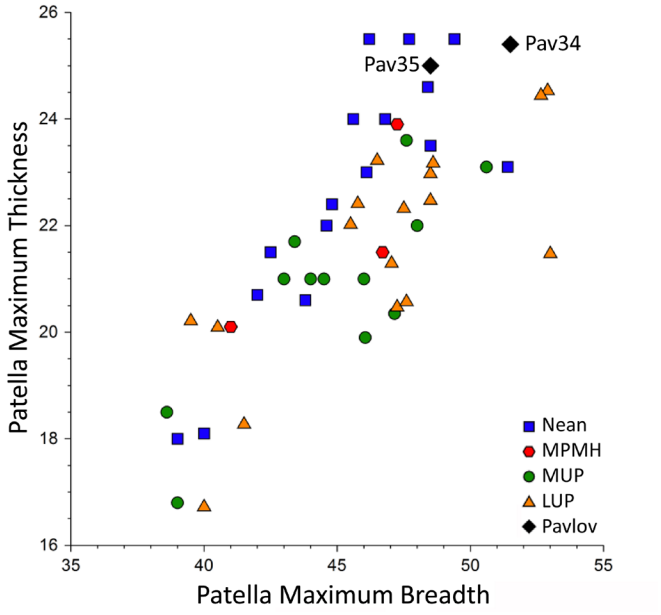

Figure 5. Bivariate plot of the patellar maximum thickness versus maximum breadth, in mm, for Pavlov 34 and 35 versus the Late Pleistocene comparative samples. The comparative samples are significantly different at p=0.017, primarily separating the Middle versus Upper Paleolithic samples. Pavlov 34 and 35 are not significantly different from the MUP sample (p=0.598 and 0.137 respectively). Abbreviations as in Figure 4.

et. There are also minor degenerative differences, in that Pavlov 34 exhibits small quadriceps femoris tendon ossifications, whereas Pavlov 35 has subchondral bone degeneration (see Figure A1 below). It is unclear whether these morphological differences are sufficient to indicate that they derive from separate individuals, but the similar exceptionally large dimensions would argue for antimeric status.

Despite considerable overlap of the comparative sample distributions (Figure 5), the comparative samples are significantly different with Middle Paleolithic humans tending to have relatively thicker patellae, at least as scaled to patellar breadth (if not body mass and leg length, cf. Trinkaus and Rhoads 1999). The Pavlov patellae have similar thicknesses and fall among the earlier samples in relative thicknesses, above those of most Upper Paleolithic patellae. Given the role of patellar thickness in quadriceps femoris moment arms, the Pavlov knees may have had an elevated mechanical advantage for that knee extensor. However, it is necessary to scale patellar thickness to femoral and tibial lengths (hence its load arm) times body mass to assess whether their knees were biomechanically more effective (see Trinkaus and Rhoads 1999).

At the same time, the medial and lateral articular facets are strongly asymmetrical, especially for Pavlov 34, placing it distinctly apart from the Neandertals and most of the early modern humans (Figure 6; cf. Trinkaus 2000). It is nonetheless similar to Dolní Věstonice 13 in these facet proportions. Pavlov 35 has less asymmetrical facets, but is

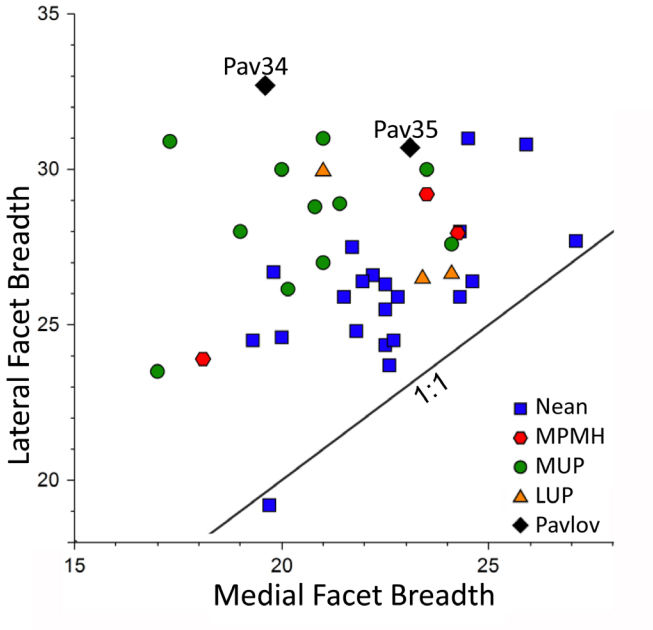

Figure 6. Bivariate plot of patellar lateral facet breadth versus that of the medial facet, in mm, for Pavlov 34 and 35 versus the Late Pleistocene comparative samples. The oblique line represents equal facet breadths. Abbreviations as in Figure 4.

still among the Upper Paleolithic humans. Neither of these patellae exhibits a vastus notch. Although the asymmetry of the patellar facets is related to lateral force vectors from normal human genu valgus (Hartigan et al. 2011), Late Pleistocene bicondylar angles are the same as recent human ones (Tardieu and Trinkaus 1994; Trinkaus 2006), and Late Pleistocene femora have asymmetrical patellar surfaces (Trinkaus 2000), there does not appear to be a tight relationship between the degrees of patellar facet asymmetry and the configurations of the distal femora (Trinkaus 2000). The significance of the Pavlov 35 and especially 34 patellar facet asymmetries, beyond indicating normal human knee function, is unclear.

THE PAVLOV 37 AND 38 PEDAL REMAINS

Despite marginal erosion and root etching, the Pavlov 37 right and left tarsal and metatarsal bones are largely complete and permit comparisons of overall length proportions as well as those of individual elements (Figure 7). Based on symmetry, of morphological details as much as of size and proportions (see Figure 7; and, see Figures 9, 13, 18, 20, 22, and 25 below), they represent a pedal pair even though their *in situ* proximities are not known; they were boxed together in storage. The Pavlov 38 tarsals and metatarsals are less complete, more extensively eroded, and primarily from the right side (Figures 8 and 9; and, see Figures 14, 18, 21, and 25 below), but the symmetry of the tali and calcanei in particular argue for the original presence of a pedal pair. Both sets of bones were boxed together (Box 177 in the Budišov Castle storage area) and initially identified as carnivore remains ("*Canis lupus*, *Ursus arctos*"), suggest-

Figure 7. The articulated Pavlov 37 right and left tarsometatarsal skeletons in dorsal views (scale bar: 10cm).

Figure 8. Pavlov 38 right tarsometatarsal skeleton and its left talus, calcaneus and metatarsal 4, in articulated dorsal views (scale bar: 10cm).

Figure 9. The Pavlov 37 right and left and Pavlov 38 right articulated medial pedal arches (scale bar: 10cm).

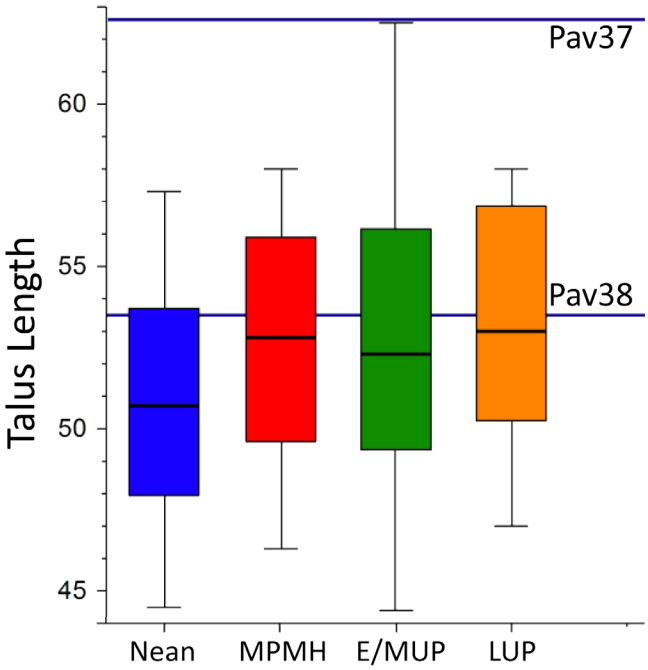

Figure 10. Boxplots of Pavlov (Pav) and Late Pleistocene talar lengths, in mm. Nean: Neandertals (n=17); MPMH: Middle Paleolithic modern humans (n=6); E/MUP: Early and Mid Upper Paleolithic humans (n=28); LUP: Late Upper Paleolithic humans (n=18). The comparative samples are not significantly different at p=0.168, nor are Pavlov 37 (p=0.036) and Pavlov 38 (p=0.888) from the E/MUP sample (after a talar multiple comparison correction).

ing that they came from the same or adjacent excavation squares.

The Pavlov 37 metatarsal 1 bases and all of its metatarsal 2 to 5 heads have fully fused epiphyses. The exposed distal trabeculae of the right metatarsals 2 to 4 and the left metatarsals 2 and 4 provide no evidence of an epiphyseal fusion line. The individual was therefore fully mature. On Pavlov 38, the only preserved metatarsal epiphyseal region is the base of the right first metatarsal. It has no evidence of a fusion line, so it was also fully mature. There is no evidence of articular or periarticular degeneration on any of the tarsals or metatarsals, although damage (especially to Pavlov 38) might obscure previous minor degenerations.

Pedal Size

Given complete medial pedal arches for both Pavlov 37 feet and the right Pavlov 38 foot (Figure 9), it is possible to assess overall foot length and proximal to distal proportions. The articular lengths of the Pavlov 37 medial arches (199mm and 201mm) are the longest known for Late Pleistocene humans, approached only by that of Předmostí 3 (Table 1). The length for Pavlov 38 is unexceptional for a Middle or Upper Paleolithic human.

It is also possible to compare talar and metatarsal 1 lengths to larger samples of Late Pleistocene humans. In the talar comparison (Figure 10), the Pavlov 38 length is among the longer Neandertal tali but only slightly above the medians for the early modern humans. The Pavlov 37 values (62.7mm and 62.5mm) are well above the Middle Paleolithic and LUP ranges, and they are at the top of the MUP range, matched only by that of Barma Grande 1 (62.5mm); the next highest values are 59.9mm for Bausu da Ture 2 and 58.0mm for Barma Grande 2. The metatarsal 1 maximum lengths follow a similar pattern; the Pavlov 38 length (≈59.2mm) is unexceptional for a Late Pleistocene human, but the lengths of ≈78.0mm and ≈76.0mm for Pavlov 37 are beyond the range of even the relatively high values for the MUP sample (Figure 11). High lengths are provided by the MUP Barma Grande 1, Bausu da Ture 1, Grotte des Enfants 4, Paviland 1, and Sunghir 1, all between 71mm and 73mm.

From these comparisons, it is evident that Pavlov 38, as with Pavlov 36, falls among the larger of the MUP (and Late Pleistocene) humans, but was similar in size to a number of the male MUP individuals. Pavlov 37, in contrast, was among the largest of the MUP individuals. It was probably close to Dolní Věstonice 14 in stature, and its stature may have reached the very tall values of some Ligurian individuals.

