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Metatarsal fusion pattern and developmental morphology of the Olduvai Hominid 8 foot: Evidence of adolescence

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ABSTRACT

The morphology of the Olduvai Hominid (OH) 8 foot and the sequence of metatarsal epiphyseal fusion in modern humans and chimpanzees support the hypothesis that OH 8 belonged to an individual of approximately the same relative age as the OH 7 subadult, the holotype of *Homo habilis*. Modern humans and chimpanzees exhibit a variety of metatarsal epiphyseal fusion patterns, including one identical to that observed in OH 8 in which metatarsal 1 fuses before metatarsals 2–5. More than the metatarsal fusion sequence, however, the principal evidence of the youthful age of OH 8 lies in the morphology of metatarsals 1, 2, and 3. Because both OH 8 and OH 7 come from the same stratum at the FLK NN type site, the most parsimonious explanation of the OH 8 and OH 7 data is that this material belonged to the same individual, as originally proposed by Louis Leakey. The proposition that OH 8 belonged to an adult is unsupported by morphology, including radiographic evidence, and the fusion sequences in human and chimpanzee skeletal material reported here and in the literature.

Introduction

Interest in the Olduvai Hominid (OH) 8 foot can be traced to the fact that it is the most complete foot in the hominin fossil record, its exceptional preservation and its derived, human-like bipedal total biomechanical pattern (Day and Napier, 1964; Susman and Stern, 1982). The importance of the OH 8 foot is underscored by the widely divergent opinions regarding its status as part of the *Homo habilis* holotype (Leakey, 1960, 1961a; Susman and Stern, 1982), the paratype (Leakey et al., 1964), or some other hominin species (Wood, 1974). Despite the fact that OH 8 is the most complete and well-preserved foot in the early hominin fossil record, its relationship to other fossils from Olduvai, its taxonomic status and its ontogenetic age have defied consensus.

The age and taxonomic status of OH 8 are intertwined due to the fact that the same "floor," Level 3 at FLK NN, has yielded remains of a subadult individual, OH 7, as well as the OH 8 remains and other fossils. While its discoverers originally considered OH 8 to be part of the OH 7 subadult (Leakey, 1961a,b), it was later suggested that OH 8 belonged to a second individual, an adult, at FLK NN Level 3 (Day and Napier, 1964). An early multivariate morphological study of the OH 8 talus prompted some to suggest that not only was OH 8 an adult, but also that it belonged to *Paranthropus boisei* (Wood, 1974). Gebo and Schwartz (2006) and Moyà-Solà et al. (2008) have also suggested that OH 8 belongs to *P. boisei*. Thus, the significance of the ontogenetic age of the OH 8 foot extends beyond its descriptive anatomy to the question of whether OH 8 is associated with the OH 7 holotype or whether it even belongs to the same species.

Susman and Stern (1982) and later Susman (2008) offered evidence of the adolescent age of the OH 8 foot based on the pattern of epiphyseal fusion in which the basal epiphysis of metatarsal 1 is fused while distal epiphyses of metatarsals 2 and 3 are unfused. In fact, Susman and Stern (1982), using modern human aging standards, suggested an age of approximately 13 years for OH 8. Most researchers agree that the distal ends of OH 8 metatarsals 4 and 5 were likely bitten or broken off peri- or postmortem, and accordingly, these bones do not retain enough of their distal ends to have captured their epiphyseal surfaces. The metatarsals that are dispositive of the issue of subadulthood in OH 8 are metatarsal 1 (OH 8 H) in which the basal epiphysis is intact on its proximal end, and metatarsals 2 (OH 8 J) and 3 (OH 8 I).

The distal ends of metatarsals 2 and 3 are essentially intact save for their epiphyses and a modest portion of the calcifying distal surface on the end of the bone that has been eroded. What remains

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of the surfaces of lesser metatarsals 2 and 3 assumes the essential contours of epiphyseal surfaces in both dorsal and lateral views (Figs. 1 and 2). Susman (2008) and Susman et al. (2010) noted that in dorsal view photographs and dorsoplantar view radiographs, metatarsals 2 and 3 display "chevron" shaped epiphyseal surfaces, characteristic of subadult metatarsals (Fig. 1C.2–3, 1D.2–3; see also Fig. 2 in Susman, 2008). The chevron contour of the end of the fossil metatarsal closely mimics its counterpart in adolescent humans (see Fig. 3), a feature that is also illustrated in the literature (e.g., see Fig. 9.23 of a c. 15 year old human individual figured in Baker et al., 2005). In lateral view, the epiphyses are clearly demonstrated by the sigmoid-shaped profile of the distal end of metatarsal 2 (Fig. 1A.2 and 1B.2) and the distinctive flare or funneling outward of metatarsals 2 and 3 near the distal ends of their metaphyses (Fig. 1A.2–3, 1B.2–3). The latter is a notable feature of most long bone metaphyses (Ham and Cormack, 1979; White, 2000).

