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The Olduvai Hominid 8 foot: Adult or subadult?

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ABSTRACT

Olduvai Hominid 8 (OH 8), an articulating set of fossil hominin tarsal and metatarsal bones, is critical to interpretations of the evolution of hominin pedal morphology and bipedal locomotion. It has been suggested that OH 8 may represent the foot of a subadult and may be associated with the OH 7 mandible, the type specimen of *Homo habilis*. This assertion is based on the presence of what may be unfused distal metatarsal epiphyses. Accurately assessing the skeletal maturity of the OH 8 foot is important for interpretations of the functional morphology and locomotor behavior of Plio-Pleistocene hominins. In this study, we compare metatarsal fusion patterns and internal bone morphology of the lateral metatarsals among subadult hominines (85 modern humans, 48 *Pan*, and 25 *Gorilla*) to assess the likelihood that OH 8 belonged to either an adult or subadult hominin. Our results suggest that if OH 8 is indeed from a subadult, then it displays a metatarsal developmental pattern that is unobserved in our comparative sample. In OH 8, the fully fused base of the first metatarsal and the presence of trabecular bone at the distal ends of the second and third metatarsal shafts make it highly improbable that it belonged to a subadult, let alone a subadult that matches the developmental age of the OH 7 mandible. In total, the results of this study suggest that the OH 8 foot most likely belonged to an adult hominin.

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Introduction

Olduvai Hominid 8 (OH 8) consists of an articulating set of seven tarsals and five metatarsals, all of which were discovered by Mary Leakey *in situ* in 1960 in the Middle Bed I deposits at the FLK NN locality (Leakey, 1960; Tobias, 1991). Fifty years have now passed since its discovery, yet OH 8 still represents one of the geologically oldest, most complete sets of foot bones in the hominin fossil record. All of the tarsals are well preserved and relatively complete except for the calcaneus, which only preserves the distal portion. All five metatarsals are missing their distal ends but their bases and shafts are reasonably well preserved.

The assumption that all twelve bones belong to a single individual is based on the fact that all were recovered within one square foot and all mutual articular surfaces appear well-matched in size and shape (Day, 1986). The morphology of the first tarso-metatarsal joint suggests that the hallux was adducted and the robusticity formula of the metatarsals is more similar to modern humans than great apes (Archibald et al., 1972). Together, these

features argue that OH 8 represents a bipedal hominin, a functional and phylogenetic interpretation generally agreed upon by most paleoanthropologists. No serious argument exists to suggest that OH 8 does not represent a single, bipedal hominin individual that lived and died approximately 1.8 Ma. Instead, debates, both past and present, are centered on the maturity and taxonomic attribution of the individual represented by OH 8.

OH 8 was originally thought to be associated with the juvenile OH 7 mandible (Leakey, 1961). This interpretation was later revised and OH 8 was interpreted as a second adult individual, based on the presence of arthritic bony growths on the lateral aspect of the tarsometatarsal region (Day and Napier, 1964; Leakey et al., 1964). Leakey (1971) also regarded the foot as belonging to an adult female. The adult status of OH 8 was reiterated in an early study of its functional morphology (Wood, 1974). Christie (1990) also found differences in adult and juvenile tali and noted specifically that the OH 8 talus was much more similar to that of an adult human talus than a subadult. However, other studies of the Olduvai fossils have suggested that OH 8 was from a subadult and that the OH 8 foot, OH 7 hand, mandible, and cranial fragments, and perhaps also the OH 35 tibia and fibula, may represent a single adolescent individual (Susman and Stern, 1982; Susman, 2008). The subadult status of the OH 7 mandible and hand is unequivocal, based on an unerupted