Tarsometatarsal Proportions

Given the role of the foot as a shock-absorber at heel-strike and a class I lever at heel-off, with rotation at the talocrural joint (Olney and Eng 2011), it is appropriate to estimate the relevant moment arms from the tarsometatarsal skeleton, using the middle of the talar trochlea to approximate the

TABLE 1. PAVLOV 37 AND 38 AND LATE PLEISTOCENE PEDAL MOMENT ARMS (in millimeters).[1]

	Subtalar Length[2]	*Proximal Moment Arm*[3]	*Distal Moment Arm*[3]
Pavlov 37 – right	199.0	52.0	147.0
Pavlov 37 – left	201.0	54.5	146.5
Pavlov 38 – right	174.7	54.3	120.4
Neandertal			
La Ferrassie 1	182.0	56.0	126.0
La Ferrassie 2	150.0	46.0	104.0
Kiik-Koba 1	181.0	58.0	123.0
Shanidar 1	185.0	58.0	127.0
Tabun 1	159.0	46.0	113.0
MPMH			
Qafzeh 8	174.0	55.0	119.0
Qafzeh 9	162.0	42.0	120.0
Skhul 4	188.0	66.0	122.0
E/MUP			
Caviglione 1	187.5	47.5	140.0
Dolní Věstonice 15	165.0	49.0	116.0
Dolní Věstonice 16	180.0	60.0	120.0
Předmostí 3	192.2	56.7	135.5
Sunghir 1	183.0	50.0	133.0
LUP			
Ohalo 2	177.0	121.0	56.0
Recent Humans[4]			
Libben Amerindians (n=40)	165.2±9.3	46.1±3.6	119.1±7.0
Keneh Egyptians (n=25)	165.1±12.2	49.6±4.8	115.2±9.1

[1]MPMH: Middle Paleolithic modern humans; E/MUP: Early/Mid Upper Paleolithic humans; LUP: Late Upper Paleolithic human.

[2]The distance from the proximal calcaneal tuberosity to the distal metatarsal 1 head, parallel to the tangent to the plantar surfaces of the metatarsal head and the calcaneal tuberosity, measured on the articulated medial arch (calcaneus, talus, navicular, medial cuneiform, and metatarsal 1) in medial view (McCown and Keith 1939; Trinkaus 1975a).

[3]The distances from the most dorsal point on the talar trochlea to the proximal and distal points of the subtalar length, measured parallel to the subtalar length.

[4]Mean ± standard deviation are provided for the recent human samples.

axis of rotation and proximal and distal ends at the calcaneal tuberosity and the metatarsal 1 head respectively (see Table 1). The distribution of these proximal and distal tarsometatarsal lengths (Figure 12) provides substantial variation for the recent and the Late Pleistocene humans. Pavlov 38 is among those with relatively shorter distal (or longer proximal) portions, along with the Neandertals and several early modern humans. Pavlov 37, in contrast, has a proportionately very long distal segment; it is joined by Caviglione 1.

Talocrural Morphology

The tibial articulations of the Pavlov 37 and 38 tali (Figures 13 and 14) exhibit the anterior extensions of the trochleae and the medial malleolar facets present on most Late Pleistocene tali (see Table A3 below), reflecting frequent talocrural dorsiflexion. Both of them also possess lateral squatting facets, which are variably present among E/MUP and other Late Pleistocene humans (Table 2).

The size of the talar trochlea relative to talar length (Figure 15), which is also reflected (inversely) in the relative length of the talar head and neck, provides only a modest separation of the Late Pleistocene samples, despite an apparently "short" talar neck among the Neandertals (Rhoads and Trinkaus 1977). The E/MUP specimen with a relatively large trochlea is the EUP Mladeč 30, and it is joined by the LUP Arancio 1, Le Peyrat 5, and San Teodoro 1 tali. The two Pavlov tali are among the tali with the relatively smallest trochleae. The proportions of the Pavlov 37 tali may be influenced by their large lengths; yet the index of talar length to medial arch length is not significantly different across the pooled Late Pleistocene and recent human samples ($p=0.507$, $n=66$), and the Pavlov 37 and 38 indices (31.3 and 30.6) are within the Late Pleistocene (28.5–31.7)

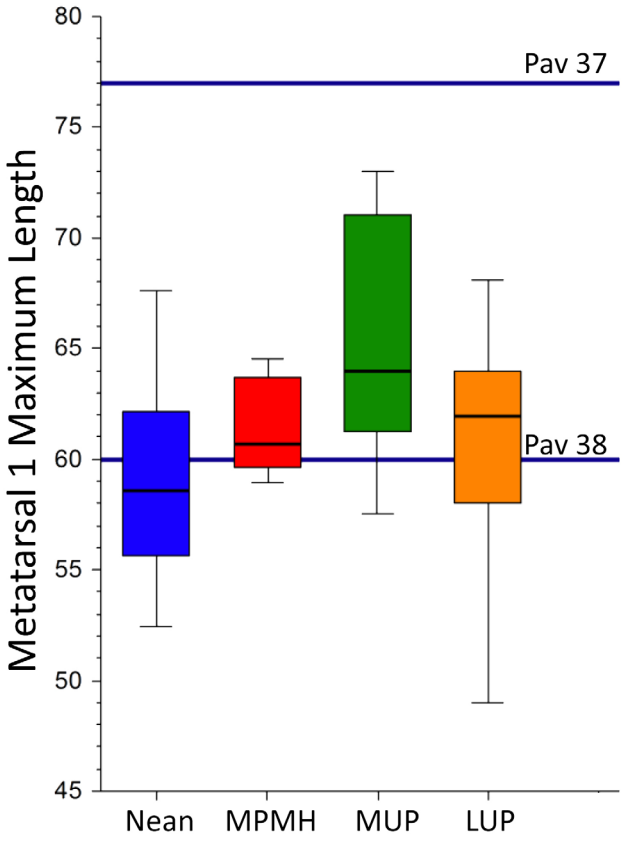

Figure 11. Boxplots of Pavlov (Pav) and Late Pleistocene metatarsal 1 length, in mm. Nean: Neandertals (n=9); MPMH: Middle Paleolithic modern humans (n=5); MUP: Mid Upper Paleolithic humans (n=17); LUP: Late Upper Paleolithic humans (n=16). The comparative samples are not significantly different at p=0.034, nor are Pavlov 37 and 38 (p=0.040 and 0.318 respectively), given multiple comparison corrections for metatarsal comparisons despite the very high value for Pavlov 37.

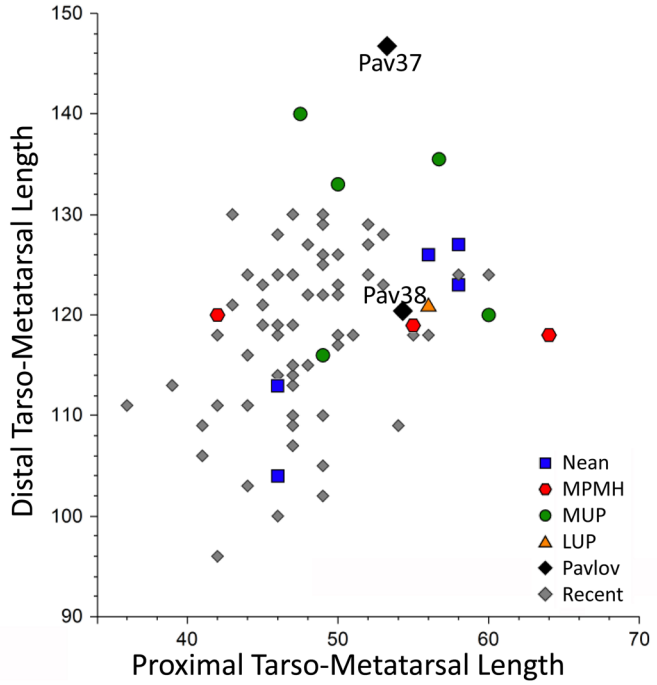

Figure 12. Bivariate plot of Pavlov 37 and 38, Late Pleistocene humans, and a pooled sample of late Holocene humans (Libben, Ohio Woodland Amerindians, and Keneh pre-dynastic Egyptians) (see Table 1) medial arch distal versus proximal tarsometatarsal lengths, in mm. Samples as in Figure 10.

and especially recent human (26.8–36.7) values.

There is also a contrast across the Late Pleistocene samples in the mediolateral projections of the malleolar facets relative to the trochlear breadth (Figure 16), with the higher values for most Neandertals contrasting with the LUP ones. The MPMH and E/MUP tali have intermediate proportions. The Pavlov 37 tali have relatively broad malleolar surfaces, whereas the Pavlov 38 ones are among the least flaring, falling below the E/MUP range albeit within the ranges of the other samples.

The differential curvatures of the talar trochlear sides, as related to the talocrural instant axis of rotation (Hicks 1953; Martin 2011), are reflected in the angle between its medial and lateral arcs, the trochlear angle (Trinkaus 1975a). There is a modest (non-significant with multiple comparison correction) shift in the median angle between the Middle and Upper Paleolithic samples (Figure 17), despite the variable and small LUP sample. All of their variation, however, is subsumed within the pooled recent human sample. The Pavlov 37 angle is principally among the lower values, whereas that of Pavlov 38 is higher.

Pedal Arches

The articulations of the medial tarsometatarsal sequences for Pavlov 37 and 38 (see Figure 9) provides them with normal human medial pedal arches. Adjustments of the assemblies, especially through the acetabulum pedis (in particular the talonavicular articulation) could raise or lower the medial arches relative to those provided. In addition, the naviculocuneiform and tarsometatarsal 1 articulations of Pavlov 38 are close to their original positions, but distal navicular and proximal metatarsal 1 erosion has required some judgment in their articulation. However, it would not be possible to position their tali and calcanei in anatomically appropriate positions without some degree of medial arch presence. In any case, arch height varies with foot posture and stance phase, and across individuals irrespective of footwear (Arulsingh et al. 2015; D'Août et al. 2009; Martin 2011; Wells 1931).

Pedal arches are reflected in the orientations of the lateral metatarsal articulations, given the plantar deviation of the tarsal articulations (vertical angles) for the longitudinal arches and given head torsion to maintain the metatarsophalangeal axes horizontal in the context of the transverse tarsometatarsal arch (Morton 1922–24; Trinkaus 1975a; Ward et al. 2011). The vertical angles of the Pavlov 37 metatarsals 3 and 4 (10° and 14°) indicate distinctly plantar orientations (Figure 18), and hence longitudinal arches, as

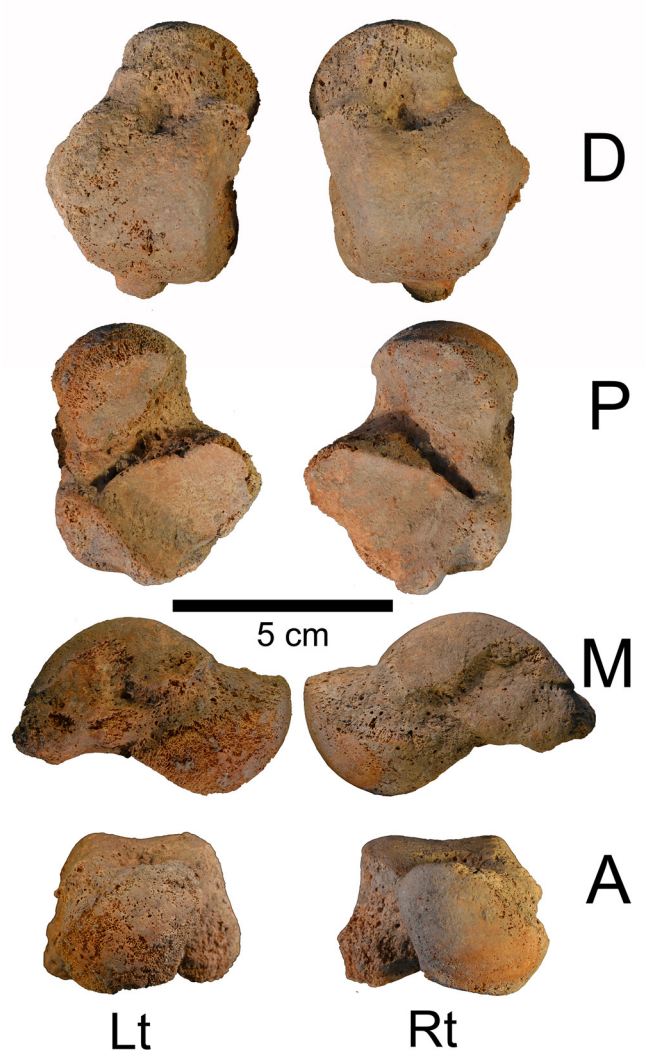

Figure 13. The Pavlov 37 left (Lt) and right (Rt) tali in dorsal (D), plantar (P), medial (M), and anterior/distal (A) views.

