Anatomical evidence for the antiquity of human footwear use

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Abstract

Archeological evidence suggests that footwear was in use by at least the middle Upper Paleolithic (Gravettian) in portions of Europe, but the frequency of use and the mechanical protection provided are unclear from these data. A comparative biomechanical analysis of the proximal pedal phalanges of western Eurasian Middle Paleolithic and middle Upper Paleolithic humans, in the context of those of variably shod recent humans, indicates that supportive footwear was rare in the Middle Paleolithic, but that it became frequent by the middle Upper Paleolithic. This interpretation is based principally on the marked reduction in the robusticity of the lesser toes in the context of little or no reduction in overall lower limb locomotor robusticity by the time of the middle Upper Paleolithic.

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1. Introduction

Since recent humans are the only extant species whose members frequently use some form of footwear for thermal protection in colder climates and mechanical protection in all environments, it is of interest to document the antiquity of the routine use of footwear as it relates to human locomotor and environmental adaptations. To date, investigation of this topic has been restricted to limited forms of evidence, given the almost universal prehistoric manufacture of foot gear out of perishable plant and/or animal materials. The earliest direct evidence for this practice dates to the terminal Pleistocene, even though it appears likely that it was engaged in for considerably greater antiquity. Given the rareness of the preservation of organic materials from which shoes could be manufactured prior to the terminal

Pleistocene, the evidence for earliest forms of foot protection is likely to be indirect. In the context of this, the relative robusticity of human lateral toes might provide insight into the frequency of use of footwear prior to the terminal Pleistocene.

2. Archeological evidence for the antiquity of footwear

Direct evidence for footwear, in the form of sandals made of plant fibers and/or leather, extends back to the early millennia of the Holocene and the terminal millennia of the Pleistocene. Ironically, all of the preserved and well dated specimens derive from North America, where largely complete sandals have been directly dated to between 6500 and 9000 years B.P. [17,18,28,29,39] and may well extend back into the terminal Pleistocene [3].

Comparable evidence for undisputed footwear of a similar antiquity is currently unknown in the Old

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World. There is one case from the late Upper Paleolithic of France, from the Grotte de Fontanet [16,22], of a footprint in a soft substrate interpreted as having been made by a foot wearing a soft and flexible moccasin-like covering. In addition, the arrangements of beads, apparently sewn onto clothing, around the feet of the Sunghir 1 adult skeleton (ca. 23,000 ^{14}C years B.P.) and the Sunghir 2 and 3 immature remains (ca. 24,000 ^{14}C years B.P.) [6,59] imply that they were buried with foot protection. Yet, there is a large variety of footprints in European Upper Paleolithic parietal art caves and karstic systems, extending back to ca. 30,000 years B.P. and made by unshod feet [8,22,27,55,56,94,100], indicating that these Paleolithic populations frequently went barefoot.

These few data points regarding Upper Paleolithic footwear are supplemented by growing data on the antiquity of the use of fibers to manufacture cordage, textiles, and other woven objects. These are reasonably well documented for the late Upper Paleolithic of Eurasia [2,3,20]. In older deposits, evidence of them has been found at Mezhirich (Ukraine) and Kosoutsy (Moldova) after ca. 17,000 ^{14}C years B.P. [2], ca. 19,000 ^{14}C years B.P. at Ohalo II (Israel) [48], and especially at the Moravian sites of Pavlov I and Dolní Věstonice I and II, dated to ca. 25,000 to 27,000 ^{14}C years B.P. [2,3]. Yet, most of these indications of weaving are either small fragments or impressions and provide little evidence of the functional objects of which they formed part. A number of the middle Upper Paleolithic (Gravettian) figurines provide indications of woven apparel [72]. None of the few human depictions that preserve feet furnish evidence of footwear [1,21], but probable depictions of boots are present among the ceramics from Pavlov I [71]. The evidence for textiles is joined by the presence of eyed needles by at least the Solutrean [76] and Gravettian faunal profiles at sites such as Pavlov I [47] suggesting the trapping of fur-bearing animals for skins and hence clothing.

Together these archeological data suggest that foot protection and insulation were readily available to people by the second half of the Upper Paleolithic (or its regional equivalent), sometime after the last glacial maximum. It is likely, based on the presence of weaving and fur-bearing animals in the Moravian sites and especially the pedal distribution of beads on the Sunghir burials and the Pavlov ceramic boots, that some form of footwear was being routinely, if not universally, employed by the middle Upper Paleolithic.

Prior to this time, however, there is no archeological evidence as to the use of artificial foot protection. The only related evidence comes from an isolated footprint in Vârtop Cave (Romania) [53], probably from a Neandertal given its age; it was made by a barefoot person and probably an habitually unshod one given the degree of medial divergence of the hallux [46].

One can nonetheless reasonably infer that, in order to survive the thermal rigors of a glacial period winter in mid-latitude Eurasia, Late Pleistocene humans must have had some form of insulation over their feet [24], and this is supported by considerations of human thermal physiology in the context of variation in Late Pleistocene human body proportions [4]. Yet, recent humans exhibit a variety of inherited and acquired vasoregulatory adjustments which limit the tendency to develop tissue damage in the hands and feet under cold stress [25,52], and it is likely that similar adjustments could have protected Pleistocene human feet from all but the most severe thermal stress. The question therefore remains archeologically open as to when, and in what context, human populations developed the frequent use of footwear.