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third molar (Leakey et al., 1964) and unfused epiphyses on the phalanges (Napier, 1962; Susman and Creel, 1979), although recent analysis of the manual remains suggest that the hand and the craniodental fossils of OH 7 may belong to different taxa (Moyà-Solà et al., 2008). Nevertheless, the association between OH 7 and OH 8 is reasonable, given that they were found in the same stratigraphic layer of FLK NN (Level 3) and the nearest scattered fragments of OH 7 are within 5 m of the OH 8 foot (Leakey, 1971). However, the evidence that the OH 8 foot is from a subadult is not as obvious as it is for the hand and craniodental remains of OH 7. The second and third metatarsals of OH 8 are missing the distal heads, a feature regarded initially as evidence for carnivore activity. It has since been suggested that instead of being broken by carnivores, the ends of the second and third metatarsals are unfused epiphyseal surfaces (Susman and Stern, 1982; Susman, 2008). Based on this interpretation of the morphology, OH 8 was suggested to have belonged to an individual of the same developmental age as the OH 7 hand and the OH 7 mandible (Susman and Stern, 1982; Susman and Brain, 1988). It is unlikely that modern humans are the appropriate model for aging hominin remains, and therefore Susman (2008) has emphasized that the *relative* ages of the OH 8 foot, OH 7 hand and OH 7 mandible are concordant. If true, then arguments that the OH 8 foot belongs to the same individual as the OH 7 material would be strengthened. Such an association would be of great importance for phylogenetic and functional interpretations of early hominins, as this individual would be represented by a mandible, skull fragments, a partial hand, and a partial foot, making it one of the more complete specimens in the hominin fossil record. Association with OH 7, the type specimen of *Homo habilis*, would refute hypotheses that the OH 8 foot belongs to *Paranthropus boisei*, as some have suggested (Wood, 1974; Grausz et al., 1988; Gebo and Schwartz, 2006). However, the hypotheses that OH 8 is: a) from a subadult, and b) associated with OH 7, has been met with skepticism (Day, 1986; White and Suwa, 1987). Despite arguments for and against the adult status of OH 8, no comparative data on tarsal and metatarsal fusion patterns in modern humans and African apes have been presented to allow a reasonable test of these hypotheses.

Modern humans and great apes share a general pattern of epiphyseal fusion in their tarsals and metatarsals. This general pattern includes distal epiphyses for the four lateral metatarsals and proximal epiphyses for the first metatarsal and calcaneus, as well as epiphyses for the medio-plantar aspect of the talus, the navicular tuberosity, and the base of the fifth metatarsal (lateral tubercle). More rarely, humans and great apes may exhibit a pseudo epiphysis for the distal end of the first metatarsal (Scheuer and Black, 2000). Typically, among modern humans, the epiphyses for the talus and navicular fuse first, followed by the epiphyses for the calcaneus and the lateral tubercle of the fifth metatarsal. These are then followed by fusion of the second through fifth metatarsal heads, generally after the eruption of the second molar but sometimes not until the third molar is erupted as well, and finally the base of the first metatarsal fuses last (Scheuer and Black, 2000; Baker et al., 2005).

In OH 8, the navicular is well preserved and has a large navicular tuberosity that appears to be already fully fused. The OH 8 talus is slightly damaged in its medio-plantar area, making it difficult to be certain of whether fusion of its epiphysis had occurred. Similarly, the OH 8 calcaneus is missing the entire proximal half of the bone; thus, whether its proximal epiphysis remains unfused cannot be evaluated. The lateral tubercle (styloid process) on the base of the OH 8 fifth metatarsal is also missing and it is unclear whether this is the result of an unfused epiphysis, antemortem trauma, post-mortem damage, or some combination of these factors. The base is rounded off proximolaterally, quite unlike the styloid-like shape of

the lateral aspect of the fifth metatarsal in most modern humans and African apes. The medial aspect of the fifth metatarsal has osteophytic growths both plantarly and dorsally that match growths on the lateral aspect of the fourth metatarsal (Fig. 1). Similar osteophytic connections occur between the bases of the fourth and third metatarsals. Reasonable arguments could be made that these pathological growths are the result of either adult age-related arthritis or a healed avulsion fracture of an unfused or partially fused lateral tubercle epiphysis, but neither are conclusive in demonstrating whether the OH 8 foot belonged to an adult or subadult. Therefore, the evidence from the tarsals and proximal fifth metatarsal is at best equivocal. If any of these areas showed clear evidence of an unfused or partially fused epiphysis, then the subadult status of OH 8 would be more than reasonably justified, whereas full fusion of these epiphyses would not necessarily preclude OH 8 from being a subadult.