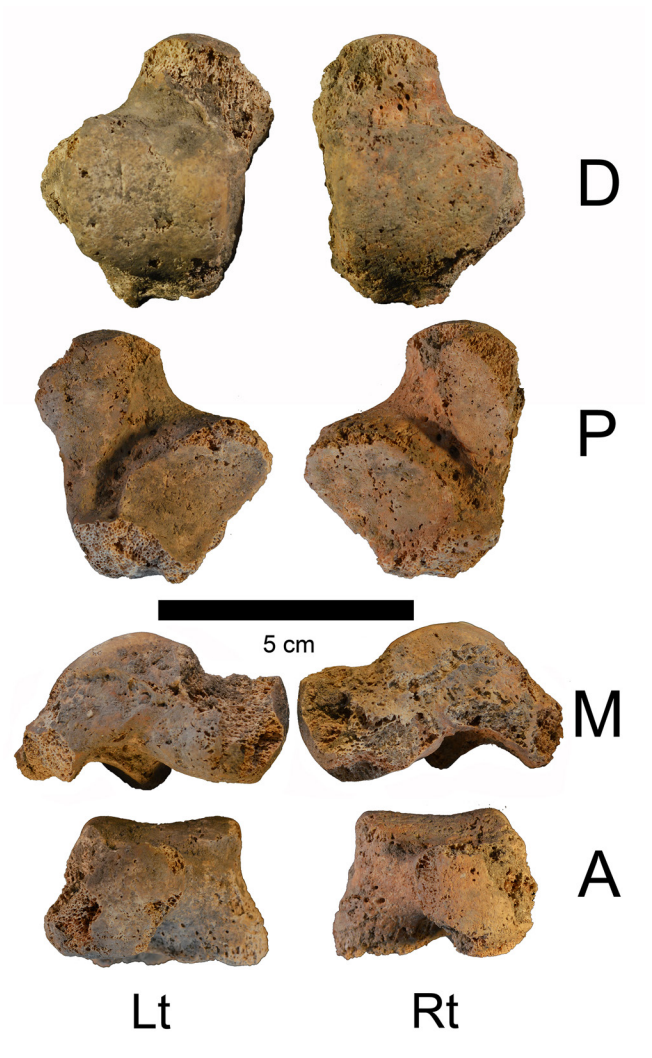

Figure 14. The Pavlov 38 left (Lt) and right (Rt) tali in dorsal (D), plantar (P), medial (M), and anterior/distal (A) views.

TABLE 2. PEDAL DISCRETE TRAITS FOR PAVLOV 37 AND 38 AND LATE PLEISTOCENE SAMPLES, PROVIDED AS THE FREQUENCY OF PRESENCE (n).[1]

	Lateral Squatting Facet[2]	*Sulcus Tali Facet*	*Talo-calcaneal Facet Fusion*[2]	*Naviculo-cuboid Facet*[3]	*Metatarsal 1-2 Facet*
Pavlov 37	present	absent	present	present	present
Pavlov 38	present	absent	present	present	--
E/MUP	50.0% (24)	62.5% (16)	88.6% (22)	36.4% (11)	9.1% (11)
MPMH	100% (6)	40.0% (5)	100% (4)	100% (3)	66.7% (3)
Neandertals	71.4% (21)	41.2% (17)	86.8% (19)	71.4% (7)	36.4% (11)
χ^2 p-value	0.051	0.120	0.834	0.092	0.095

[1]MPMH: Middle Paleolithic modern humans; E/MUP: Early/Mid Upper Paleolithic humans; insufficient Late Upper Paleolithic data are available (cf. Trinkaus 2015).

[2]The presence / absence of squatting facets pools together observations from tali and distal tibiae, and the presence of talocalcaneal facet fusion includes observations from tali and calcanei.

[3]Four recent human samples provide frequencies of 24.0%, 45.5%, 50.4%, and 62.0% (Trinkaus 1975a; Trinkaus et al. 2014). The data include observations from both navicular and cuboid bones.

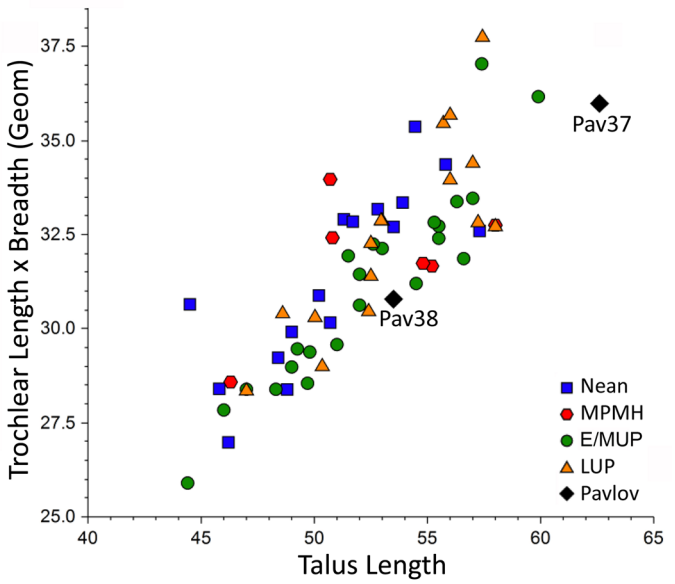

Figure 15. Bivariate plot of the geometric mean of the trochear length and breadth versus talar length for the Pavlov (Pav) and Late Pleistocene tali (in mm). Nean: Neandertals; MPMH: Middle Paleolithic modern humans; E/MUP: Early and Mid Upper Paleolithic humans; LUP: Late Upper Paleolithic humans. The comparative samples are not significantly different at p=0.060, nor are Pavlov 37 (p=0.123) or 38 (p=0.280) from the E/MUP sample.

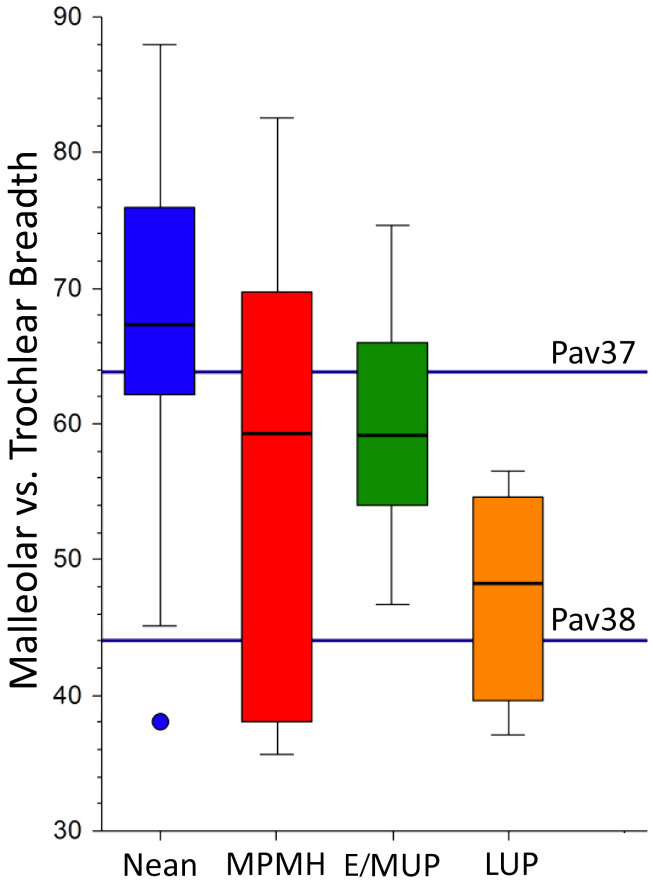

Figure 16. Boxplots of the index of the summed medial and lateral malleolar breadths versus trochlear breadth (in mm) for the Pavlov (Pav) and Late Pleistocene tali. Nean: Neandertals (n=16); MPMH: Middle Paleolithic modern humans (n=7); E/MUP: Mid Upper Paleolithic humans (n=15); LUP: Late Upper Paleolithic humans (n=4). The comparative samples are not significantly different at p=0.027, given a multiple comparison correction for talar comparisons. Pavlov 37 and 38 remain insignificantly different from the E/MUP sample (p=0.634 and 0.087 respectively).

do those of almost all Late Pleistocene and recent humans (Trinkaus 1975a, 1983, 2016). The Pavlov 37 metatarsal 3 and 4 torsion angles (20° and 24°) are in the middles of values for a small and variable pooled Late Pleistocene sample (20.5°±11.5°, n=7 and 28.1°±9.9°, n=10), which are modestly higher than those of a late prehistoric Amerindian sample (17.5°±6.1°; 18.9°±6.7°; n=40). The vertical and torsion angles of the Pavlov 38 metatarsals cannot be measured, given articular erosion; its fourth metatarsal diaphyses indicate torsion angles well within recent human variation, and the base of its left metatarsal 4 was distinctly plantarly deviated (see Figure 18).

A more indirect indication of the presence of pedal arches is the talar head torsion angle, in which angles substantially greater than zero serve to stabilize the transverse tarsal articulation in supination (Elftman 1960; Martin 2011). The variable Late Pleistocene angles are generally lower than those of the recent human sample (p=0.002), but the sample ranges overlap (Figure 19). The Pavlov 37 values (46°, 43°) are moderately but insignificantly higher than most of the Late Pleistocene ones, whereas those of Pavlov 38 (≈36°, ≈40°) are unexceptional.

Subtalar Morphology

The Pavlov tali and calcanei have fused anterior and medial talocalcaneal facets, as with 90% of the Late Pleistocene ones (see Figures 13, 14, 20, and 21; see Table 2; see Tables A3 and A4 below). There is little or no indication of a notch along the sulcus tali margins of the facets on the tali, but the facets on the calcanei narrow from the medial to the anterior ones, such that the anterior facet breadths are half to two-thirds of the medial facet breadths (see Table A4 below). The result is a modest notch between the two portions of the fused facet on the Pavlov 37 calcanei and the left Pavlov 38 one. All of the medial facets are separated from the posterior ones. The talocalcaneal facets form even anterolateral to posteromedial curves. This curve implies smooth rotation of the subtalar articulation, although none of the Pavlov tali exhibit a sulcus tali facet from marked pronation of the subtalar joint (see Table 2).

The Pavlov 37 navicular bones and its left cuboid bone have relatively large naviculocuboid facets (Figure 22; see Table 2; see Tables A5 and A6 below), although they do not approach those evident in the australopith OH-8 and A.L. 333-36 navicular bones in size, orientation, or extent (see Latimer et al. 1982). A facet is also present on the Pavlov 38 right navicular bone, but erosion precludes assessing its

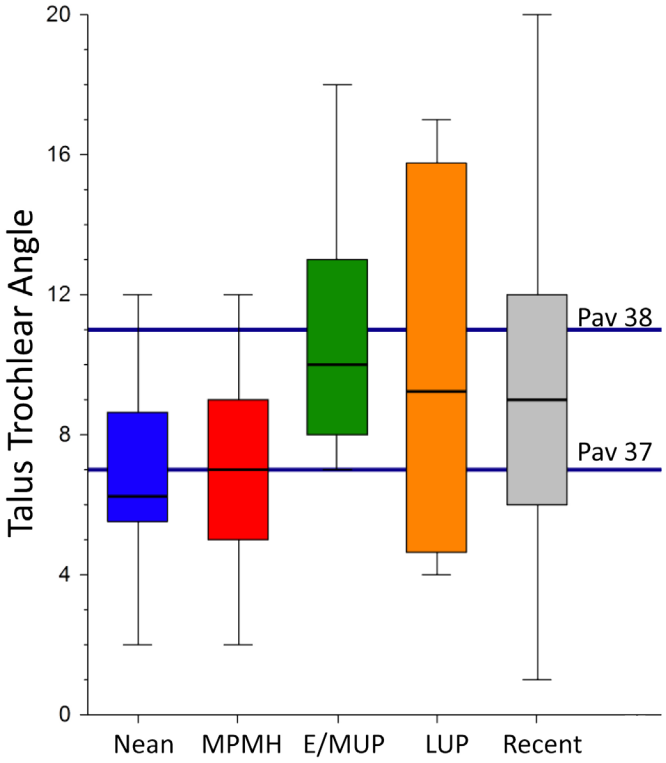

Figure 17. Boxplots of the Pavlov (Pav), Late Pleistocene, and recent human talus trochlear angles (°). Nean: Neandertals (n=16); MPMH: Middle Paleolithic modern humans (n=7); E/MUP: Early and Mid Upper Paleolithic humans (n=11); LUP: Late Upper Paleolithic humans (n=4); Recent (n=140). The Late Pleistocene comparative samples are not significantly different at p=0.020, given a multiple comparison correction for talar comparisons; Pavlov 38 is in the middle of the E/MUP sample (p=0.947), and Pavlov 37, although the lowest E/MUP value (along with Tianyuan 1), is not significantly different either (p=0.286).