3. A biomechanical scenario for the antiquity of footwear

In the context of these archeological observations, it is appropriate to ask whether there might be human anatomical reflections of the antiquity of footwear. Since the foot provides the contact between the body and the substrate, and since the use of footwear with a semi-rigid sole will alter the distribution of mechanical forces through the foot, it might be possible to perceive differences in the relative hypertrophy of portions of the foot in response to changes in habitual biomechanical loads through the pedal skeleton. It should be noted that all of these Late Pleistocene humans, on the basis of footprints and skeletal remains, had feet which functioned in the same basic manner as those of recent humans [43,82,86,95].

Unfortunately, analyses of frequently unshod extant humans and their footprints [7,44,46,57] provide little data on pedal loading patterns. They have primarily established similar patterns of subtalar weight-distribution across human populations, and they have noted the generally lower levels of hallux valgus and greater anterior pedal breadth in feet without constricting footwear. A framework based on clinical data from (albeit habitually shod) recent humans has therefore been constructed to permit inferences of pedal loading patterns among Late Pleistocene humans.

During the stance phase of a normal striding bipedal gait, the ground reaction force (GRF) is principally transmitted through the subtalar skeleton, with peak forces at heel-strike through calcaneus and at heel-off through the metatarsophalangeal articulations. These GRFs are continued but reduced at toe-off, principally through the hallux. Whether shod or unshod, these reaction forces should remain consistent for a given level and pattern of locomotion, the resultant forces through the foot being altered principally by any elasticity in the

footwear and minor changes in foot position constrained by the shoe. It is primarily the diffusion of forces across the plantar foot that is produced by footwear, such that peak forces on portions of the foot are frequently reduced [10,50]. The forces in the lesser toes (rays 2 to 5) should be also be markedly altered by the use of footwear.

During heel-off in barefoot locomotion, the toes are passively dorsiflexed, producing tension in the plantar aponeurosis [34]. The elastic tensile force in the plantar aponeurosis is accompanied by contraction of the flexor hallucis longus and flexor digitorum longus muscles [30,78], both of which produce digital plantarflexion and increase GRF on the toes. The tensile force in the plantar aponeurosis is accompanied during the second half of stance phase by contraction of the intrinsic plantar muscles, in particular abductor hallucis, flexor hallucis brevis and flexor digitorum brevis [42]. It is of note that once the ipsilateral heel-strike occurs, it is principally flexor hallucis longus (plus peroneus longus and brevis, which evert the foot and thereby shift the point of GRF medially), which continues to show contraction [78].

The combined effect of tension in the extrinsic and intrinsic flexor muscles and the plantar aponeurosis is to increase the GRF under the pedal digits, especially under the hallux during active propulsion [31]. In standing, the GRF is borne principally by the heel and the ball of the foot, with the forces across the toes, both medially and laterally, being half to a third of those across the ball of the foot [15]. A lower pedal arch, a common configuration in individuals without constricting footwear [57], increases the hallucal plantar pressure and has little effect on the lateral toes [14]. With walking, the GRFs are generally tripled in the forefoot, and the pressure on the hallux matches or exceeds that on the metatarsal heads, whereas the GRFs through the lateral toes remain at about one-third to one half of those on the hallux and anterior subtalar skeleton [14,97], although collectively the pressure on the lateral toes may approach that of the hallux [23]. The mediolateral contrast increases with greater speed, such that the augmentation in GRF is principally on the hallux with little increase on the lateral toes [77,97], and in active running there is little significant GRF through the toes [13].

From these anatomical and ground reaction force considerations, it is reasonable to infer that the principal locomotor forces across the anterior foot during heel-off to toe-off occur across the metatarsal heads and, to a lesser degree, the hallux, with the lateral toes having a minor role in propulsion. Yet, in barefoot locomotion on an uneven or compliant substrate, in contrast to the level, firm and smooth surfaces used in force plate analyses, the passive plantarflexion of the lateral toes from the plantar aponeurosis and digital flexor muscles

will curl the lateral toes into the ground during mid-stance to heel-off. This action will increase the traction during heel-off, and it will also induce bending forces on the lateral toes, from both the vertical component of GRF (which will be resisted in part by the flexor tendons) and from the transverse component of GRF (which will laterally bend the toes in most individuals given toeing-out) [88]. These biomechanical forces on the lesser toes will vary with locomotor mode and with substrate texture and hardness, producing a complex mosaic of bending forces on the toes during barefoot locomotion in a natural environment.

The introduction of footwear has little effect on the basic pattern of heel to forefoot patterns of GRF during walking, as clinical studies with and without shoes demonstrate [10,14,35,49,77]. It will, however, affect the bending forces through the hallux by diffusing them broadly across the medial forefoot. Moreover, footwear, with a compliant sole and especially a rigid one, will eliminate the traction role of the lesser toes. Although this effect will not eliminate vertical GRF on the lateral toes, since they will still flex against the sole of the shoe, it should reduce the overall level of vertical GRF by distributing it across the forefoot. Yet, it will remove the lateral bending on the lesser toes. Since lateral toe hypertrophy in part involves the mediolateral expansion of the phalangeal diaphyses to resist mediolateral bending forces [88], this should be reflected in reduced robusticity of those lateral phalanges.

From these considerations, it is therefore hypothesized that the robusticity of the hallucal phalanges should be largely proportional to general levels of locomotion and the associated forces on the forefoot. Yet, they should show some degree of relative reduction in robusticity with the use of shoes, given the resultant diffusion of GRF through the anteromedial foot during heel-off and toe-off. At the same time, the levels of robusticity of the lateral toes should be directly proportional to locomotor levels but strongly influenced by, and inversely proportional to, the degree to which supportive footwear is used.