Thus, the best available evidence for evaluating whether OH 8 is a subadult or adult lies in its metatarsals. The OH 8 foot does not preserve any of the five metatarsal heads. The fourth and fifth metatarsals are broken distal to the midshaft and preserve the proximal portions. Alternatively, the second and third metatarsals preserve almost their entire length and both have a proximodorsal to distoplantar angulation to their terminal surfaces. The end of each bone occurs just as the diaphyseal surface begins to expand into the metatarsal heads. If these are unfused epiphyses (Susman and Stern, 1982; Susman, 2008), then it is curious that the proximal epiphysis of the first metatarsal is fully fused to the diaphysis and the diaphyseo-epiphyseal junction is completely obliterated both visually and in published radiographs (Susman, 2008). The purpose of this study is to compare metatarsal fusion patterns among African apes and modern humans to determine the frequencies of varying fusion patterns. Such frequencies can then be used to establish the likelihood of finding a subadult hominin with a particular fusion pattern. To address the possibility that early *Homo* may have possessed a metatarsal fusion pattern unlike that



Figure 1. Osteophytic growths on adult fifth metatarsals. The medial side of fifth metatarsals in an adult human (left) and OH 8 (right) are shown. Notice the osteophytic growths emanating distally and plantarly from the fourth metatarsal facet. This condition was not seen in any of the juvenile metatarsals examined in this study.

in either modern humans or African apes, we also compare the fusion pattern of the OH 8 foot with the associated pedal and craniodental remains of a roughly contemporaneous early *Homo* juvenile from Dmanisi, Georgia.

Materials and methods

The metatarsal fusion pattern of 158 extant subadult hominines was studied (85 *Homo*, 25 *Gorilla*, 48 *Pan*) and compared with those of OH 8. A breakdown of specimens by taxonomy and place of curation is given in Table 1. Study was restricted to a range of individuals whose second molar had erupted and whose third molar was either unerupted or not fully in occlusion. For specimens without associated craniodental remains, only those where the distal humerus was fully fused were included. This typically occurs in modern humans at approximately 10–14 years of age (White, 2000).

The original OH 8 foot was also compared with fossil metatarsals listed in Table 1. Original mandibles D2735 and D211 were studied at the Georgia National Museum and compared with high-quality casts of OH 7 and OH 13 from the National Museums of Kenya.

Fusion of all epiphyses was visually scored as unfused (epiphyses separate from the diaphysis), partially fused (epiphyses attached to diaphysis with epiphyseal lines present), or fully fused (epiphyseal lines obliterated). Distal metatarsal shafts (unfused or fused but broken postmortem) were examined further and the visible bone scored as either irregular woven bone or trabecular bone. These qualitative data were then used to evaluate the likelihood that OH 8 belonged to an adult versus a subadult individual.

Results

The observed metatarsal fusion patterns and their relative frequencies in *Gorilla*, *Pan*, and *Homo* are summarized in Tables

Table 1
Metatarsals examined in this study

Species	Sample size	Collection
<i>Homo sapiens</i>	16	Raymond Dart Collection, University of Witwatersrand
	13	Mistihalj Collection, Harvard Peabody Museum
	17	Hamann-Todd Collection, Cleveland MNH
	39	Libben Collection, Kent State University
<i>Pan</i>	48	Cleveland MNH, Harvard MCZ, University of Zürich, Royal Museum for Central Africa, Smithsonian NMNH
<i>Gorilla</i>	25	Cleveland MNH, Harvard MCZ, University of Zürich, Royal Museum for Central Africa, Smithsonian NMNH