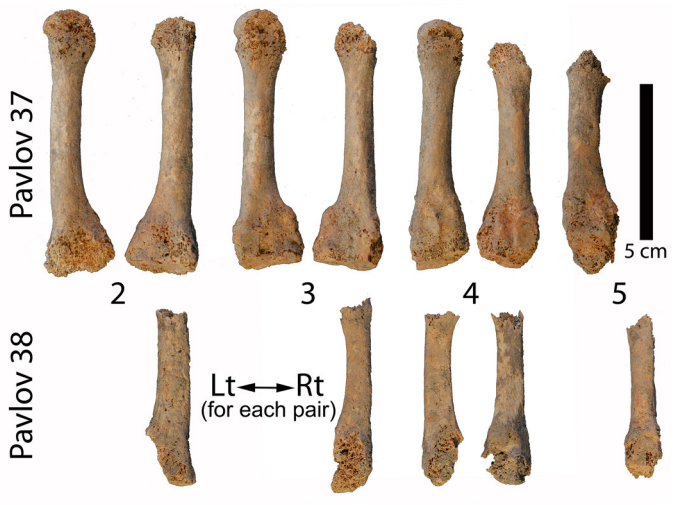

Figure 18. The Pavlov 37 and 38 metatarsals 2 to 5 in medial view.

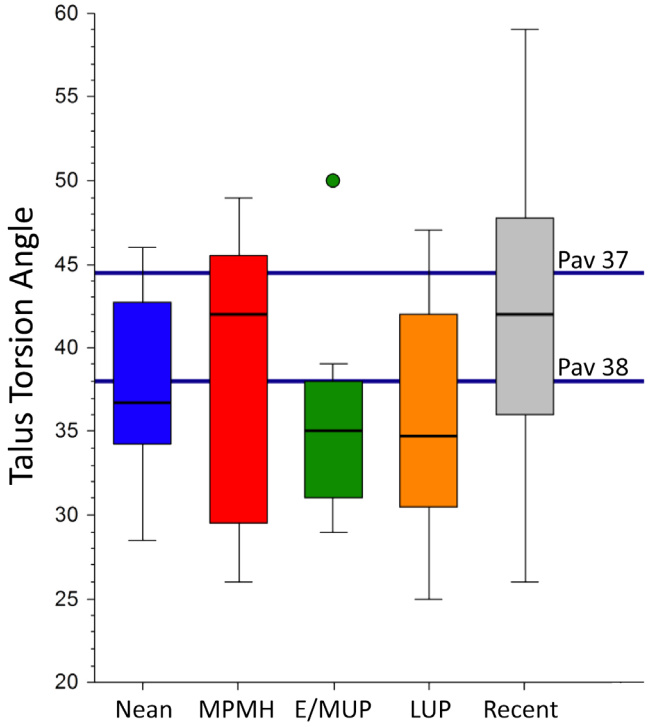

Figure 19. Boxplots of the Pavlov (Pav), Late Pleistocene, and recent human talus torsion angles (°). Nean: Neandertals (n=16); MPMH: Middle Paleolithic modern humans (n=5); E/MUP: Early and Mid Upper Paleolithic humans (n=11); LUP: Late Upper Paleolithic humans (n=10); Recent (n=140). The Late Pleistocene comparative samples are not significantly different at p=0.514; Pavlov 38 is at the upper quartile of the E/MUP sample (p=0.665), and Pavlov 37, although the second highest value (below Tianyuan 1), is not significantly different either (p=0.162).

size. Naviculocuboid facets, as opposed to a ligamentous surface, are moderately common among Late Pleistocene and recent humans (see Table 2).

Late Pleistocene humans have a modest medial positioning of the acetabulum pedis, as is reflected in the talar head-neck angle and the medial projection of the sustentaculum tali. The Pavlov 37 and 38 tali have average head-neck angles, ones well within Late Pleistocene (and especially recent) human ranges of variation (see Figures 13 and 14; Figure 23). The Upper Paleolithic ones are generally lower than the Middle Paleolithic ones, but not significantly so (see Figure 23).

Yet, these Pavlov talar head-neck angles are associated with sustentacula tali that are among the more modest of the Late Pleistocene ones relative to calcaneal length. An index of sustentacular projection (medial breadth [lateral posterior talar surface to medial sustentaculum tali] to calcaneal total length; Figure 24) does not separate the Late Pleistocene samples, and it places Pavlov 37 and 38 within the MUP interquartile range. An index of sustentacular breadth [sustentacular breadth / body breadth (Bräuer

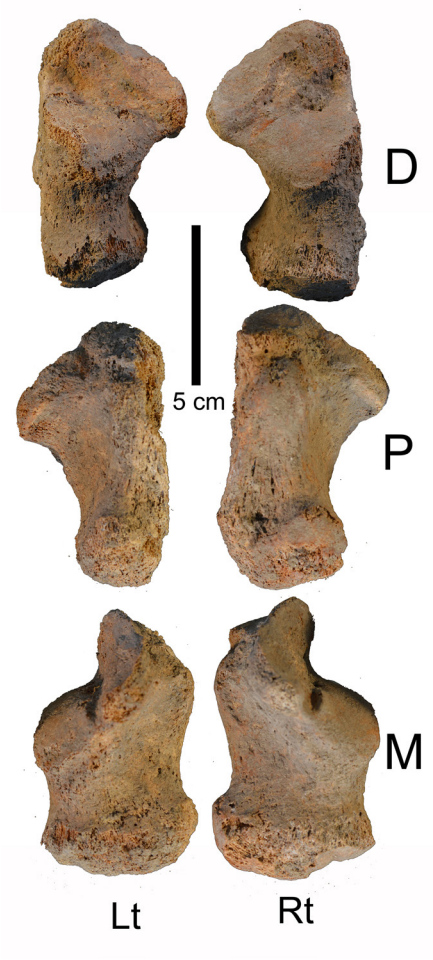

Figure 20. The Pavlov 37 calcanei in dorsal (D), plantar (P), and medial (M) views.

Figure 21. The Pavlov 38 calcanei in dorsal (D), plantar (P), and medial (M) views.

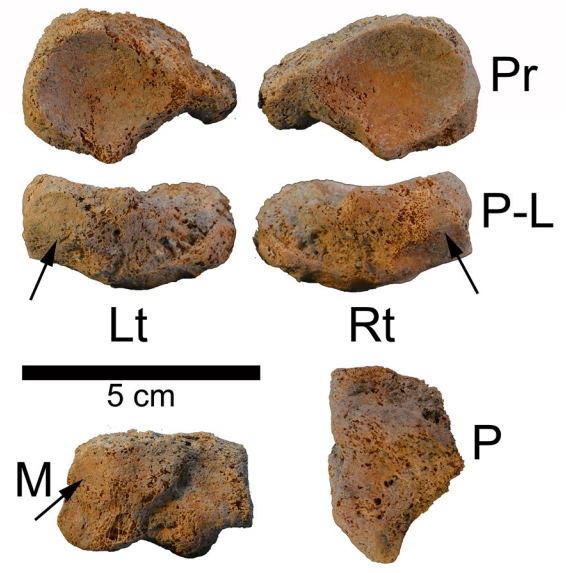

Figure 22. The Pavlov 37 right (Rt) and left (Lt) navicular bones in proximal (Pr) and planto-lateral (P-L) views and the left cuboid bone in medial (M) and plantar (P) views. The arrows indicate the naviculocuboid facets.

1988; data not shown] would make the Pavlov ones appear smaller, but it is susceptible to variation in the determination of the medial border of the flexor hallucis longus sulcus.

Hallucal Considerations

The Pavlov halluces are represented by the largely complete medial cuneiform bones and first metatarsals of Pavlov 37, and the same bones, but rather eroded, for the right hallux of Pavlov 38. These metatarsals (Figure 25) are notable primarily for the marked length of the Pavlov 37 metatarsals, the Pavlov 38 one being more modest, especially for a Mid Upper Paleolithic human (see Figure 11).

The first tarsometatarsal articulations of Pavlov 37 exhibit only a minimal degree of mediolateral distal convexity. The left distal medial cuneiform is flat dorsally and has a slight convexity plantarly, with a dorsoplantar twist. The right one has a suggestion of convexity but little difference in the orientations of the dorsal versus plantar halves of the facet. The associated metatarsal 1 bases are distinctly concave mediolaterally on the dorsal portion but only shallowly so plantarly. The Pavlov 38 metatarsal 1 has a concave facet dorsally, but the other portions of the first tarso-

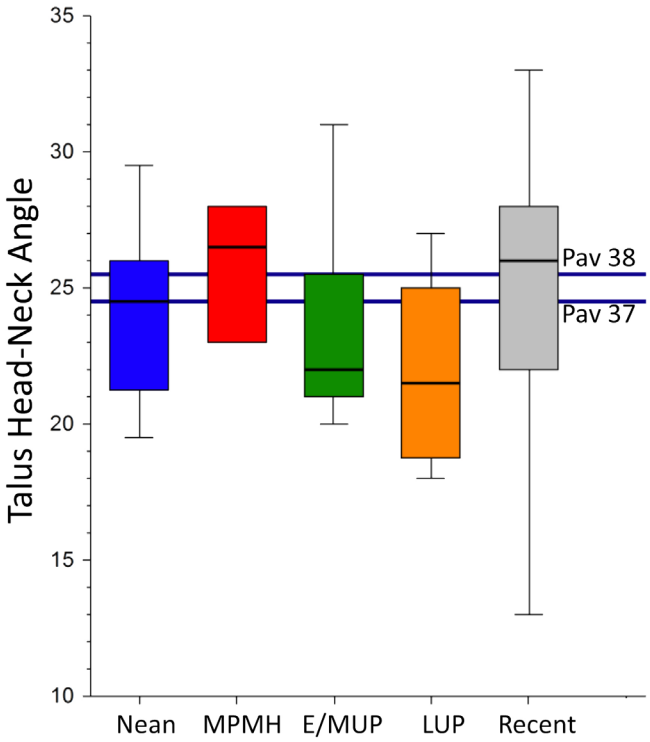

Figure 23. Boxplots of the Pavlov, Late Pleistocene, and recent human talus head-neck angles (°). Nean: Neandertals (n=16); MPMH: Middle Paleolithic modern humans (n=6); E/MUP: Early and Mid Upper Paleolithic humans (n=19); LUP: Late Upper Paleolithic humans (n=9); Recent (n=140). The Late Pleistocene comparative samples are not significantly different at p=0.087, and Pavlov 37 and 38 are similar to the E/MUP sample (p=0.700 and 0.496 respectively).

