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Paranthropus boisei: Fifty Years of Evidence and Analysis

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KEY WORDS   *Paranthropus*; *boisei*; *aethiopicus*; human evolution; Africa

ABSTRACT   *Paranthropus boisei* is a hominin taxon with a distinctive cranial and dental morphology. Its hypodigm has been recovered from sites with good stratigraphic and chronological control, and for some morphological regions, such as the mandible and the mandibular dentition, the samples are not only relatively well dated, but they are, by paleontological standards, reasonably-sized. This means that researchers can trace the evolution of metric and nonmetric variables across hundreds of thousands of years. This paper is a detailed[1] review of half a century's worth of fossil evidence and analysis of *P. boisei* and traces how both its evolutionary history and our understanding of its evolutionary history have evolved during the past 50 years. Yrbk Phys Anthropol 50:106–132, 2007.   © 2007 Wiley-Liss, Inc.

Australopithecus boisei, which for reasons explained later in this article we refer to as *Paranthropus boisei*, is a hominin best known for its large jaws and large postcanine teeth. It is unusual among hominins for several reasons. First, because *P. boisei* is an easily recognized (Tobias, 1967; Rak, 1978) and an apparently derived (Wood, 1991; Kimbel et al., 2004; Strait and Grine, 2004) taxon its hypodigm is well circumscribed and relatively uncontroversial. Second, most of the fossil record of *P. boisei* comes from sites with good stratigraphic and chronological control (Feibel et al., 1989; McDougall and Brown, 2006). Third, the hypodigm is heavily biased towards jaws and teeth so that for some morphological regions such as the mandible and the mandibular dentition, samples are not only relatively well-dated, but by paleontological standards they are reasonably-sized. This means that researchers can trace the evolution of metrical and nonmetrical variables across hundreds of thousands of years. Finally, because 50-years have elapsed since its discovery, it is possible to use *P. boisei* as an example of how our understanding of a hominin taxon has itself evolved over time. We review half a century's worth of fossil evidence and analysis of *P. boisei* to trace how both its evolutionary history and our understanding of its evolutionary history have evolved over that time.

son suggested that the genus *Zinjanthropus* be abandoned and he proposed that the new specimen should be included within the existing genus *Paranthropus*. In doing so, he pointedly referred to the existence of "nearly 200 specimens of *Paranthropus*"(Robinson, 1960b, p. 458), presumably to emphasize that Leakey was unfamiliar with the range of variation included in this hypodigm. Robinson acknowledged there were size differences between OH 5 and the *Paranthropus* remains from southern Africa, but he interpreted these as being of relatively minor significance. Subsequently, a detailed and meticulous analysis of the OH 5 cranium (Tobias, 1967) also found no grounds for a generic distinction between *Zinjanthropus* and *Australopithecus* (i.e., *Paranthropus*).

Most researchers now include the East African megadont archaic hominins in *Australopithecus* as *A. boisei* (e.g., Tobias, 1967; Kimbel, 1984; Suwa et al., 1994). The researchers who favor the hypothesis that the East and southern African megadont taxa form a monophyletic group (e.g., Grine, 1988; Wood, 1991) retain *Paranthropus* as the genus name for that clade and use *P. boisei* as the species name for the group to which OH 5 belongs. For the reasons given in the sections on Taxonomy and Phylogenetic Analysis, we suggest that until uncertainties about the taxonomy of the East African