Species	Accession #	Collection
<i>Australopithecus afarensis</i>	AL 333-78	Cast. Cleveland Museum of Natural History
<i>Australopithecus africanus</i>	StW 377	School of Anatomical Sciences and Institute for Human Evolution, University of Witwatersrand
	StW 435	
	StW 477	
	StW 496	
<i>Homo habilis?</i>	OH 8	Tanzania National Museum and House of Culture
<i>Homo erectus</i>	KNM-ER 803	Kenya National Museum
<i>Homo sp.</i>	Omo F.511-16	Cast. School of Anatomical Sciences and Institute for Human Evolution, University of Witwatersrand
	D 2021	Photographs courtesy of David Lordkipanidze
	D 2669	
	D 2671	

Table 2
Metatarsal fusion pattern in *Gorilla*

1st Metatarsal base	Lateral metatarsal heads		
	Unfused	Partially fused	Fused
Unfused	12	1	0
%	48.0	4.0	0.0
Partially fused	2	7	0
%	8.0	28.0	0.0
Fully fused	0	2	1
%	0.0	8.0	4.0

2–4, respectively. In our *Gorilla* sample, 24 have unfused or partially fused lateral metatarsal heads. Of these, 22 (91.7%) have an unfused or partially fused first metatarsal base and two (8.3%) have a fully fused base. The one remaining *Gorilla* displays fully fused epiphyses for all of the metatarsals. In our *Pan* sample, 37 have unfused or partially fused lateral metatarsal heads. Of these, 36 (97.3%) have an unfused or partially fused first metatarsal base and one (2.7%) has a fully fused base. Of the 11 *Pan* with fused lateral metatarsal heads, seven have a fully fused base (63.6%) and four have a partially fused base (36.3%). In our *Homo* sample, all 67 (100%) that have unfused or partially fused lateral metatarsal heads also have an unfused or partially fused first metatarsal base. The 18 remaining *Homo* specimens have fully fused epiphyses for all of the metatarsals. None of the 89 African ape and human feet with unfused lateral metatarsal heads had a fully fused base of the first metatarsal (Tables 2–4). Only three individuals (1.9%; two *Gorilla*, one *Pan*) had partially fused lateral metatarsals along with fully fused first metatarsal bases.

In individuals that had unfused epiphyses for the lateral metatarsals, a subsample ($n = 79$) was examined by one of us (JD) for the type of bone present on the epiphyseal surface of each metatarsal. In all 79 cases, the epiphyseal surface of each metatarsal consisted of roughened, unorganized bone. Even unfused metatarsals that were eroded still had a film of unorganized bone covering the most distal aspect of the epiphyseal surface. There were no cases of subadult human or African ape metatarsals with trabecular bone only at the most distal end of the bone. However, trabecular bone was present in adult specimens that were damaged or broken in the region of the metatarsal heads.

Discussion

It has generally been reported that in modern humans, fusion of the base of the first metatarsal occurs slightly after the fusion of the second through fifth metatarsal heads. Hoerr et al. (1962) describe the fusion of the first metatarsal base as “beginning” when the fusion of the metatarsal heads is already “in progress.” According to a comprehensive survey of the literature on human skeletal growth, Scheuer and Black (2000, 2004) report that fusion of the

Table 3
Metatarsal fusion pattern in *Pan*

1st Metatarsal base	Lateral metatarsal heads		
	Unfused	Partially fused	Fused
Unfused	17	1	0
%	35.4	2.1	0.0
Partially fused	3	15	4
%	6.3	31.3	8.3
Fully fused	0	1	7
%	0.0	2.1	14.6