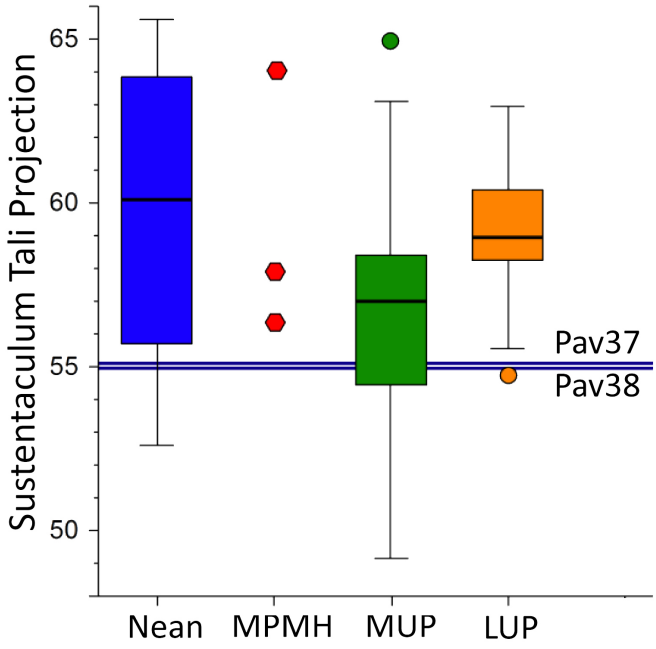

Figure 24. Box plots of the relative calcaneal sustentaculum tali projection, as an index of medial breadth to total length. Nean: Neandertals (n=8); MPMH: Middle Paleolithic modern humans (n=3); MUP: Mid Upper Paleolithic humans (n=12); LUP: Late Upper Paleolithic humans (n=13). The comparative samples are not significantly different at p=0.246, and Pavlov 37 (p=0.718) and 38 (p=0.693) are not significantly different from the MUP sample.

metatarsal articulation are eroded.

On the lateral base of the Pavlov 37 left metatarsal 1, there is a distinct facet for the metatarsal 2 (see Figure 25; see Table 2; see Table A10 below). The right bone also exhibits one, but it is too eroded to measure. The medial base of the right metatarsal 2 retains the first metatarsal 1 facet area, but it is eroded (see Figure 18). There is a hint of a facet by the raised area just distal of the medial cuneiform facet, but it is insufficient to confirm it. The Pavlov 38 metatarsal 1 entirely lacks the lateral base, and its second metatarsal preserves only the distal edge of the raised area (see Figures 18 and 25). It is insufficient to indicate whether a facet was present, although the marked proximomedial metatarsal 2 ligamentous markings support a fully adducted hallux for it, as with those of Pavlov 37.

Distally, the plantar intersesamoid crests are damaged (see Figure 25), but they are sufficiently preserved to provide horizontal angles (between the crest axis and the diaphyseal axis) of ≈5° and ≈9° for Pavlov 37 and 38. These values, indicating lateral deviation of the head for mild hallux valgus (Meyer 1979), are similar to those of the few other MUP humans providing the angle (5.0°±3.1°, n=6), as well as those of Middle Paleolithic humans (5.8°±3.1°, n=9). The three comparative samples (no LUP data are available) are not significantly different (p=0.343).

Figure 25. Medial (M), lateral (L), and plantar (P) views of the Pavlov 37 right and left first metatarsals and the Pavlov 38 right one.

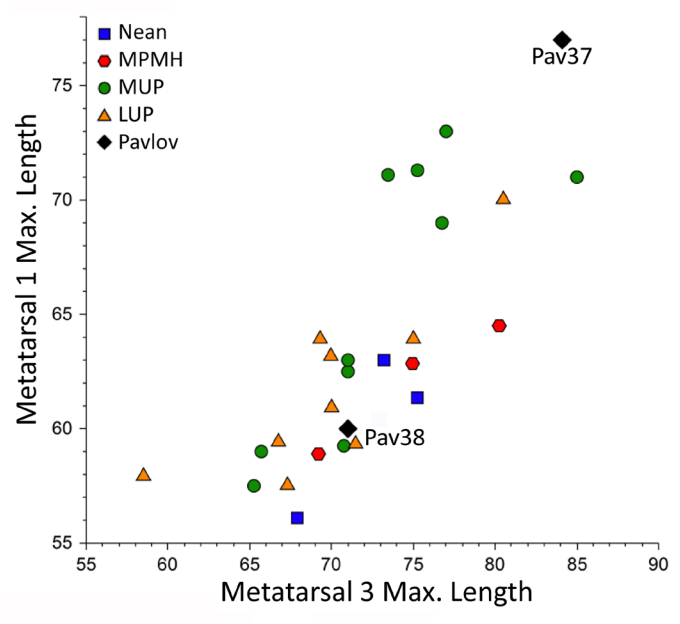

Figure 26. Bivariate plot of metatarsal 1 maximum length versus that of metatarsal 3 for Pavlov 37 and 38 and the Late Pleistocene comparative samples (in mm). Abbreviations as in Figure 24. The comparative samples are not significantly different at p=0.038, given a multiple comparison correction for metatarsal comparisons. Pavlov 37 and 38 are not significantly different from the MUP sample (p=0.680 and 0.320 respectively).

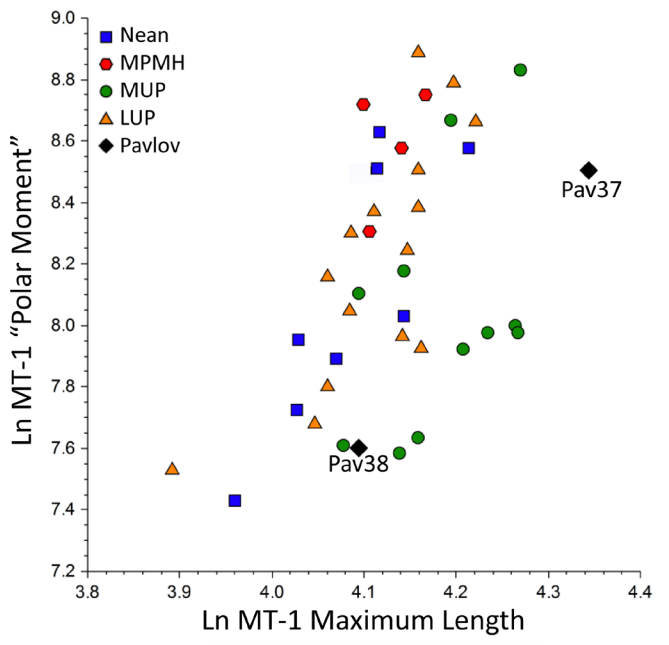

Figure 27. Bivariate plot of ln_e metatarsal polar moment of area (from external diameters) versus ln_e maximum length for Pavlov 37 and 38 and Late Pleistocene comparative samples. Abbreviations as in Figure 24. The comparative samples are significantly different at p=0.001; and Pavlov 37 (p=0.471) and 38 (p=0.993) are not significantly different from the MUP sample.

Samples sizes are small for comparisons of metatarsal 1 to 3 lengths, but the available paired lengths provide a modest difference across the comparative samples (Figure 26). The difference is largely a contrast of the Middle versus Upper Paleolithic remains. The Pavlov 38 proportions, even taking the estimations of its lengths into account (see Tables A10 and A12 below), fall among the Middle Paleolithic remains and the Upper Paleolithic ones with the relatively shorter hallucal metatarsals. Pavlov 37, in addition to having an absolutely long metatarsal 1 (see Figure 11), is among the Mid Upper Paleolithic ones (Grotte des Enfants 4, Paviland 1 and Sunghir 1) with the relatively longer first metatarsals.

In this context, it is possible to assess the diaphyseal hypertrophy (robusticity) of the metatarsal 1 diaphyses comparing a subperiosteal polar moment of area to metatarsal length (Figure 27). The samples are significantly different, but principally the Mid Upper Paleolithic sample deviates from the others. It may be that the relatively long lengths of the Pavlov 37 metatarsals account in part for its apparent gracility, but smaller MUP individuals (including Pavlov 38) remain among the more gracile Late Pleistocene individuals. Alternatively, it may be due to the more linear body proportions of some MUP remains (Holliday 1997), since lower limb diaphyseal rigidity should be scaled to bone length times body mass (Ruff 2000). Metatarsal 1 length relative to estimated body mass is not significantly different (p=0.189) across the Late Pleistocene samples (n=35), and it is very similar (p=0.695) across the three early modern human samples (n=30). Moreover, the more linear Middle Paleolithic modern human sample exhibits among the more robust metatarsals, and most of the Late Upper Paleolithic ones are more robust than the Pavlov and other MUP ones.

DISCUSSION AND CONCLUSION

The Pavlov 34 to 38 appendicular remains add to our growing sample of Mid Upper Paleolithic human remains, reinforcing and expanding the ranges of variation of this Late Pleistocene human group. The Pavlov 36 metacarpal 2 adds little to our assessment of hand morphology, although the pronounced radial diaphyseal sulcus is unusual. The lower limb elements are unexceptional in terms of basic functional implications, but they add to several aspects of genual and pedal variation.

The probably paired Pavlov 34 and 35 patellae are notable for being among the largest Late Pleistocene ones, well above those of the Dolní Věstonice 13 and 14 and Předmostí 3 males, and further above those of the Dolní Věstonice 3 and Předmostí 4 females. They are absolutely thick, approached only those of Dolní Věstonice 15 and 16 and the Ligurian Barma Grande 2 and Bausu da Ture 1. In relative thickness, Pavlov 35 is separate from other Upper Paleolithic patellae, falling among the Middle Paleolithic ones, and Pavlov 34 is similar. Even if they derive from a tall individual, similar to Dolní Věstonice 14 and the tallest Ligurian males, as is implied for the long Pavlov 37 pedal remains, their patellae would remain among the largest

and especially thickest of the Mid Upper Paleolithic ones.

The Pavlov 34 patella also stands out for the marked asymmetry of its medial versus lateral articular facets and the pronounced vertical sulcus in the lateral facet. Yet, in these aspects it is close to the pattern evident on the Dolní Věstonice 13 patellae, but not on the other Pavlovian patellae.

The Pavlov 37 and 38 tarsometatarsal skeletons, despite erosion especially of the latter one, present only a few features of note. The primary aspects for Pavlov 37 are its large dimensions. It is the longest Mid Upper Paleolithic (or Late Pleistocene) one for which data are available. This overall length is reflected as well in its talar and metatarsal 1 lengths. Pavlov 38, by comparison, is generally average in size, although its talar and metatarsal 1 lengths are among those of the Dolní Věstonice 13 and 16 (pelvically sexed) males, albeit also close to those of the females from Předmostí.

The various proportions of the Pavlov 37 and 38 pedal remains related to articular hypertrophy provide a mixed picture, although one in which they fall comfortably within Late Pleistocene and recent human ranges of variation. Both of their tali are among the ones with moderately small trochleae relative to talar length, but they differ with respect to malleolar projections (the former being broader). Their talar head-neck angles are average for the Late Pleistocene, but their sustentacular projections are moderately low. They both have evenly curved and fused anterior and medial talocalcaneal facets, as well as naviculocuboid facets. In this context, they both have relatively gracile metatarsal 1 diaphyses, although that of Pavlov 37 (and possibly Pavlov 38) might appear less so if appropriately scaled to body mass as well as bone length. Yet, the Pavlov 37 gracility is approached by the Cro-Magnon 4345, Paviland 1, Předmostí 3, and Sunghir 1 first metatarsals.

The Pavlov 34 to 38 human postcranial remains therefore amplify and reinforce the appendicular patterns evident in other Mid Upper Paleolithic human remains. In this, they show affinities in a number of aspects to the other central European Pavlovian human remains, from the regional Dolní Věstonice II and Předmostí sites, as well as generally to remains from across western Eurasia.