4. Phalangeal diaphyses and load levels on the forefoot

Inferences of differential anterior pedal load levels from phalangeal diaphyseal robusticity assumes that phalangeal diaphyses respond through hypertrophy or atrophy to variation in the habitual loads placed upon them. As tubular structures of cortical bone, similar to the diaphyses of the major long bones, this is reasonable, given the abundant literature on cortical bone response during both development and maturity to differential levels of biomechanical loading [12,58,64,87]. Moreover, as previously argued [88], the relatively wide

diaphyses of the middle three proximal pedal phalanges in part reflects differential mediolateral expansion of their diaphyses in the context of elevated overall loads, given the trussing role played by the extensor and flexor tendons; the diaphyseal response to changing loads is therefore related to both the magnitudes and the effective orientations of those loads.

It could be argued that diaphyseal changes in pedal phalanges might be reflecting similar changes in homologous manual structures, given the parallels in differential phalangeal lengths between Neandertal versus modern human pollices and halluces and the presence of expanded apical tuberosities in both limbs of the former [80,81,85,96]. However, whereas Neandertal manual proximal phalanges exhibit both radioulnar and dorsopalmar diaphyseal expansion relative to recent humans, Upper Paleolithic modern humans only exhibit radioulnar expansion [45]. In contrast, the principal contrast in pedal proximal diaphyseal proportions between Neandertals and Upper Paleolithic humans is in diaphyseal breadth [86,88]. It is therefore unlikely that the patterns of diaphyseal hypertrophy documented here can be considered secondary to more stringent demands on homologous structures in the upper limb.

5. Late Pleistocene locomotor robusticity and pedal phalanges

Research has shown that there was little change in average locomotor anatomy hypertrophy during the Late Pleistocene, and that a significant decrease in robusticity occurred principally with the emergence of sedentism and especially industrialization during the Holocene. This is evident in the robusticity of femoral and tibial diaphyses which, when appropriately scaled to estimates of body mass and ecogeographically-patterned body proportions, shows little shift between late archaic and early modern humans and within early modern humans [37,65,90−92]. It is apparent in femoral anterior curvature [69], relative power arms for quadriceps femoris [89], and scaled dimensions of discrete muscle insertion areas [84]. The only consistent changes concern femoral shaft shape, which relate to changing body proportions between late archaic humans and early/middle Upper Paleolithic humans [90,98] and mobility levels through the Upper Paleolithic [37]. Femoral neck-shaft angles increase slightly among late Upper Paleolithic humans, despite being anomalously high among the Qafzeh-Skhul early modern humans [83].

It is therefore to be expected that there would be little change in pedal phalangeal robusticity through the Late Pleistocene, if the use of footwear remained consistent through this time period. However, if there was a significant increase in the use of footwear, one would predict a modest reduction in hallucal phalangeal robusticity but a clear decrease in the robusticity of the lesser digits. Conversely, therefore, if a decrease in lateral pedal phalangeal robusticity is perceived in the context of relatively less change in hallucal hypertrophy, it should indicate an increase in the use of protective footwear.

6. Materials and methods

6.1. Samples

In order to assess pedal phalangeal reflections of footwear use in the Late Pleistocene, two sets of samples of phalanges were employed. The primary one consists of Middle and Upper Paleolithic late archaic and early modern humans from western Eurasia. The first sample includes Middle Paleolithic Neandertals from La Chapelle-aux-Saints, La Ferrassie, Kiik-Koba, Regourdou, Shanidar, Spy and Tabun. The second one is of Middle Paleolithic early modern humans from Qafzeh and Skhul. The third sample is of middle Upper Paleolithic (Gravettian) humans predating ca. 18,000 ^{14}C years B.P. from the sites of Barma Grande, Caviglione, Cro-Magnon, Dolní Věstonice I & II, Ohalo II, Paglicci, Pataud, Předmostí and Veneri (Parabita). Data are from the original specimens, except for Kiik-Koba 1 and Skhul 4 which derive from casts. For body mass estimation, the femoral length of Kiik-Koba 1 was estimated prior to the stature calculation using other Neandertal specimens, thereby reducing the effect of their low crural indices on perceived body mass.

Sufficiently complete (providing both a diaphysis and a length measurement) similarly aged proximal phalanges are only also available from Bordul Mare, Livadilţa and Minatogawa, but they are insufficiently described [5,26,79]. Geologically older isolated phalanges are known from Krapina, Sima de los Huesos and Gran Dolina [41,61], but it remains uncertain to what extent the Krapina remains are fully mature given the high proportion of adolescents in the craniodental sample [99]. Data are only available for isolated hallucal proximal phalanges from Sima de los Huesos and Gran Dolina [41], and they show considerable variation in diaphyseal size scaled to phalanx length. It should be noted that pedal phalanges, especially of the lesser toes, are rarely preserved and only occasionally recognized in Pleistocene human fossil assemblages. As a result, most of the remains come from partial skeletons or mixed assemblages of multiple individuals, and sample sizes are corresponding low.

To provide a recent human comparative framework, phalanges and associated postcrania of three North American recent human samples were assessed. These include a range of activity levels and degrees of being habitual shod.

The first sample is from Pecos Pueblo (New Mexico) and consists of late prehistoric/early historic Native Americans from the southwestern American high desert (formerly in the Harvard Peabody Museum, now repatriated). Their lower limbs remains are relatively robust among recent human samples [65]. Sandals have been documented from areas of American Southwest back to ca. 9000 years B.P. [29], and sandals and moccasins/boots were present and the latter worn especially during winter at higher altitudes. However, most of the southwest American Native Americans at the time of European contact were habitually barefoot, and those who wore shoes were specially remarked upon by the 16th century Spanish chroniclers [11,32]. Moreover, moccasins/boots were made of deerskin (*Odocoileus*), which remains soft and conforms to the substrate.