Table 4
Metatarsal fusion pattern in *Homo sapiens*

1st Metatarsal base	Lateral metatarsal heads		
	Unfused	Partially fused	Fused
Unfused	48	0	0
%	56.5	0.0	0.0
Partially fused	7	12	0
%	8.2	14.1	0
Fully fused	0	0	18
%	0.0	0.0	21.2

first metatarsal base occurs between the ages of 13 and 15 years in females and between 16 and 18 years in males; whereas fusion of the metatarsal heads occurs between the ages of 11 and 13 years in females and 14 and 16 in males. Similarly, Baker et al. (2005) also suggest that fusion of the first metatarsal base is slightly delayed relative to fusion of the metatarsal heads. Radiographic data from Whitaker et al. (2002) indicate that metatarsal heads become fully fused slightly before the base of the first metatarsal fuses to the diaphysis.

The results of this study suggest that African apes and humans share a typical pattern of metatarsal fusion pattern, wherein fusion of the base of the first metatarsal closely matches fusion of the lateral metatarsal heads. For instance, 80.0% of *Gorilla*, 81.3% of *Pan*, and 91.8% of *Homo* occur along the main diagonal of each genus matrix (Tables 2–4). Moreover, although 13.6% of the entire sample displayed a metatarsal fusion pattern off the main diagonal of each genus matrix, not a single individual was observed with a fully fused epiphysis of the first metatarsal in combination with unfused epiphyses of the lateral metatarsals (Bolded in Tables 2–4). These data suggest that if the OH 8 foot is from a subadult with unfused second and third metatarsals, then the base of the first metatarsal should also be unfused. At the very least, the epiphyseal line on the proximal end of the first metatarsal should be detectable, particularly in radiographs, which is not the case for OH 8 (Susman, 2008). Instead, the epiphyseal line on the first metatarsal base is fully obliterated, which suggests that the second and third metatarsal heads were either fully fused or at least partially fused in the OH 8 hominin. If the metatarsal heads were fully fused, then there is little likelihood that OH 8 is from a subadult, but if they were partially fused, then we should consider the possibility that they may have been broken off postmortem.

The absence of metatarsal heads in hominin fossils is not an unusual preservation pattern, even from individuals who were likely adults. All but the head of the metatarsal is preserved in Sterkfontein metatarsals StW 377, StW 435, StW 477, and StW 496. Third metatarsals Omo F.511–16, KNM-ER 803, and Dmanisi D2021 also have a similar pattern of damage with the lateral metatarsal head broken off just as the distal diaphysis begins to expand (Fig. 2). It is certainly possible that some of these individuals are juveniles. However, based on the wear of associated teeth, KNM-ER 803 is clearly from an adult (Day and Leakey, 1974) and D2021 is associated with an adult skeleton (Lordkipanidze et al., 2007). It has also been suggested that StW 435 is associated with the adult male *Australopithecus africanus* partial skeleton, StW 431 (Toussaint et al., 2003).

Trabecular bone at the broken distal end of the D2021 third metatarsal was presented as evidence that the bone was from an adult (Gabunia et al., 1999). Trabecular bone is also present in the distal ends of metatarsals StW 377, 435, 477, 496, Omo F.511–16, and the OH 8 second and third metatarsals (Fig. 3). This is in contrast to modern human and African ape subadult metatarsals, which have a layer of roughened bone at the metaphyseal growth plate (Baker et al., 2005). It is possible that this layer is eroded away in the Olduvai fossils. The possibility that the absence of the woven bone was an artifact of fossilization was assessed by examining the metatarsals of the eight to ten-year-old Skhul VIII individual and images of a Neandertal metatarsal from an ~15-year-old individual from Valdegoba (Quam et al., 2001). Though covered with a preservative, it is clear that the end of the third metatarsal of the Skhul VIII foot does not present trabecular bone, and instead preserves a layer of unorganized bone at the distal metaphysis (Fig. 3). A similar morphology is observed in the Valdegoba subadult metatarsal. This is in contrast to adult metatarsals that are broken at their distal ends, which instead show a layer of trabecular bone, as found in the D2021, StW 477, and OH 8 (Fig. 3).