NOMENCLATURE

In the "preliminary diagnosis" of what was then referred to as *Zinjanthropus boisei*, Leakey (1959) drew attention to 20 "major differences" (p. 493) between *Z. boisei* and "the genera *Australopithecus* and *Paranthropus*" (p. 492). Because at the time OH 5 was both the holotype and the only evidence of that taxon, these were effectively differences between a single specimen, OH 5, and two relatively well sampled established genera (see Smith (2005) for a sober warning about this and other studies that claim taxonomic distinction on the basis of a single specimen). The following year Robinson (1960b) went through Leakey's claimed "major differences" and to the former's satisfaction refuted the vast majority. Robin-
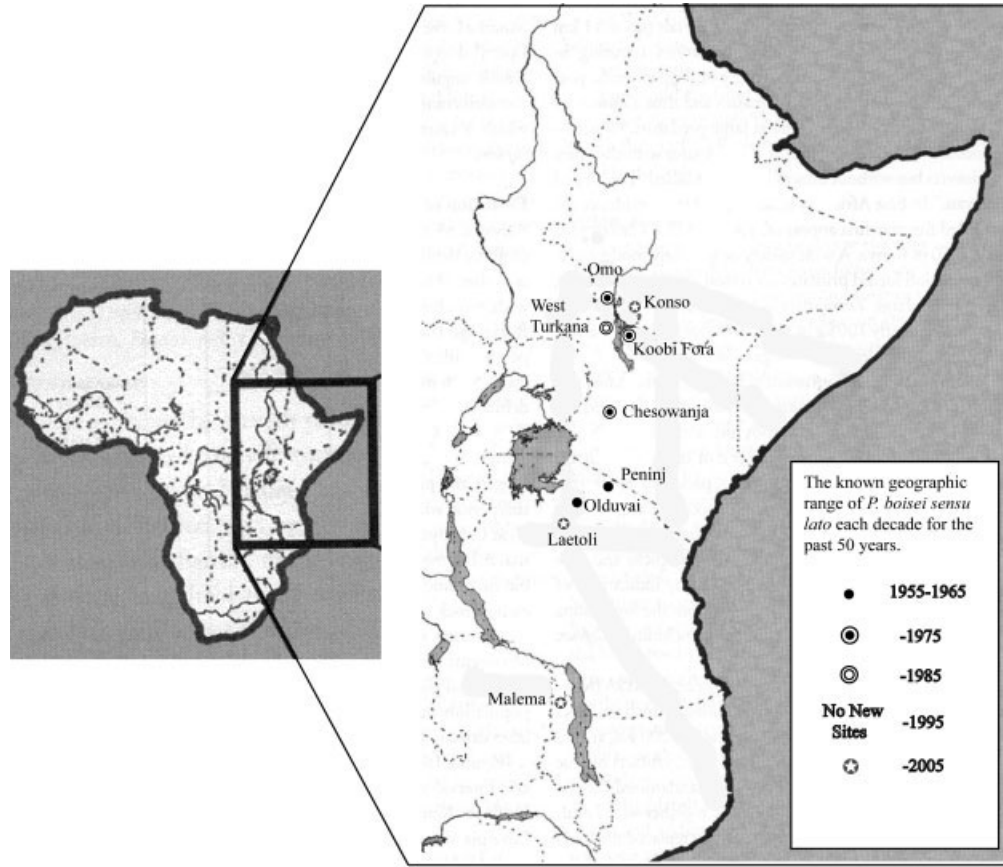
Fig. 1. Map of *P. boisei* sites in East Africa highlighting the change in its known geographic range over the past five decades. The only new site discovered between 1975 and 1985 was West Turkana, and no new sites were discovered between 1985 and 1995. The last decade has seen a significant increase in the range of *P. boisei* due mainly to the recovery of additional fossils from Malema in Malawi and from Konso in Ethiopia. Adapted from Delson et al. (2000).

taxa and the phylogenetic relationships of both the East African and southern African megadont taxa are resolved, the term *Paranthropus* should be used to recognize the strong possibility that megadont taxa in both regions form an adaptively distinctive monophyletic group. Furthermore, as will be discussed in the Taxonomy section, there is some debate as to whether *P. boisei* is the only species of "robust" hominin in East Africa, or whether the pre-2.3 Ma fossils constitute a second species called *P. aethiopicus*. We recognize *P. aethiopicus* as a valid species and hence use *P. boisei* to refer solely to the post-2.3 Ma "robust" fossil specimens. However, in some places we use the term *P. boisei sensu stricto* to reinforce the fact that we are excluding *P. aethiopicus*, and we use *P. boisei sensu lato* when the discussion refers to a hypodigm that subsumes both *P. boisei sensu stricto* and *P. aethiopicus*.

HISTORY OF DISCOVERY

The first evidence of a megadont hominin (i.e., a hominin with absolutely and relatively very large postcanine tooth crowns) from East Africa was OH 3, a specimen comprising a deciduous canine and a large deciduous molar crown (Leakey, 1960; Robinson, 1960a; Howell, 1978; Grine, 1984). These teeth were found at locality BK in Lower Bed II at Olduvai Gorge in Tanzania in 1955 (Leakey, 1958)[2] (Fig. 1), but their taxonomy remained uncertain until the recovery of a well-preserved subadult cranium, OH 5, in 1959 (Fig. 2).

No mandibles matching the OH 5 cranium have been found at Olduvai Gorge, but in 1964 a well-preserved, robust-bodied, adult mandible with megadont postcanine tooth crowns was recovered from a site on the western shore of Lake Natron which lies to the north of Olduvai Gorge in the Great Rift Valley. The official accession number of this specimen is NMT-W64-160, but it is almost universally referred to as Peninj 1. It seemed to provide evidence of the type of mandible that would be compatible with the OH 5 cranium (Leakey and Leakey, 1964). Another hominin mandible with postcanine megadontia, Omo 18.18, was recovered from the Omo Shungura Formation in southern Ethiopia in 1967 (Arambourg and Coppens, 1968). It was initially included in a separate genus and species, *Paraustralopithecus aethiopicus*, but this genus name has been abandoned and it is universally regarded as a junior synonym of either *Paranthropus* or