The second sample consists of some prehistoric (Ipiutak) and primarily protohistoric (Tigara) Inuits from Point Hope (Alaska), engaging in terrestrial and maritime foraging [40] (collections of the American Museum of Natural History, New York). Their lower limb remains are robust compared to other recent human samples [68]. As arctic Native Americans, they would have worn thermally effective footwear most, if not all, of the year [38,40,74,75]. Although arctic footwear largely consisted of moccasins and boots [33], the primary construction consisted of stiff sealskin (*Phoca*) soles with upper portions of softer caribou (*Rangifer*) or other fur-bearing animal skin [51,75].

The third sample is made up of late 20th century Euroamericans (collections of the Maxwell Museum of Anthropology, University of New Mexico), all of whom habitually wore industrially manufactured rigid-soled shoes. Their limbs tend to be among the most gracile of recent humans, as with most modern urban populations.

It is predicted, given the above anatomical considerations, that the Pecos sample should exhibit the most robust lateral pedal phalanges and the Euroamericans the least robust lesser toes, when appropriately scaled. The Point Hope sample should have pedal phalanges which may be more robust that those of the Euroamericans, given the generally greater robusticity of the lower limbs of non-industrial recent human populations [65,68], yet less so than the more habitually barefoot southwestern American Native American sample.

6.2. Methods

The analysis of hallucal and lesser toe robusticity is based principally on the articular lengths (M-1a: mid metatarsal concavity to mid trochlea) and midshaft dorsoplantar and mediolateral diameters (M-2 & M-3) of proximal pedal phalanges. These measurements, as well as those employed for body mass estimation [bi-iliac breadth (M-2), femoral bicondylar length (M-2) and femoral sagittal head diameter (M-19), are standard osteometrics [9] and are accurate to within 0.5 mm for the phalangeal measurements and within 1 mm for bi-iliac breadth and the femoral measurements. The first figure is substantiated by intraobserver mean errors of 0.2, 0.2 and 0.1 mm for phalangeal length, midshaft height and midshaft breadth on a sample of recent human phalanges ($N = 22$).

Weight-bearing diaphyses should normally be scaled to an estimate of the beam length (articular bone length for the phalanges) times body mass [63,65], but it remains unclear to what extent pedal phalanges are truly "weight-bearing." There are GRFs below them in standing and under the hallux during the latter portion of heel-off, but it is uncertain whether, and undoubtedly highly variable in the extent to which, there is direct weight-bearing such as provides the baseline load on the femoral and tibial diaphyses. For this reason, the phalangeal midshaft dimensions are compared to both phalangeal length and to phalangeal length times estimated body mass (for those partial skeletons providing reasonable estimates of the latter).

The specimens (both recent and especially Pleistocene) also vary in the extent to which there are sufficient associated postcranial remains for appropriate body mass estimation. As a result, the samples are larger for the comparisons involving only phalangeal diaphyseal strength (J) versus length than for those comparing phalangeal J versus length times a body mass estimate (Table 1).

Lean body mass was estimated for Pleistocene and recent humans following Ruff et al. [66]. The average of the results of the three available regression formulae (sex-specific as appropriate) from femoral head diameter was then averaged with the (sex-specific as appropriate) estimate from stature and bi-iliac breadth, when both were available or estimatable (see Trinkaus et al. [92] for bi-iliac breadth estimation). The Trotter and Gleser [93] Euroamerican femoral formulae were employed for recent individuals; all available long bones were used for Pleistocene specimens. For individuals with less complete data, the average femoral head value or the stature and bi-iliac breadth value was employed. Femoral head based estimates tend to provide slightly higher values (average difference: 2.0 kg), which is within the estimation error of either approach.

Articular phalangeal length was directly measured on most of the original phalanges. To maximize sample size, phalanx length was estimated for a couple of specimens. For Předmostí 3, for whom maximum lengths are published [43], articular length was estimated using least squares regressions based on recent human samples of phalanges [r^2: 1: 0.862 ($N = 44$), 2: 0.961 ($N = 45$), 3: 0.971 ($N = 44$), 4: 0.957 ($N = 43$), 5: 0.963 ($N = 42$)]. The La Ferrassie 1 proximal phalanx 1 length was estimated from the lengths of the second to fourth proximal phalanges using a pooled Late Pleistocene and

Table 1
Summary statistics for phalanx length, phalanx midshaft polar moment of area (modeled as a solid beam – see text), and estimated body mass for individuals preserving the phalanx/phalanges in question (see text)