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Appendix I:
Preservation and Pathology of the Pavlov 34 to 38 Human Postcranial Remains

The human remains from Pavlov–Centre, identified in the course of zooarchaeological analysis of the faunal remains by PW and JW, are variably preserved. The Pavlov 36 metacarpal 2 is missing its proximal portion, but the other remains have been reduced through abrasion of the margins or portions of the trabecular bone. All of them are fragile, and all of the surfaces exhibit some degree of etching. Yet, a number of the articular subchondral bone surfaces are solid, with those of the Pavlov 38 pedal remains being most affected.

The bones are variably covered with thin gray encrustations, which are harder than the bone tissue and hence not practical to remove without damage to the underlying fragile bone. None of them obscure the skeletal morphology or affect their dimensions. The primary surfaces not affected are portions of the tarsal and metatarsal articulations, which appear reddish and were apparently in close articulation *in situ*.

There is extensive root etching of most of the bones. The evidence consists of both grooves into the surfaces, obvious especially on subchondral bone, and of fine tunnels into the trabecular bone.

PAVLOV 34: PATELLA – RIGHT (SEE FIGURE 3)

The bone is largely intact with minimal marginal abrasion (see Table A1 below; see Figure 3). The anterior surface and the superior quadriceps femoris surfaces are complete, but there is abrasion to the posterior half to one-third of the medial proximal surface. The anterior surface is preserved close to the apex inferiorly, but the non-articular surface between the femoral facets and the apex is absent posteriorly. The articular facets are largely intact, with minimal medial and superomedial marginal abrasion and more extensive bone loss along the inferior facet margins.

There are small, non-projecting spicules of bone on the lateral ≈12mm superiorly, for the quadriceps femoris insertion. There is thin surface erosion of the lateral one-quarter of the articular facets, which is not pathological.

PAVLOV 35: PATELLA – LEFT (SEE FIGURE 3)

The bone is a complete bone, but with etching/erosion on the margins, especially around the medial side, on the lateral edge, and the mid-inferior facet margin. There are encrustations on the articular facets, especially the lateral one, with subchondral erosion on the mid to mid-superior facets.

On the lateral side of the crest, between the medial and lateral facets, there is a small bony growth with its posterior surfaces smoothed over (Figure A1; see Table A1 below). The more evident portion is vertical and to the medial side, but additional growth is evident superolateral of it below gray encrustation. The area lateral and inferior of these growths exhibits bony resorption and trabecular rounding.

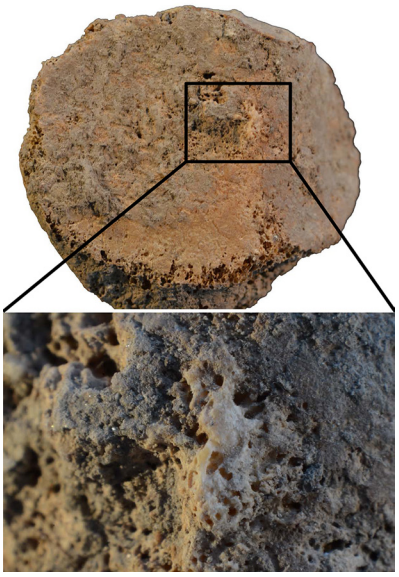

Figure A1. Posterior view of the Pavlov 35 left patella, with the position of the bony growth indicated, plus an enlargement of the additional bone.

It should reflect minor patellofemoral osteoarthritis.

PAVLOV 36: METACARPAL 2 – LEFT (SEE FIGURE 2)

The bone retains the distal portion and about three-quarters of the diaphysis, for a preserved length of 54.4mm (see Table A2 below; the original length of the bone should have been ≈68–69mm (see text). The bone is identified and sided by the beveling of the right head (in dorsal view).

The preserved portion of the diaphysis is intact, but with thin encrustations and minor surface etching. The head sustained a mid-dorsal depression and an ulnar puncture. The ulnar head damage and the proximal break are recent. There are no lesions.

PAVLOV 37: TARSOMETATARSAL SKELETONS – RIGHT AND LEFT (SEE FIGURES 7 AND 9)

Pavlov 37 retains thirteen of the tarsals (missing only the right cuboid bone) and nine of the metatarsals (lacking only the right metatarsal 5). None of the phalanges or sesamoid bones are preserved, nor are any portions of the distal tibiae and fibulae. They are associated as right and left pedal remains of one individual based on the strong symmetry of the individual paired elements, despite minor differences in osteometrics between sides (see Tables A3 to A14 below). There are no lesions on the bones.

Pavlov 37a: Talus – Right (see Figure 13)
A complete bone with abrasion to the plantar lateral malleolar surface, including the plantar tip of the surface, and slight abrasion to the dorsal head.

Pavlov 37b: Talus – Left (see Figure 13)
A complete bone but with abrasion to almost all of the margins, and especially around the anterolateral lateral malleolar/posterior calcaneal surfaces.

Pavlov 37c: Calcaneus – Right (see Figure 20)
Largely complete bone with surface bone loss across the entire lateral side and with erosion of the lateral cuboid and posterior talar facets. The tuberosity is intact for the Achilles tendon insertion, but the surface is eroded plantarly of it and across the dorsal margin.

Pavlov 37d: Calcaneus – Left (see Figure 20)
The bone is largely present, but there is extensive erosion to the lateral side, especially anteriorly, loss of most of the cuboid surface, and erosion to most of the tuberosity.

Pavlov 37e: Navicular – Right (see Figure 22)
Complete bone with erosion across the dorsal surface and around the tuberosity.

Pavlov 37f: Navicular – Left (see Figure 22)
Largely complete bone, but with more extensive dorsal erosion than the right one, bone loss on the dorsal tuberosity, and a general pitting of the cuneiform facets that obscures the articular margins.

Pavlov 37g: Cuboid – Left (see Figure 22)
Largely present with surface erosion dorsally and laterally, plus pitting of the metatarsal facets, especially of the metatarsal 5 facet.

Pavlov 37h: Medial Cuneiform – Right (see Figures 7 and 9)
Complete bone with gentle erosion to all of the medial side, resulting in medial marginal loss to the navicular and metatarsal 1 facets.

Pavlov 37i: Medial Cuneiform – Left (see Figures 7 and 9)
Intact bone with generalized erosion to all of the surfaces and the facet margins.

Pavlov 37j: Intermediate Cuneiform – Right (see Figure 7)
A complete bone with minor abrasion to the dorsal navicular facet and the lateral metatarsal 2 facet.

Pavlov 37k: Intermediate Cuneiform – Left (see Figure 7)
Largely present bone but with erosion and pitting to all of the surfaces except the dorsal navicular and lateral cuneiform facets.

Pavlov 37l: Lateral Cuneiform – Right (see Figure 7)
A complete bone with surface erosion to the medial and proximal tuberosity and to the dorsal margins of the navicular and metatarsal 3 facets.

Pavlov 37m: Lateral Cuneiform – Left (see Figure 7)
Complete tarsal with dorsolateral erosion and a hollowing out of the proximal tuberosity.

Pavlov 37n: Metatarsal 1 - Right (see Figure 25)
Intact bone with epiphyseal abrasion, especially on the dorsomedial base, the lateral head, and the medioplantar head.

Pavlov 37o: Metatarsal 1 – Left (see Figure 25)
The intact base and shaft with erosion of most of the lateral base, plus of the head midline, plantar intersesamoid crest, and medial sesamoid sulcus.

Pavlov 37p: Metatarsal 2 – Right (see Figure 18)
The complete shaft and base are present with minor erosion around the base. The head is a trabecular core with the lateral dorsal tubercle, which does not extend to the distal head.

Pavlov 37q: Metatarsal 2 – Left (see Figure 18)
The shaft is intact. The base is eroded medially and proximally such that none of the tarsal facets remain, but the proximolateral corner is very close to the original maximum extent. The distal end retains the dorsal tubercles and the trabecular head core, but articular bone is present only on the dorsal margin. Despite the absence of distal subchondral bone, the maximum preserved length of 87.3mm is very close to the original maximum length, anatomically estimated at 88mm (see Table A11 below).

Pavlov 37r: Metatarsal 3 – Right (see Figure 18)
The diaphysis and proximal articulations, with minor erosion to the dorsal base. The distal end is an eroded trabecular core of the head.

Pavlov 37s: Metatarsal 3 – Left (see Figure 18)
The complete bone with minor erosion to the lateral base and the medial and lateral head.

Pavlov 37t: Metatarsal 4 – Right (see Figure 18)
The diaphysis, the base eroded around the cuboid facet, and the proximal trabecular core of the head.

Pavlov 37u: Metatarsal 4 – Left (see Figure 18)
The diaphysis, the base with trivial dorsal cuboid facet erosion, and the trabecular core of the head with subchondral bone preserved on the mid-dorsal half of the trabecular core. The lengths (see Table A13 below) therefore require only minimal estimation of the missing distal head.

Pavlov 37v: Metatarsal 5 – Left (see Figure 18)
The diaphysis and the base with erosion to the plantar base and around the tubercle.

PAVLOV 38: TARSOMETATARSAL SKELETON – RIGHT; TALUS, CALCANEUS AND METATARSAL 4 – LEFT

Pavlov 38 consists of an extensively eroded right tarsometatarsal skeleton, missing only the cuboid bone, plus the talus, calcaneus, and one partial metatarsal (the fourth) from the left side (see Figures 8 and 9). As with Pavlov 37, the two sides are associated as a result of a high degree of symmetry, especially between the tali and the calcanei. None of the phalanges or sesamoid bones are retained, and the all of the metatarsals except the right metatarsal 1 lack their distal articulations. There is extensive loss of surface bone. There is no evidence of any lesions, but the degree of surface bone loss would make most minor lesions unrecognizable.

Pavlov 38a: Talus – Right (see Figure 14)
A complete bone with damage to the dorsomedial head and the posterior tubercles, plus minor abrasion to all of the articular margins and a general porosity of the subchondral bone.

Pavlov 38b: Talus – Left (see Figure 14)
The bone is largely intact, although it is missing the dorsomedial head. There is less pronounced damage to the plantolateral head, the lateral malleolar facet tip, and the posteromedial tubercle.

Pavlov 38c: Calcaneus – Right (see Figure 21)
A largely complete bone with erosion to the medial sustentaculum tali and the dorsal and lateral tuberosity, but it is missing the plantar half of the cuboid facet.

Pavlov 38d: Calcaneus – Left (see Figure 21)
A complete bone with marginal erosion, especially to the lateral cuboid facet, the dorsolateral posterior talar facet, and around the tuberosity.

Pavlov 38e: Navicular – Right (see Figures 8 and 9)
The core of the bone with the middles of the talar and cuneiform facets, with the circumferential margin present only for part of the cuboid facet. The tuberosity is absent.

Pavlov 38f: Cuboid – Right (see Figure 8)
An eroded and porous bone, but it retains most of the calcaneal facet, the medial side with the lateral cuneiform facet, the metatarsal 4 facet, and part of the dorsal surface.

Pavlov 38g: Medial Cuneiform – Right (see Figures 8 and 9)
The eroded core of the bone with the dorsal metatarsal 1 facet, the middle of the navicular facet, and part of the plantar intermediate cuneiform facet.

Pavlov 38h: Intermediate Cuneiform – Right (see Figure 8)
The dorsal half of the bone with the dorsal half of the metatarsal 2 facet.

Pavlov 38i: Metatarsal 1 – Right (see Figure 25)
The diaphysis, the dorsolateral corner of the tarsal facet, and the medial half of the head without the plantar edge of the intersesamoid crest. Although both articulations are incomplete, they are sufficient to estimate the articular length at ≈ 57mm, from which the maximum length can be estimated (see Table A10 below).

Pavlov 38j: Metatarsal 2 – Right (see Figure 18)
The proximal three-quarters of the shaft with the dorsal third of the base.

Pavlov 38k: Metatarsal 3 – Right (see Figure 18)
The diaphysis, the eroded base with the plantolateral tarsal facet, and the medial dorsal distal tubercle. Although the head is absent and the base is incomplete, the distance from the mid-base to the distal dorsal tubercle is sufficient to estimate the length of the bone (see Table A12 below).