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[2]The discovery of OH 3 was also reported in the Illustrated London News (Leakey, LSB [1958]. A giant child among the giant animals of Olduvai? A huge fossil milk molar which suggests that Chellean Man in Tanganyika may have been gigantic. *Illustrated London News*, **232**:1104–1105), but because the *Illustrated London News* is a non-specialist magazine and not a scientific publication, we suggest that the paper in *Nature* be given precedence.
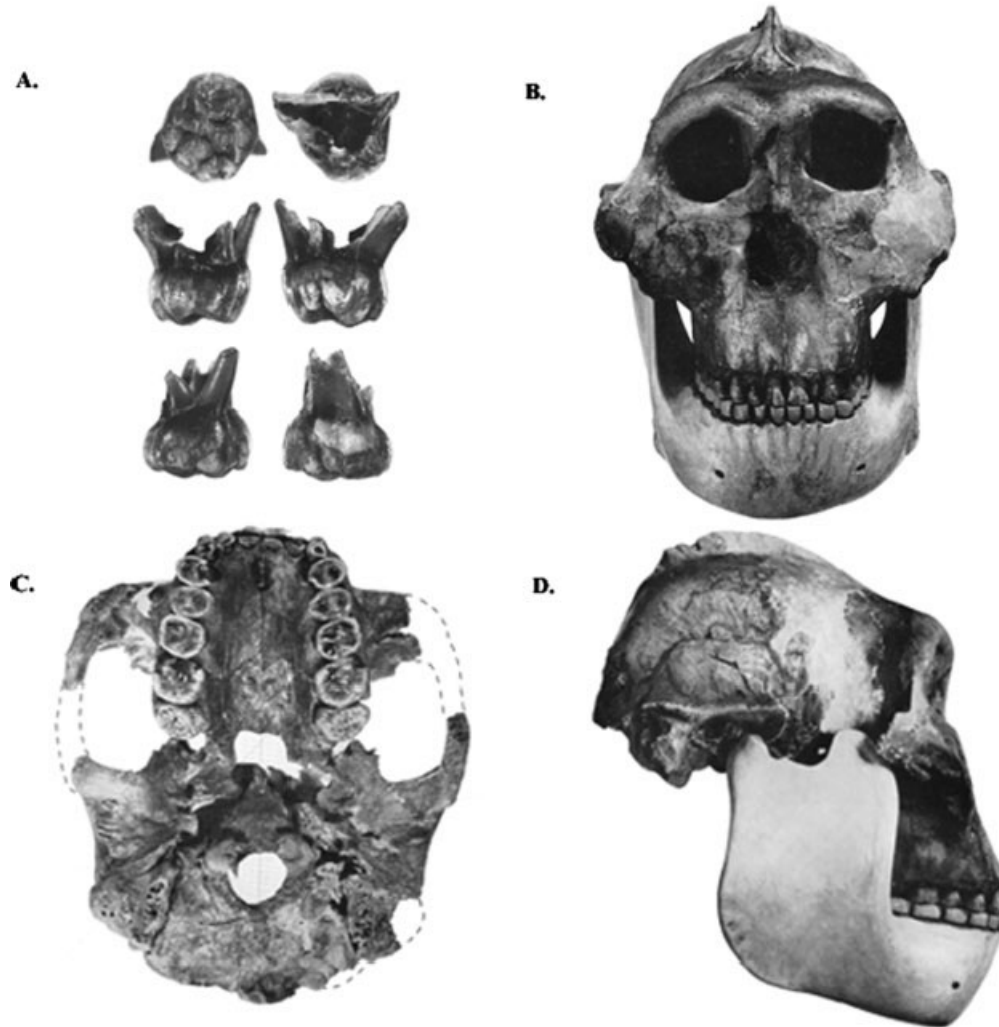
Fig. 2. The initial evidence of the taxon originally referred to as *Zinjanthropus boisei*. (**A**) the OH 3 deciduous molar, (**B**) OH 5 (anterior view), (**C**) OH 5 (inferior view), (**D**) OH 5 (right lateral view). Adapted from Tobias (1967).

Australopithecus. Some researchers still prefer to retain a specific distinction for this mandible and other similar pre-2.3 Ma megadont specimens from the Omo region (see below), hence their being referred to as either *Paranthropus* or *Australopithecus aethiopicus*.