	Neandertals	Qafzeh-Skhul	Middle Upper Paleolithic	Pecos Pueblo Native Americans	Point Hope Inuits	Modern Euroamericans
PP1 Length (mm)	26.7±2.7 (9)	31.0±1.7 (4)	30.8±3.0 (13)	25.8±2.8 (39)	27.0±2.3 (30)	29.1±2.6 (35)
PP1 J (mm^4)	1960±663 (9)	2232±246 (4)	1904±642 (13)	1409±472 (39)	861±314 (30)	1228±576 (35)
PP1 BM (kg)	74.9±10.1 (6)	64.8, 72.1, 78.5	72.2±5.3 (9)	57.7±7.9 (31)	63.3±5.8 (30)	65.9±7.3 (34)
PP2-4 Length (mm)	23.3±2.5 (9)	25.5±0.8 (4)	25.2±2.3 (10)	22.8±2.2 (64)	23.6±2.8 (31)	24.7±2.1 (35)
PP2-4 J (mm^4)	349±137 (9)	335±55 (4)	155±72 (10)	124±61 (64)	96±56 (31)	88±42 (35)
PP2-4 BM (kg)	75.7±8.0 (8)	64.8, 72.1, 78.5	68.6±9.4 (9)	57.1±7.2 (46)	62.6±5.8 (31)	65.9±7.3 (34)
PP5 Length (mm)	19.4±2.4 (5)	23.0, 23.8	22.7±2.0 (7)	19.3±1.7 (34)	19.6±2.1 (20)	21.1±1.8 (34)
PP5 J (mm^4)	187±107 (5)	170, 249	104±25 (7)	98±34 (34)	64±39 (20)	56±25 (34)
PP5 BM (kg)	75.5±7.4 (4)	64.8, 78.5	67.7±8.6 (6)	59.1±6.4 (25)	62.2±6.5 (20)	66.1±7.3 (33)

Lengths and polar moments of area for phalanges 2 to 4 are the average of the values for ones preserved for that individual. Smaller sample sizes for body mass estimates reflect the absence of associated long bone and pelvic data for some of the individuals. Mean±standard deviation (N) provided; individual values for $N < 4$. PP: proximal phalanx; J: polar moment of area; BM: body mass.

recent human sample ($r^2 = 0.747$, $N = 117$), the Regourdou 1 proximal phalanx 3 length was estimated from the second phalanx length using a similar sample ($r^2 = 0.877$, $N = 137$), and for Qafzeh 6 the proximal phalanx 4 length was estimated from its first, second and third phalangeal lengths using a similar sample ($r^2 = 0.850$, $N = 110$); all standard errors of the estimates are <1% of the resultant values.

Relative phalangeal diaphyseal rigidity was quantified by computing the midshaft dorsoplantar and mediolateral second moments of area with the shaft modeled as a solid beam. For this, standard ellipse formulae [54] and the subperiosteal mediolateral and dorsoplantar diameters were employed. The perpendicular second moments of area were summed to provide a polar moment of area (J) for each phalanx, a measure of overall bending and torsional rigidity [65] especially given the subcircular contours of pedal phalangeal diaphyses [19]. Since femoral and tibial relative cortical area differs little across the Late Pleistocene and tends to be modestly lower in recent human samples [65,90,91], quantifying the cross sections as solid beams should make little difference in the Late Pleistocene comparisons and will be conservative in comparisons between Late Pleistocene and recent human samples. Since pedal phalangeal diaphyses closely approach ellipses in cross-sectional shape, except for minor ridges for the flexor tendon sheaths on the lateral phalanges, formulae based on the diameters of an ellipse should closely approximate the total subperiosteal bone distribution and not be subjected to the overestimation inherent in using them on femora, tibiae and humeri [54,67].

Comparisons were done separately for the hallucal and fifth proximal phalanges, which are morphologically distinct. However, it is often difficult to assign phalanges 2, 3 or 4 reliably to digit, especially when only one or two of them is present; digit assignment is often based on an assumption of decreasing length laterally. Consequently, to maximize sample sizes without overly representing individuals with multiple phalanges preserved (whose measurements are not independent within individuals), the available lengths and polar moments of area for phalanges 2 to 4, as present, were averaged to provide an individual middle proximal phalangeal value for each measurement. The resultant values were then employed in the comparisons. For the recent human samples, only one of each symmetrical pair of phalanges was measured; for the paleontological samples, raw measurements from antimeres, when present, were averaged prior to the calculation of second moments of area, length times body mass, and subsequent values.

To assess the patterns and degrees of differences between the samples, reduced major axis regression was done on the natural log transformed data, and linear residuals were computed from the reduced major axes through the pooled recent human sample (Table 2). The data were log transformed, since the variables are in different powers of linear dimensions; the lengths are in mm, the polar moments of area are in mm^4, and length times body mass is effectively in mm^4 (mm×mass ∝ mm×volume ∝ mm×mm^3). The correlation coefficients for the regression equations are generally low, but the slopes of all of them except those for the fifth digit are significantly different from zero at the $P < 0.001$ level, and those for the fifth digit remain significant at the $P < 0.05$ level. The low level of correlation is produced by individual variation in phalangeal robusticity and inter-populational differences in average robusticity [as reflected in the significantly different residual distributions of the three samples (Table 3) despite generally similar phalangeal lengths (Table 1)], compounded by minimal functional constraints on the fifth digit. Since these correlation levels are low, and since all of the variables are measured

Table 2
Reduced major axis regressions for the pooled recent human samples of proximal pedal phalanx midshaft polar moments of area (J) versus phalangeal length (Len) and versus phalangeal length times estimated body mass (Len×BM)

	RMA equation	r	P	N
PP-1 J/Length	$\ln J = 4.23 (\ln Len) - 6.9$	0.364	0.0001**	104
PP-1 J/Length×Body Mass	$\ln J = 2.14 (\ln (Len \times BM)) - 8.9$	0.360	0.0003**	95
PP-2-4 J/Length	$\ln J = 5.47 (\ln Len) - 12.7$	0.545	<0.0001**	130
PP-2-4 J/Length×Body Mass	$\ln J = 2.73 (\ln (Len \times BM)) - 15.4$	0.465	<0.0001**	111
PP-5 J/Length	$\ln J = 5.20 (\ln Len) - 11.4$	0.255	0.017*	88
PP-5 J/Length×Body Mass	$\ln J = 2.74 (\ln (Len \times BM)) - 15.3$	0.264	0.020*	78