Pavlov 38l: Metatarsal 4 – Right (see Figure 18)
The diaphysis extending proximolaterally with the metatarsal 5 facet, the mid-lateral edge of the cuboid facet, and the distal flare for the dorsal tubercles.

Pavlov 38m: Metatarsal 4 – Left (see Figure 18)
The diaphysis and the base, with a hole in the plantar base.

Pavlov 38n: Metatarsal 5 – Right (see Figure 18)
The diaphysis with the trabecular core of the base and the metatarsal 4 facet.

APPENDIX II: OSTEOMETRIC MEASUREMENTS OF THE PAVLOV 34 TO 38 POSTCRANIAL REMAINS

(##) indicates a measurement with minor estimation due to skeletal damage; [##] indicates one that has been predicted from a smaller but preserved dimension; ((##)) indicates a more tenuous estimation due to skeletal damage. "M-#" refers to the Martin system measurement definition in Bräuer (1988).

TABLE A1. PAVLOV 34 AND 35 PATELLAR DIMENSIONS (in millimeters) AND A DISCRETE TRAIT.

	M-#	*Pavlov 34 right*	*Pavlov 35 left*
Maximum height	1	(44.6)	46.3
Maximum breadth	2	51.5	48.5
Maximum thickness	3	25.4	25.0
Maximum dimensions geometric mean[1]	--	38.8	38.3
Middle thickness[2]	--	23.0	23.0
Articular breadth	--	48.8	48.5
Medial facet breadth[3]	--	32.7	30.7
Lateral facet breadth[3]	--	19.6	23.1
Vastus notch	--	absent (flat)	absent (convex)

[1]The geometric mean of the maximum height, breadth, and thickness.
[2]The anteroposterior thickness at the proximodistal middle of the articular facet.
[3]The distance from the middle of the articular ridge to the medial or lateral articular margin (Trinkaus 2000).

TABLE A2. LINEAR DIMENSIONS OF THE PAVLOV 36 LEFT SECOND METACARPAL (in millimeters).

	M-#	*Pavlov 36*
Midshaft dorsopalmar diameter	7	8.7
Midshaft radioulnar diameter	6	8.5
Distal height	11	12.8
Distal dorsal tubercle breadth [1]	--	13.2
Distal palmar tubercle breadth[1]	--	12.3
Distal dorsal articular breadth[2]	--	9.0
Distal palmar articular breadth[2]	9	10.7

[1]Radioulnar breadth across the external margins of the dorsal or palmar tubercles.
[2]Radioulnar breadth across the external margins of the dorsal or palmar articulation.

TABLE A3. DIMENSIONS (in millimeters and degrees) AND DISCRETE TRAITS OF THE PAVLOV 37 AND 38 TALI.

	M-#	*Pavlov 37*		*Pavlov 38*	
		right	*left*	*right*	*left*
Maximum length	1a	69.6	68.8	--	(57.0)
Talar length	1	62.7	62.5	53.3	53.7
Articular breadth	2b	(55.0)	(53.0)	(43.0)	(43.0)
Articular height	3b	31.4	29.2	27.0	25.5
Trochlear length	4	39.6	39.0	31.6	31.9
Trochlear breadth	5	33.3	32.6	29.8	29.9
Trochlear anterior breadth	--	(34.1)	--	(29.3)	31.1
Trochlear posterior breadth	--	25.0	(24.5)	--	--
Head-neck length	8	26.4	27.5	18.7	19.3
Head length	9	41.2	41.3	--	--
Head breadth	10	26.3	27.7	--	--
Anteromedial calcaneal facet length[1]	--	33.4	--	--	28.3
Anteromedial calcaneal facet breadth	--	17.7	--	--	16.9`
Posterior calcaneal facet length	12	(41.0)	--	(31.5)	--
Posterior calcaneal facet breadth	13	24.3	25.0	19.8	20.4
Trochlear angle[2]	--	8°	6°	12°	10°
Head-neck angle	16	25°	24°	24°	27°
Torsion angle (trochlear)	17	46°	43°	(36°)	(40°)
Medial malleolar extension[3]	--	present	present	present	present
Medial trochlear extension	--	present	present	present	present
Lateral trochlear extension	--	present	present	present	absent
Lateral squatting facet	--	present	present	present	present
Sulcus tali facet[4]	--	absent	--	absent	absent
Anteromedial calcaneal fusion	--	complete	complete	complete	complete

[1]The length and breadth of the combined anterior and medial calcaneal facets. The breadth is the maximum anteromedial to posterolateral dimension.

[2]The angle in the horizontal plane of the talus between the medial and lateral trochlear margins (Trinkaus1975a).

[3]The discrete traits follow Barnett (1954) and Trinkaus (1975b). The "extensions" are anterior extensions of the malleolar facet and the trochlear margins relative to the primary trochlear anterior margin.

[4]A distinct facet on the posterior surface of the sulcus tali, rounding anteriorly from the posterior calcaneal articulation (Trinkaus1975b), also known as a *facies inferior accesoria corporis tali* (Baba and Endo 1982). To be scored as present, it must be a distinct facet and not merely a rounding of the margin.

TABLE A4. DIMENSIONS (in millimeters) AND DISCRETE TRAITS OF THE PAVLOV 37 AND 38 CALCANEI.

	M-#	*Pavlov 37*		*Pavlov 38*	
		right	*left*	*right*	*left*
Maximum length	1	91.6	--	(75.0)	--
Total (articular) length	1a	85.5	--	(71.0)	--
Body length	5	65.2	--	(55.0)	--
Medial breadth	2	(48.0)	(46.2)	--	39.0
Sustentacular breadth	6	14.8	14.0	--	10.5
Body breadth[1]	--	(33.2)	(32.2)	--	28.5
Minimum body height[2]	--	42.0	41.6	36.3	38.7
Tuberosity height	7	49.0	--	--	43.5
Tuberosity breadth	8	--	--	--	28.7
Medial process length[3]	--	34.5	--	(27.0)	--
Anteromedial talar facet length[4]	--	(42.5)	(40.0)	28.8	28.6
Anterior talar facet breadth[4]	--	9.4	8.5	9.0	9.3
Medial talar facet breadth[4]	--	13.9	15.1	13.6	(14.3)
Posterior talar facet length	9	36.6	35.7	28.4	29.4
Posterior talar facet breadth	10	24.5	25.6	18.9	--
Anteromedial talar facet fusion[5]	--	complete	complete	complete	complete
Anteromedial talar facet curvature[5]	--	even	even	even	even

[1]Medial breadth minus sustentacular breadth.

[2]Minimum body height between the posterior talar facet and the tuberosity, anterior of the medial process's anterior extent.

[3]Most posterior point on the tuberosity to the most anterior point on the medial process, measured along the long axis of the calcaneal body.

[4]The maximum length of the combined anterior and medial talar facets, and the maximum breadths of each facet.

[5]The degree of fusion of the anterior and medial talar facets, and whether the two facets make an even curve or are angled relative to each other.

TABLE A5. DIMENSIONS (in millimeters) AND A DISCRETE TRAIT OF THE PAVLOV 37 AND 38 NAVICULAR BONES.

	M-#	*Pavlov 37*		*Pavlov 38*
		right	*left*	*right*
Maximum thickness	8	22.0	21.5	--
Minimum thickness	7	11.6	12.2	--
Mediolateral breadth[1]	1	45.1	43.0	--
Dorsoplantar height[1]	2	29.6	(30.0)	--
Talar facet length[1]	3	30.5	(31.0)	--
Talar facet breadth[1]	4	26.1	26.0	--
Cuboid facet	--	present	present	present[5]
Cuboid facet mediolateral dimension[2]	--	--	13.3	--
Cuboid facet proximodistal dimension[2]	--	7.3	9.5	--
Medial cuneiform facet breadth[3]	--	14.9	--	--
Intermediate cuneiform facet breadth[3]	--	17.7	--	--
Lateral cuneiform facet breadth[3]	--	14.8	--	--
Tuberosity projection[4]	--	(13.0)	--	--
Tuberosity thickness[4]	--	--	21.0	--

[1]The breadths and lengths of the navicular bone overall and of the talar facet are taken parallel and perpendicular to the dorsal margin of the talar facet.
[2]The maximum dimensions of the articular facet for the cuboid bone. Note that a facet is present on the Pavlov 38 navicular bone, but the margins are too abraded to measure the diameters.
[3]The maximum mediolateral breadths of the facets for each cuneiform bone.
[4]The medial projection of the navicular tuberosity from the medial extent of the talar facet and the maximum proximodistal thickness of the tuberosity.
[5]Only a portion of the cuboid facet is preserved; it measures 4.2mm wide and 4.9mm deep.

TABLE A6. DIMENSIONS (in millimeters) OF THE PAVLOV 37 AND 38 RIGHT CUBOID BONES AND A DISCRETE TRAIT.

	M-#	*Pavlov 37*	*Pavlov 38*
Height	3	26.6	21.4
Medial length	1	39.0	30.0
Lateral length	2	((20.0))	--
Calcaneal facet height	--	(20.0)	--
Calcaneal facet breadth	--	(30.0)	--
Navicular facet height	--	13.2	--
Navicular facet breadth	--	10.0	--
Lateral cuneiform facet height	--	13.2	--
Lateral cuneiform facet breadth	--	12.8	--
Navicular facet	--	present	--

TABLE A7. DIMENSIONS (in millimeters) AND A DISCRETE TRAIT OF THE PAVLOV 37 AND 38 MEDIAL CUNEIFORM BONES.

	M-#	*Pavlov 37*		*Pavlov 38*
		right	*left*	*right*
Dorsal length	3	30.0	--	--
Middle length	2	27.3	26.1	21.6
Plantar length	1	29.7	29.1	--
Total breadth	8	--	20.3	--
Navicular facet height	4	(26.5)	--	--
Navicular facet breadth	--	17.2	--	--
Metatarsal facet height	5	31.5	--	--
Metatarsal facet convexity[1]	--	minimal	absent	--

[1]Whether the articular facet for the first metatarsal is distinctly distally convex in a mediolateral sense, as opposed to being transversely flat.

TABLE A8. DIMENSIONS OF THE PAVLOV 37 AND 38 INTERMEDIATE CUNEIFORM BONES (in millimeters).

	M-#	*Pavlov 37*		*Pavlov 38*
		right	*left*	*right*
Dorsal length	1	22.1	21.6	17.9
Middle length	--	19.1	--	--
Navicular facet height	--	18.7	--	--
Navicular facet breadth	4	15.3	(16.0)	--
Metatarsal facet height	--	25.0	(22.0)	--
Metatarsal facet breadth	3	13.2	13.9	--

TABLE A9. DIMENSIONS OF THE PAVLOV 37 LATERAL CUNEIFORM BONES (in millimeters).

	M-#	*right*	*left*
Dorsal length	1	28.2	28.0
Middle length	--	26.2	26.0
Navicular facet height	--	16.3	18.3
Navicular facet breadth	--	14.8	14.2
Metatarsal facet height	--	23.1	24.5
Metatarsal facet breadth	4	17.0	16.0
Tuberosity height[1]	--	(28.5)	--
Tuberosity breadth[1]	3	23.5	22.0

[1]The height from the dorsal lateral cuneiform bone to the plantar surface of the plantar tuberosity, and the maximum proximodistal breadth of the tuberosity. Tuberosity height minus navicular facet height provides a measure of the plantar projection of the proximal end of the tuberosity.

TABLE A10. DIMENSIONS (in millimeters and degrees) AND DISCRETE TRAITS OF THE PAVLOV 37 AND 38 FIRST METATARSALS.