The 1.77 mya site of Dmanisi has also yielded a subadult mandible (D2735), along with an associated skull (D2700), fourth metatarsal (D2669), and first metatarsal (D2671) (Vekua et al., 2002; Lordkipanidze et al., 2007). Both of the OH 7 and D2735 mandibles display a similar pattern of dental eruption and wear of the preserved dentition and both preserve all of the dentition, excluding the lower third molar (M_3). In D2735, the M_3 is congenitally absent on the left side, while a preserved and open alveolus on the right side suggests the M_3 was just beginning to erupt. The right side of OH 7 is broken just distal to M_1 , but preserves a complete M_2 and the beginnings of the M_3 alveolus. It is difficult to know with certainty what state of eruption the M_3 was

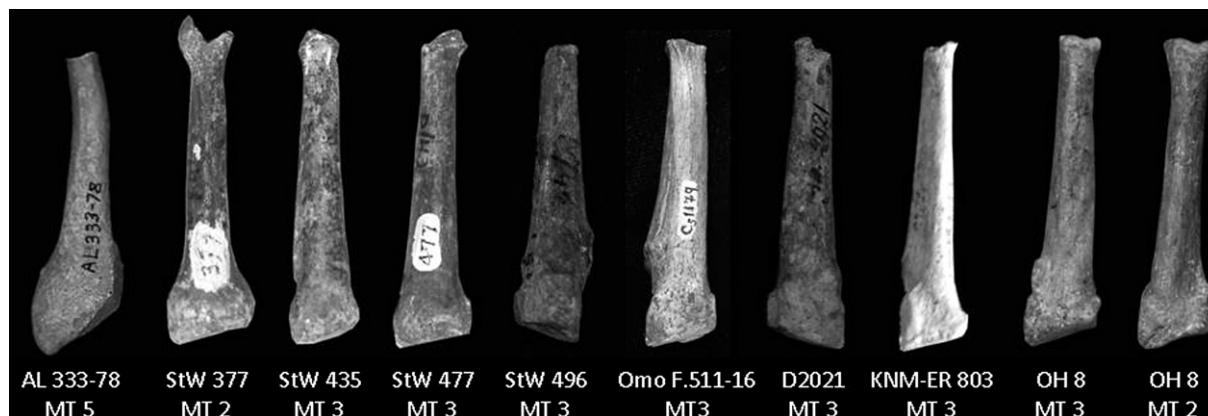


Figure 2. Hominin metatarsals with the common taphonomic signature of a missing head. Hominin metatarsals are all in dorsal view. Note that the preservation of all but the metatarsal head is common in the fossil record. This condition does not necessarily imply juvenile status, as both KNM-ER 803 and D2021 are known to have come from adult hominins.