* $P<0.05$, ** $P<0.01$, each with a sequentially reductive Bonferroni multiple comparison correction [60,62].

with error, reduced major axis regression is the appropriate approach for computing the residuals [73]. Since the analysis involves controlling for size, rather than determining proportionality, the alternative approach (using ratios of the variables, even if adjusted for powers of linear dimensions) is not appropriate [70], especially given the frequent non-independence of ratios from overall size in morphometric analyses. In any case, the pronounced overlap in size across the samples (Table 1) and the high levels of contrasts across the samples in the resultant residuals (Table 3) indicate that minor deviations of the regression lines from the "true" relationships between the variables are likely to have little effect on the results.

The resultant residual distributions are presented as box plots (Figs. 1–3), and Kruskal–Wallis P-values were computed across the residuals of the total samples and the temporal sets of samples (Table 3). Sequentially reductive Bonferroni multiple comparison corrections [62] were employed within sets of comparisons [60].

7. Results

The comparisons of the hallucal proximal phalangeal robusticity (Fig. 1; Table 3) provide highly significant differences across the recent humans samples, in which the Native American sample is relatively robust and the

Inuit and Euroamerican samples are similar to each other and more gracile. In this, post-hoc Wilcoxon tests provide P-values of <0.001 between the Native American sample and each of the other two, but a $P = 0.333$ between the Inuit and Euroamerican samples. In the polar moment of area to length comparison, there is
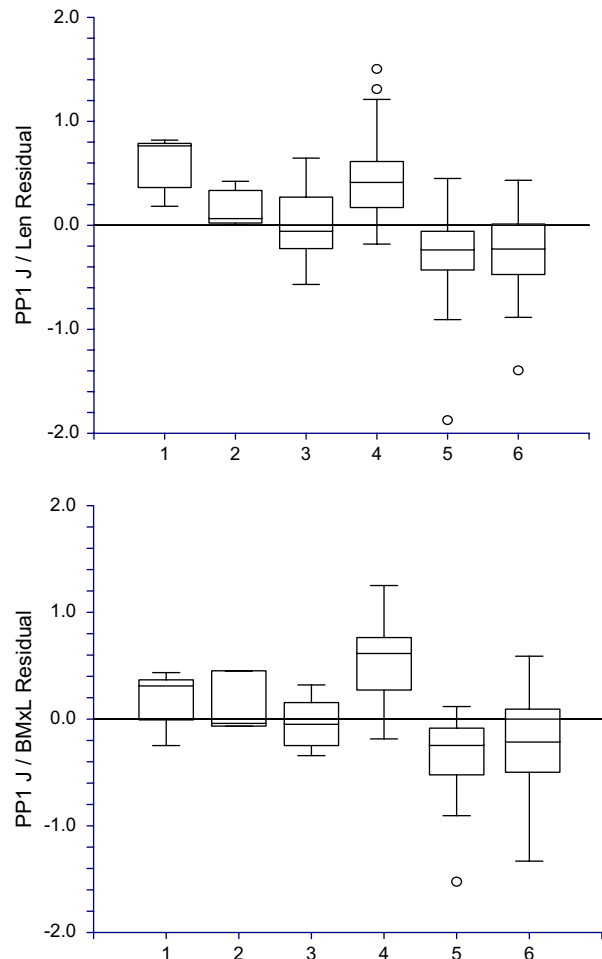

Fig. 1. Box plots of linear residuals from the pooled recent human reduced major axis line (0) for the hallucal proximal phalangeal midshaft polar moment of area (J) versus phalanx length (above) and versus phalanx length times body mass (below). Samples: 1: Neandertals; 2: Qafzeh-Skhul; 3: middle Upper Paleolithic; 4: Pecos Pueblos Native Americans; 5: Point Hope Inuits; 6: Modern Euroamericans.

Table 3
Kruskal–Wallis P-values for comparisons of residuals from reduced major axis regressions across all samples, within the recent humans, and across the Late Pleistocene samples

	All 6 Samples	Recent Humans	Late Pleistocene
PP-1 J/Length	<0.001**	<0.001**	0.001*
PP-2-4 J/Length	<0.001**	<0.001**	<0.001**
PP-5 J/Length	<0.001**	<0.001**	0.011
PP-1 J/Length×Body Mass	<0.001**	<0.001**	0.176
PP-2-4 J/Length×Body Mass	<0.001**	<0.001**	0.002*
PP-5 J/Length×Body Mass	<0.001**	<0.001**	0.080