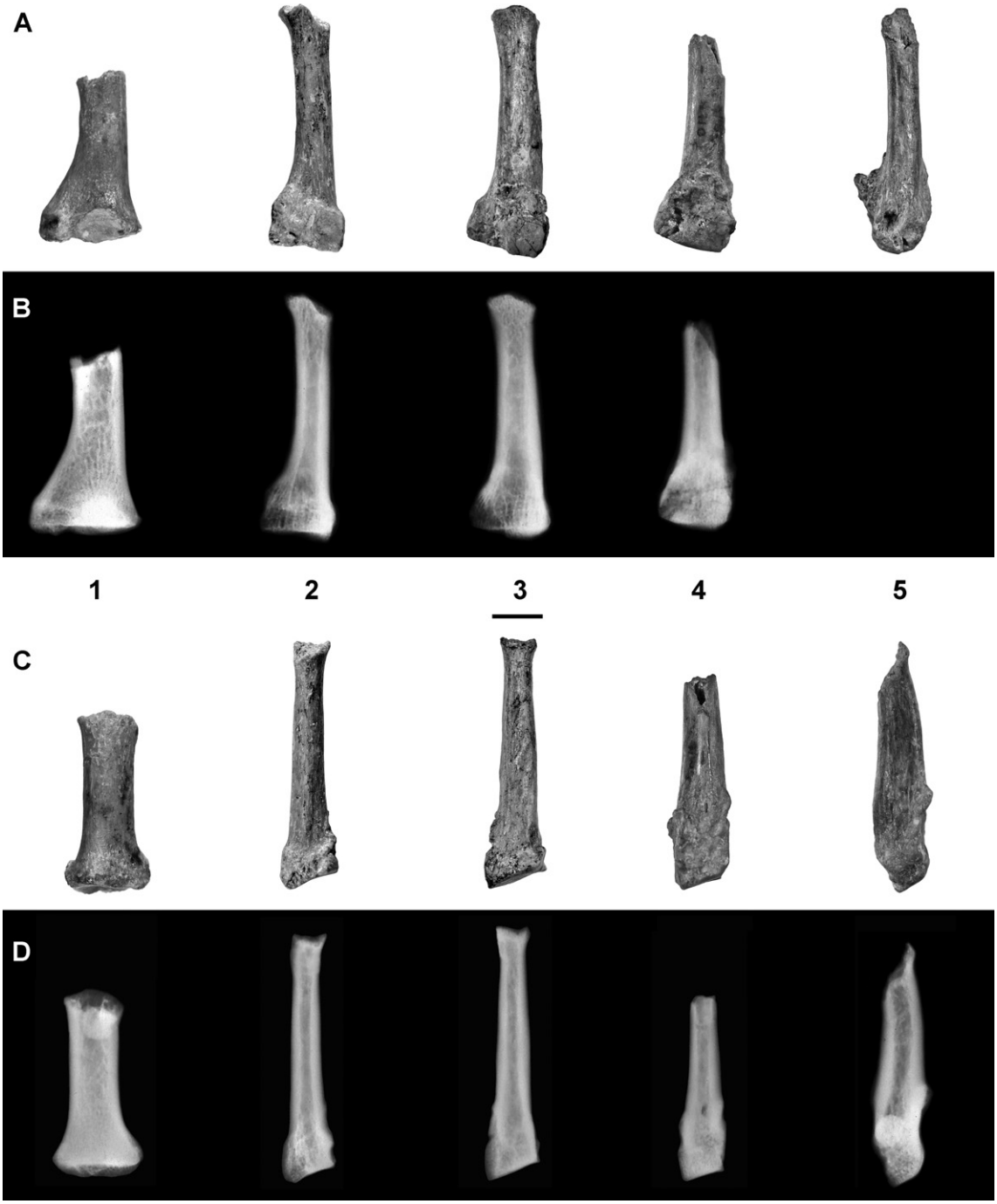

Figure 1. (A) Lateral view photographs, and (B) mediolateral plain X-rays of OH 8 metatarsals 1–4/5. The broken distal ends of metatarsals 1, 4 and 5 are evident (see also Fig. 2). The epiphyseal surface contours are evident on the proximal ends of metatarsals 2 and 3. The X-ray of metatarsal 1 shows the fused basal epiphysis and the epiphyseal line (see also Fig. 4B). The latter is an indicator of a recently fused epiphysis (DeSilva et al., 2010:421). (C) Dorsal view photographs, and (D) dorsoplantar plain X-rays of OH 8 metatarsals 1–5. The adolescent status of OH 8 is manifest in the shapes of the distal ends metatarsals 2 and 3. These unfused fossil metatarsals display a characteristic "chevron" at the distal epiphyseal surfaces, typical of modern humans. Compare the distal ends of OH 8 metatarsals 2 and 3 in row D with their human counterparts in Figs. 3 and 6 (see also Fig. 9.23 in Baker et al., 2005). Also indicative of the young age of OH 8 is the outward flare or funneling of the diaphyses of metatarsal 2 and 3 as they reach their epiphyses. This feature is absent in metatarsals 1, 4, and 5. Scale bar = 1 cm.