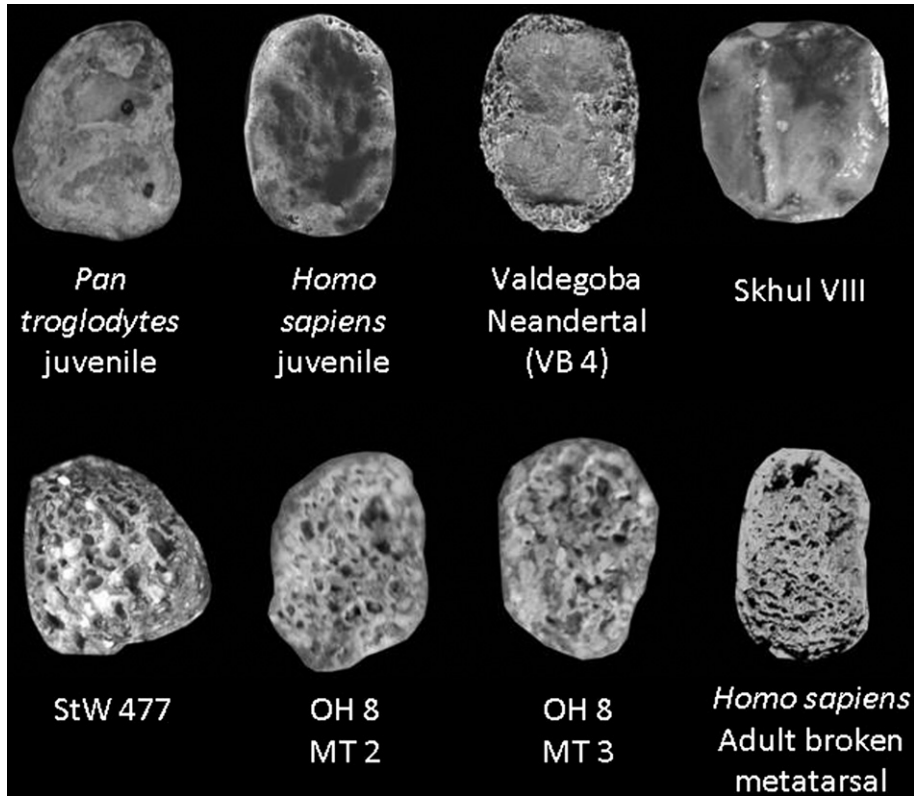


Figure 3. Distal view of epiphyseal surfaces in unfused juvenile compared with broken adult metatarsals. Juveniles present a layer of unorganized, irregular bone at the epiphyseal surface (chimpanzee and human upper left). This morphology can be preserved in the fossil record as demonstrated by the Neandertal metatarsal and the *Homo sapiens* Skhul VIII specimens (PMAE 46-49-60/N7448.0) (upper right). The OH 8 second and third metatarsals display trabecular bone at their most distal ends, similar to what is seen in adult metatarsals that have been damaged postmortem (bottom). The presence of trabecular bone precludes these from being epiphyseal surfaces.