* $P<0.05$ with a Bonferroni multiple comparison correction [60,62] within the sample set; ** $P<0.01$ with similar criteria. PP: proximal phalanx; J: polar moment of area.
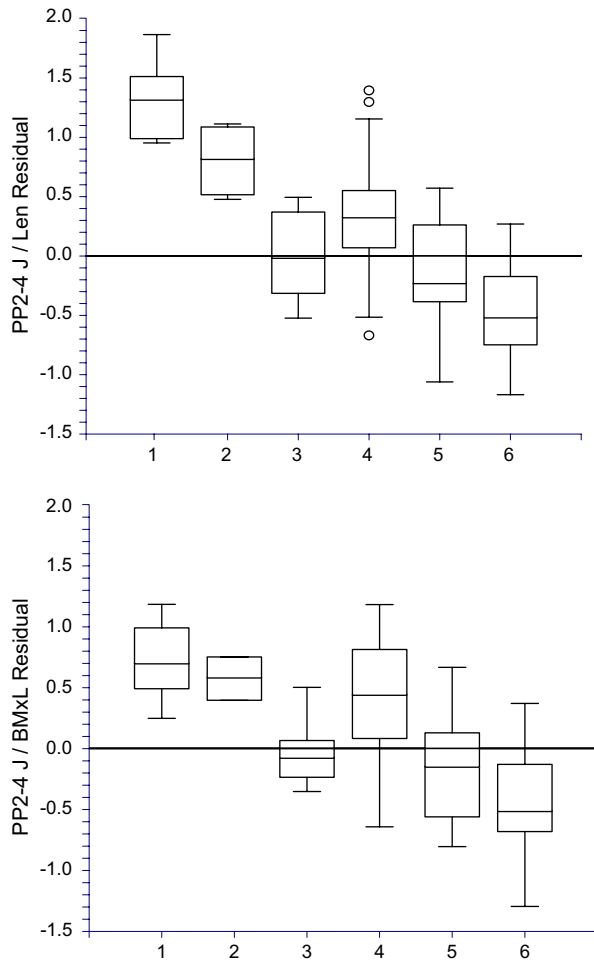
Fig. 2. Box plots of linear residuals from the pooled recent human reduced major axis line (0) for the average of the middle three proximal phalangeal midshaft polar moment of area (J) versus phalanx length (above) and versus phalanx length times body mass (below). Samples: 1: Neandertals; 2: Qafzeh-Skhul; 3: middle Upper Paleolithic; 4: Pecos Pueblos Native Americans; 5: Point Hope Inuits; 6: Modern Euroamericans.
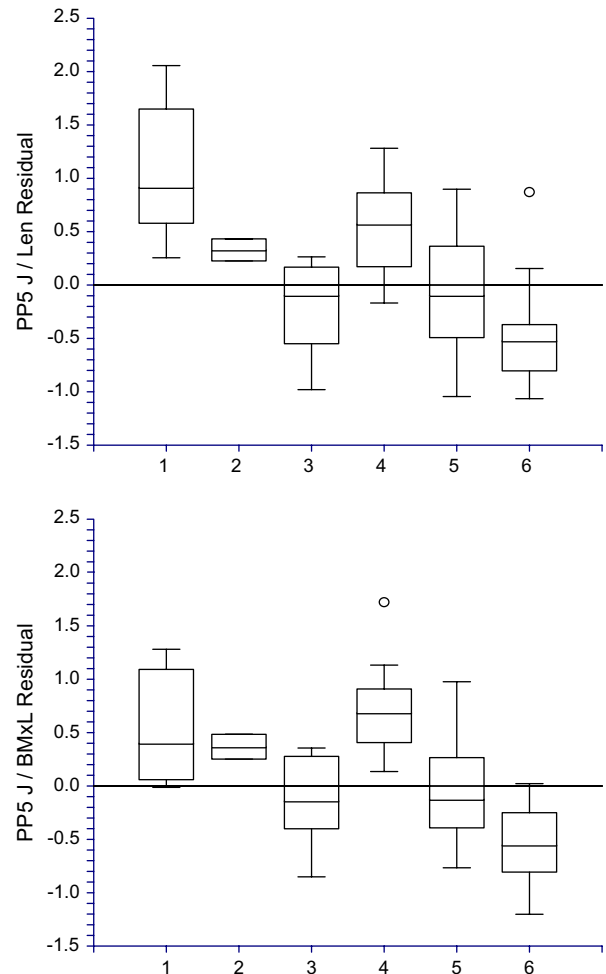

Fig. 3. Box plots of linear residuals from the pooled recent human reduced major axis line (0) for the fifth toe proximal phalangeal midshaft polar moment of area (J) versus phalanx length (above) and versus phalanx length times body mass (below). Samples: 1: Neandertals; 2: Qafzeh-Skhul; 3: middle Upper Paleolithic; 4: Pecos Pueblos Native Americans; 5: Point Hope Inuits; 6: Modern Euroamericans.

consistent reduction in apparent robusticity from the Neandertals to the Qafzeh-Skhul sample to the middle Upper Paleolithic one, with the last falling very close to the recent human average.

However, the Neandertals possessed elevated body mass relative to limb length [36], which would have increased relative loads on the phalanges, assuming that they can be considered weight-bearing (see above). Moreover, the Neandertals appear to have had slightly abbreviated proximal hallucal phalangeal lengths relative to recent humans [80], a pattern homologous to the foreshortening of their pollical proximal phalanges [96]. It therefore appears appropriate to scale their hallucal phalangeal diaphyses to length times a body mass estimate. The resultant distribution of residuals (Fig. 1) reveals reduced contrasts across the Late Pleistocene samples. The remaining shift is between the Middle

Paleolithic Neandertal and Qafzeh-Skhul samples and the middle Upper Paleolithic one, although neither the overall comparison nor any of the post-hoc pairwise comparisons reach significance at the 5% level. There is a maintenance of the significant recent human contrasts with the incorporation of body mass into the phalangeal diaphyseal scaling.

In the comparisons of the middle toe proximal phalangeal robusticity (Fig. 2; Table 3), the three recent human samples closely parallel the pattern predicted from their levels of postcranial robusticity and footwear use, with the Native American sample having the most robust phalanges, followed by the Inuit sample and then the recent Euroamerican one. In the assessment of polar moment of area relative to phalangeal length, the Neandertals are significantly more robust than other samples, Pleistocene or recent, with the Qafzeh-Skhul

sample falling between it and the Upper Paleolithic and recent samples.