	M-#	*Pavlov 37*		*Pavlov 38*
		right	*left*	*right*
Maximum length	1	(78.0)	(76.0)	[59.2][5]
Articular length	1b	75.5	75.2	(57.0)
Midshaft height	4	15.8	15.6	10.6
Midshaft breadth	3	14.0	14.5	13.3
Midshaft circumference	--	47.0	47.0	40.0
Proximal maximum height	7	32.8	33.3	--
Proximal maximum breadth	6	(22.5)	--	--
Proximal articular height	7b	31.2	31.3	--
Proximal articular breadth	6b	17.1	--	--
Tarsal facet concavity-dorsal[1]	--	present	present	(present)
Tarsal facet concavity-plantar[1]	--	shallow	shallow	--
Metatarsal 2 facet[2]	--	present	present	--
Metatarsal 2 facet height[2]	--	--	7.8	--
Metatarsal 2 facet breadth[2]	--	--	6.7	--
Distal height	9	(25.0)	24.5	--
Distal medial height[3]	--	22.0	22.5	(15.6)
Horizontal head angle[4]	--	--	(5°)	(9°)
Subperiosteal polar moments of area[6]	--	4838	5036	2001

[1]Whether the proximal (medial cuneiform) facet is mediolaterally distinctly concave and its degree if more modestly concave, scored for the dorsal and plantar halves of the facet as preserved.

[2]Whether a distinct facet is present for the second metatarsal, and its height and breadth if present.

[3]The dorsoplantar distance from the medial sesamoid sulcus to the dorsal head; the lateral side is not sufficiently preserved on the Pavlov 37 and 38 first metatarsals.

[4]The angle between the intersesamoid crest on the plantar head and the diaphyseal axis, in the horizontal plane of the bone. A positive angle indicates a lateral deviation of the distal crest. Note that both of the Pavlov metatarsals have eroded crests (see Figure 25), and hence the angles are approximate but sufficiently reliable to indicate a distolateral deviation.

[5]The maximum length of the Pavlov 38 metatarsal 1 (59.2±0.9mm) is estimated from its articular length using a least squares regression based on recent human first metatarsals (MaxLen = 0.930 x ArtLen + 6.21, r^2=0.961, n=29).

[6]Computed from the midshaft height and breadth using standard ellipse formulae (O'Neill and Ruff 2004), modeling the diaphysis as a solid beam. As such, they are greater than polar moments of area employing only the distribution of cortical bone.

TABLE A11. DIMENSIONS (in millimeters and degrees) OF THE PAVLOV 37 AND 38 SECOND METATARSALS.

	M-#	*Pavlov 37*		*Pavlov 38*
		right	*left*	*right*
Maximum length	2	--	(88.0)[1]	--
Articular length	1b	--	[83.5][1]	--
Midshaft height	4	9.6	9.9	10.3
Midshaft breadth	3	8.2	8.0	7.9
Proximal articular height	7b	(22.0)	--	--
Proximal articular breadth	6b	(15.3)	--	14.7
Proximal vertical angle[2]	--	7°	--	--

[1]The maximum length is estimated from the preserved portions of the bone (length: 87.3mm), given that the proximal and distal extents are very close the original landmarks. The articular length (83.5±1.1mm) is predicted from the maximum length using a least squares regression based on recent human second metatarsals (ArtLen = 0.918 x MaxLen + 2.73, r^2=0.966, n=27).

TABLE A12. DIMENSIONS (in millimeters and degrees) OF THE PAVLOV 37 AND 38 THIRD METATARSALS.

	M-#	*Pavlov 37*		*Pavlov 38*
		right	*left*	*right*
Maximum length	2	--	84.1	[71.0][1]
Articular length	1b	--	81.8	[69.0][1]
Midshaft height	4	10.5	10.0	8.7
Midshaft breadth	3	8.2	8.2	6.2
Proximal articular height	7b	(21.5)	20.1	--
Proximal articular breadth	6b	16.0	15.2	--
Metatarsal 2 facet height: dorsal	--	--	6.4	--
Metatarsal 2 facet height: plantar	--	6.0	5.4	--
Metatarsal 2 facet breadth: dorsal	--	10.9	8.9	--
Metatarsal 2 facet breadth: plantar	--	4.5	3.0	--
Metatarsal 4 facet height	--	9.7	8.6	--
Metatarsal 4 facet breadth	--	12.6	12.7	--
Torsion angle	11	--	20°	--
Proximal horizontal angle[2]	--	15°	20°	--
Proximal vertical angle[3]	--	11°	10°	--

[1]The Pavlov 38 maximum and articular lengths are estimated from the distance between the mid-tarsal facet to the middle of the distal dorsal tubercles (60.1mm), using least squares regressions based on recent human third metatarsals (ArtLen = 1.058 x TubLen + 5.36, r^2=0.950, n=40; MaxLen = 1.175 x TubLen + 0.34, r^2=0.920, n=40). The predicted values are 68.9±1.1mm and 70.9±1.6mm respectively, rounded off to 69mm and 71mm.

[2]The angle, in the horizontal plane of the bone, between the proximal (cuneiform) facet and the diaphyseal axis. An angle >0° indicates a proximomedial facing of the facet.

[3]The angle, in the sagittal plane of the bone, between the proximal (cuneiform) facet and the diaphyseal axis. An angle >0° indicates a proximoplantar facing of the facet.

TABLE A13. DIMENSIONS (in millimeters and degrees) OF THE PAVLOV 37 AND 38 FOURTH METATARSALS.

	M-#	*Pavlov 37*		*Pavlov 38*	
		right	*left*	*right*	*left*
Maximum length	2	--	(81.5)	--	--
Articular length	1b	--	(78.0)	--	--
Midshaft height	4	10.2	10.2	8.9	9.5
Midshaft breadth	3	8.4	8.3	5.4	6.0
Proximal articular height	7b	--	(17.6)	--	--
Proximal articular breadth	6b	--	13.8	--	--
Metatarsal 3 facet height	--	--	10.4	--	9.4
Metatarsal 3 facet breadth	--	--	11.6	--	--
Metatarsal 5 facet height	--	8.1	10.6	--	--
Metatarsal 5 facet breadth	--	(14.0)	15.0	--	--
Torsion angle	11	--	24°	--	--
Proximal horizontal angle[1]	--	--	16°	--	16°
Proximal vertical angle[2]	--	--	14°	--	--

[1]The angle, in the horizontal plane of the bone, between the proximal (cuboid) facet and the diaphyseal axis. An angle >0° indicates a proximomedial facing of the facet.

[2]The angle, in the sagittal plane of the bone, between the proximal (cuboid) facet and the diaphyseal axis. An angle >0° indicates a proximoplantar facing of the facet.

TABLE A14. DIMENSIONS (in millimeters and degrees) OF THE PAVLOV 37 AND 38 FIFTH METATARSALS.

	M-#	*Pavlov 37*	*Pavlov 38*
		right	*right*
Midshaft height	4	13.4	9.1
Midshaft breadth	3	9.7	7.1
Proximal articular height	7b	14.6	--
Proximal articular breadth	6b	15.9	--
Metatarsal 4 facet height	--	12.5	9.5
Metatarsal 4 facet breadth	--	12.0	10.1
Proximal horizontal angle[1]	--	45°	--
Proximal vertical angle[2]	--	0°	--

[1]The angle, in the horizontal plane of the bone, between the proximal (cuboid) facet and the diaphyseal axis. An angle >0° indicates a proximomedial facing of the facet.

[2]The angle, in the sagittal plane of the bone, between the proximal (cuboid) facet and the diaphyseal axis. The angle of 0° indicates a vertical tangent to the facet perpendicular to the diaphyseal axis.

APPENDIX III: LATE PLEISTOCENE HUMAN REMAINS INCLUDED IN THE COMPARATIVE SAMPLES, BY BONE[1]

	Patella	*Talus*	*Calcaneus*	*MT-1*	*MT-3/4*
Neandertals					
Amud 1	--	1, 15	1	15	--
La Chapelle-aux-Saints	1	1	1	--	--
La Ferrassie	2	1, 2	1, 2	1, 2	1, 2
Kiik-Koba 1	1	1	1	1	1
Krapina	see note 2	see note 2	see note 2	see note 2	see note 2
Okladnikov	--	10	--	--	--
La Quina	--	1	--	--	--
Regourdou	1	1	1, 2	--	--
St. Césaire	1	--	--	--	--
Shanidar	1, 4, 5, 6	1, 3	1, 3	1	1, 4, 6, 8
Spy	2	2	2	1	1
Subalyuk	1	--	--	--	--
Tabun	1	1	1	1	1
Middle Paleolithic Modern Humans					
Qafzeh	3, 9	3, 8, 9	8, 9	3, 8, 9	8
Skhul	4	4 to 7	4	4, 5	4
Early/Mid Upper Paleolithic					
Barma Grande	--	1, 2	--	1	--
Bausu da Ture	1, 2	2	--	2	--
Caviglione	1	--	1	1	--
Cro-Magnon	--	see note 3	see note 3	see note 3	see note 3
Dolní Věstonice	3, 13 to 16	3, 13, 15, 16	13, 15	14 to 16	--
Grotte des Enfants	--	4 to 6	--	4	--
Mladeč	--	30	--	--	--
Nazlet Khater	--	2	--	--	--
Nahal En-Gev	--	1	1	--	--
Ostuni	1	1	--	--	--
Paglicci	25	25	--	--	--
Pataud	1	1	1	1	1
Paviland	--	1	1	1	--
Předmostí	3, 4, 14	3, 9, 10, 14	3, 9, 10, 14	3, 4, 9, 10, 14	--
Sunghir	1	1	1	1	1
Tianyuan	--	1	--	--	--
Veneri (Parabita)	--	1, 2	--	--	--

	Patella	*Talus*	*Calcaneus*	*MT-1*	*MT-3/4*
Late Upper Paleolithic					
Arancio	1	1	1	1	--
Arene Candide	2, 5, 10	2. 4. 5. 10	2. 4. 5. 10, 13	2, 3, 5, 10	--
Bichon	1	1	--	--	--
Cap Blanc	1	1	1	1	--
Chancelade	1	1	--	1	--
Continenza	--	1	--	--	--
En-Gev	--	1	--	1	1
Lafaye (Bruniquel)	1	--	--	1	--
Laugerie Basse	4	4	--	--	--
La Madeleine	--	--	--	1	1
Maritza	--	--	2	--	--
El Mirón	1	1	1	1	--
Neve David	--	1	1	--	--
Oberkassel	--	--	1	1	--
Oetrange	--	--	--	--	unn.
Ohalo	2	2	2	2	2
Le Peyrat	5	5	--	5	--
Rochereil	1	--	--	--	--
San Teodoro	1, 4	1, 4	--	--	--
Tagliente	1	1	1	1	--

[1]The numbers of the individual specimens providing data are indicated for each site and by bone(s). Not all bones provide the full suite of comparative measurements, and some elements only provide discrete trait data (see Table 2).

[2]The Krapina sample includes various isolated elements (Trinkaus 2016). The patellae providing data for the comparisons include Krapina 215.1 to 215.3, 215.5, 216.1, 216.3, 216.4, 216.6, 216.8, and 216.9. The tali providing comparative data are Krapina 235 to 237, 238.1 to 238.5, 239.1 and 239.2. The first metatarsals providing comparative data are Krapina 245 and 246. The third and fourth metatarsals providing angles are Krapina 247.1 to 247.3 and 248.1 to 248.3. The Krapina 240 and 240.1 calcanei provide discrete data, as do the Krapina 246.1 and 246.2 second metatarsals and the Krapina 218 and 219 distal tibiae.

[3]The Cro-Magnon sample includes various isolated elements. The tali providing data for the comparisons are Cro-Magnon 4337 and 4338. The one Cro-Magnon calcaneus is unnumbered. The first metatarsals providing data are Cro-Magnon 4345 and 4345bis, plus the Cro-Magnon 4346 metatarsal 2 providing metatarsal 1-2 facet data. The Cro-Magnon fourth metatarsals providing base angles are Cro-Magnon 4347 and 4348.