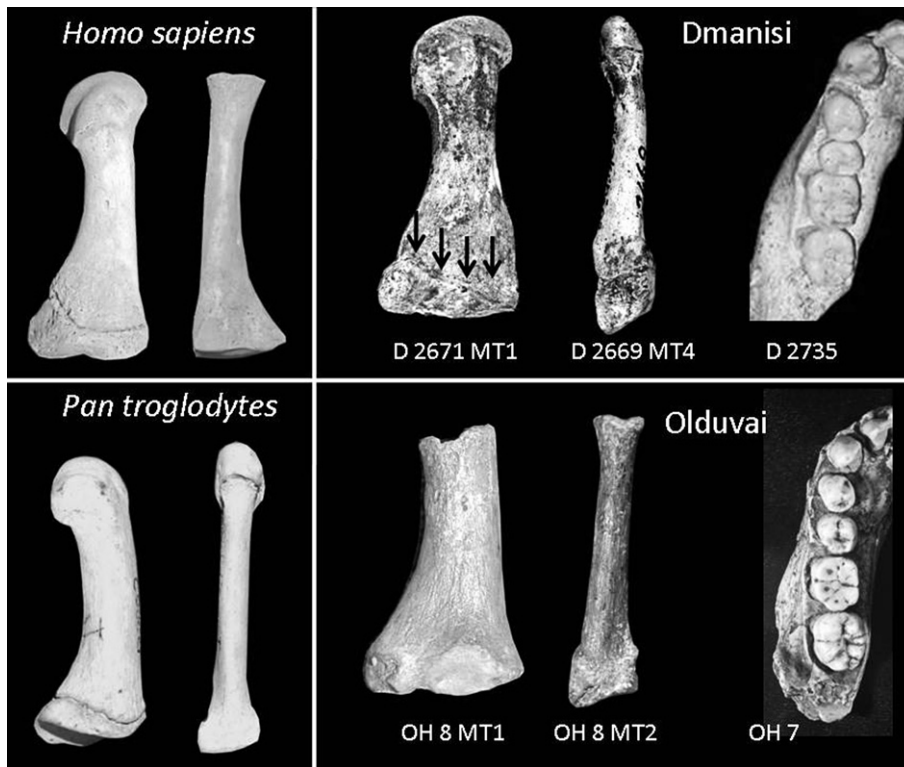


Figure 4. Comparison of metatarsal fusion patterns in Dmanisi and Olduvai hominins. Both the human (upper left) and chimpanzee (lower left) had second mandibular molars that were erupted and in occlusion, but had not erupted the third molars. This is the developmental status of both mandibles (D 2735, upper right; OH 7, lower right). Note the strong epiphyseal line present in the subadult human and chimpanzee metatarsals. The epiphyseal line can also be seen in the D 2671 metatarsal from Dmanisi (indicated with arrows). The fourth metatarsal (D 2669) also has a distal epiphyseal line present. However, the base of the OH 8 first metatarsal is fully fused and the epiphyseal line is obliterated. The images of the Dmanisi metatarsals (right-side) have been reversed to facilitate direct comparison with OH 8 (left-side).

in, but it is doubtful that it was much advanced beyond that of D2735 on the basis of comparative dental wear between the two specimens. Both specimens display moderate cusp flattening on M_1 with several isolated pockets of dentin exposure. They both display only mild dental wear on M_2 , with much of the cusp morphology preserved and only the slightest beginnings of dentin exposure. The premolars and canines of both mandibles show only slight polishing with weak apical wear. The Dmanisi specimen preserves only its lateral incisors, which show moderate wear along the occlusal surface comparable with that seen on OH 7. The corpus of D2735 shows additional subadult characteristics; it lacks much of the superficial topography (i.e., anterior marginal tubercle, lateral torus) typically associated with adult or even late adolescent mandibular development, such as seen on the D211 mandible from Dmanisi or OH 13 from Olduvai. Unfortunately, the absence of the basal half of the OH 7 mandible does not allow for similar comparisons with D2735, but what is preserved of the alveolar region does not suggest substantive differences in the stage of development between these two subadult hominin mandibles.

Given that the OH 7 and D2735 mandibles are so similar in terms of dental development and geological age, it is particularly informative to compare the epiphyseal fusion patterns of the metatarsals in relation to our extant comparative data. D2669, the fourth metatarsal, clearly possesses a partially fused metatarsal head (Fig. 4). As we would predict based on the comparative data presented herein, D2671, the accompanying first metatarsal, is also partially fused with a clear epiphyseal line across its base, and unlike the fully fused condition in the OH 8 first metatarsal (Fig. 4).

In total, the comparative evidence of metatarsal fusion patterns and internal bone morphology of distal metatarsals among modern humans, African apes, and fossil hominins, suggests that it is highly improbable that OH 8 possessed unfused lateral metatarsal heads. Rather, it is more probable that, at the time of death, the lateral metatarsal heads of OH 8 were fully fused, reducing the likelihood that the individual was a subadult and, in particular, a subadult that reasonably matches the developmental age of the OH 7 mandible. The missing metatarsal heads may be the result of crocodylian activity, suggested to have left bite marks on the OH 8 talus and calcaneus as well (Njau and Blumenschine, 2007), or some other taphonomic process.

Conclusion

The results of our comparative analyses of metatarsal fusion patterns and internal bone morphology of distal metatarsals suggest that the OH 8 foot more likely belonged to an adult hominin. If OH 8 did belong to a subadult, then it displays a metatarsal developmental pattern that is rare for extant African apes and humans and fossil hominins. Close examination of the distal metatarsal surfaces reveals them to be broken ends, rather than epiphyseal surfaces. Given the dental development of the OH 7 mandible and the results of our comparative analysis the hypothesis that the OH 8 foot and the OH 7 mandible are from the same individual is unlikely to be correct.

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