Although there is little difference in relative lateral proximal phalangeal length between the Neandertals and recent humans [80], the differential body mass to limb length of the Neandertals may have elevated the loads on the lateral phalanges. When body mass is included with length to scale the phalangeal diaphyses, the recent human pattern remains, the middle Upper Paleolithic sample remains similar to the recent human ones, the difference between the Neandertal and Qafzeh-Skhul sample disappears (Wilcoxon $P = 0.414$), and the two Middle Paleolithic samples are within the distribution of the largely barefoot Native American sample.

Assessment of relative robusticity of the fifth proximal pedal phalanges provides a similar pattern to the middle three (Fig. 3). The contrasts between the Late Pleistocene samples are less than with the middle phalanges, but the differences among the recent human samples remain marked.

8. Discussion

The pattern of pedal proximal phalangeal robusticity among the recent human samples is one in which there is a general correlation between the use of footwear and the robusticity of the phalanges. This is readily apparent in the lateral digits, both the pooled middle three and the fifth one. It is present at least between the Native American sample and the two others in the hallux, sufficient to make the difference among the samples highly significant. However, in femoral and tibial robusticity, the Inuit and Native American samples should be similar and both more robust than the Euroamerican one [65,68].

This hallucal result is in contrast with the general prediction above that hallucal robusticity would largely follow the pattern of overall lower limb robusticity. It suggests (as noted above) that hallucal robusticity can be significantly affected by the use of footwear, through the diffusion of GRF across the plantar foot. This effect would distribute GRF during heel-off and toe-off across the hallux and medial metatarsal heads. The similarity of the Inuit and Euroamerican hallucal phalanges, and their contrast with the Native American ones, therefore imply that the rigid soles of Inuit sealskin boots and modern industrial shoes would have a similar effect in reducing the role of the hallux during the latter portions of the stance phase.

In the context of these recent human patterns, the Late Pleistocene proximal pedal phalanges provide little difference between the two Middle Paleolithic samples when body mass is taken into account and a higher but non-significant distribution for the Neandertals when only phalangeal length is employed for scaling. How-

ever, the middle Upper Paleolithic sample is consistently more gracile in its pedal proximal phalanges, although the difference reaches significance only among the middle three toes in both comparisons and the hallux in the length-only assessment. This is in contrast to analyses of their femoral and tibial diaphyseal, muscular and articular robusticity, in which there are no consistent differences between the samples once body size and proportions are taken into account (see above).

Given the patterns evident in the three recent human samples and the correlations with levels of footwear use, it is likely that these Late Pleistocene phalangeal differences are due to contrasts in the extent to which they were shod. The lack of a significant sample separation in hallucal robusticity may be taken to infer that the footwear were insufficiently rigid to effectively diffuse GRF. However, the contrast in middle toe proximal phalangeal robusticity (and a more modest one in the little toe), despite small sample sizes, indicates a reduction in the habitual loads on these toes in the context of little change elsewhere in the leg. It is hard to explain these differences other than through the increased use of a device that reduced the role of the lesser toes in locomotion and thereby decreased habitual loads on them.

It therefore appears probable that there was a significant increase in the use of footwear between Middle Paleolithic humans (both late archaic and early modern) and middle Upper Paleolithic early modern humans. Middle Paleolithic humans may well have had forms of foot gear, to provide insulation during cold weather and possibly mechanical protection from the substrate. However, the robusticity of their lateral toes suggests that such foot protection was worn irregularly and/or provided little mechanical separation between the foot and the ground. By the middle Upper Paleolithic, the anatomical evidence presented here, along with limited archeological evidence of foot covering, suggests that people were routinely using semi-rigid to rigid soled shoes, boots or sandals to protect the foot. They may have gone barefoot frequently, as the footprints in caves attest, but their toes indicate that they had footwear available as needed for stressful locomotion. The rare archeological suggestions of such footwear, as at Sunghir and Pavlov, were therefore part of a much more widespread phenomenon.

In addition, there is no perceptible difference between human morphological groups in the Middle Paleolithic and none between those in different climatic regimes within archeological phases. European (La Chapelle-aux-Saints, La Ferrassie, Kiik-Koba, Regourdou and Spy) and southwest Asian (Shanidar and Tabun) Neandertals are similar, as they are to the Qafzeh-Skhul sample. Ohalo 2 from southwest Asia is in the middle of the European middle Upper Paleolithic distribution (Barma Grande, Caviglione, Cro-Magnon, Dolní

Věstonice, Paglicci, Pataud, Předmostí and Veneri). And the Mediterranean specimens (Barma Grande, Caviglione, Ohalo, Paglicci and Veneri) are similar to those from further north in Europe. It is therefore apparent that the shift in phalangeal robusticity and inferred footwear use is principally a cultural phenomenon, at least within the Late Pleistocene of western Eurasia.

9. Conclusion

The archeological record has suggested that footwear was present during the Upper Paleolithic, at least in portions of Europe extending back to the middle Upper Paleolithic. An assessment of the relative robusticity of their pedal proximal phalanges indicates that there was a significant increase in the use of protective and mechanically effective footwear between the Middle Paleolithic and the middle Upper Paleolithic. These data also suggest that the use of protective footwear was independent of morphological group and general climatic setting during the Late Pleistocene of western Eurasia and was therefore an element of cultural change through the earlier Upper Paleolithic.

Acknowledgments

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