Since 1967, teeth like those of OH 5 and Peninj 1 (e.g., Omo L628-1) and mandibles similar to Peninj 1 (e.g., L74-21 and L7A-125), have been found in the Shungura Formation in the Omo region of southern Ethiopia, and they have been assigned to either *A. boisei* or *A. aethiopicus* (taxa we refer to here as *P. boisei* and *P. aethiopicus*) (Coppens, 1978, 1980). A fragmentary adult cranium, Omo 323-1976-896, recovered from Member G of the Shungura Formation in 1976, almost certainly belongs to *P. boisei* (Coppens and Sakka, 1983; Alemseged et al., 2002). The fragmented immature cranium from Member E, L338y-6, was initially considered to belong to *P. boisei*, but its age of ca. 2.4 Ma and the morphology it shares with KNM-WT 17000 are also consistent with it belonging to *P. aethiopicus* (Rak and Kimbel, 1991, 1993; but see Walker et al., 1993 White and Falk, 1999).

The abraded robust mandibular corpus KNM-ER 403 recovered in 1968 was the first in a series of discoveries of *P. boisei* from what was then known as East Rudolf

(now called Koobi Fora or East Lake Turkana) on the east side of Lake Turkana in northern Kenya. The same year researchers recovered KNM-ER 404, another hemi-mandible resembling Peninj 1, and an abraded and edentulous palate, KNM-ER 405. The mandibular hypodigm at Koobi Fora has since expanded so that numerically it is the best-sampled region of the *P. boisei* skeleton (Wood, 1991). More cranial evidence of *P. boisei* from Koobi Fora came in 1970 with the recovery of KNM-ER 406, a well preserved but edentulous adult cranium, and KNM-ER 407, the posterior part of an adult calvaria. A year later, researchers recovered KNM-ER 732, an adult hemi-cranium preserving the majority of the vault, the right side of the face, and part of the right side of the cranial base, and KNM-ER 733, a fragmented adult skull that preserves sufficient taxonomically-valent morphology to allow it to be assigned to *P. boisei* (Wood, 1991).

Soon after the initial discoveries of *P. boisei* at Koobi Fora, another significant addition to the hypodigm came in 1970 with the recovery of KNM-CH 1, a right hemiface and anterior cranial base from the Chemoigut Formation at Chesowanja in Kenya. The generally massive build of the face, the absolute and relative size of the dentition, and details of facial morphology were all judged to be
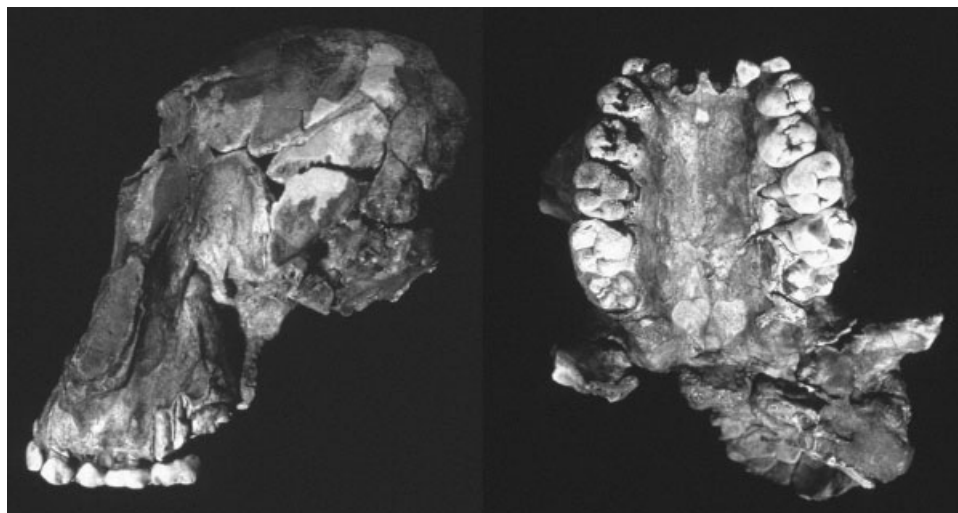
Fig. 3. The subadult cranium KNM-WT 17400 in lateral and inferior views. This specimen is from West Turkana and it is approximately 750 ky younger than KNM-WT 17000. See Walker and Leakey (1988) for a detailed description.

characteristic of *P. boisei* (Carney et al., 1971). However, the ways that the facial and cranial morphology of KNM-CH 1 departs from that of OH 5, especially the greater postorbital breadth and the apparent absence of temporal ridges, were interpreted in the initial description as evidence that KNM-CH 1 sampled "... a population of evolved robust australopithecines, most likely descended from *A. boisei*" (Carney et al., 1971, p. 513). Szalay (1971) and others were not persuaded that the cranial capacity of KNM-CH 1 was large, nor were they convinced that its morphology departed from that of *P. boisei*. The Chesowanja cranium is now more usually interpreted as a small-bodied, probably female member of the species (Howell, 1978; Wood, 1991), and two more hominin specimens from Chesowanja, KNM-CH 302 and KNM-CH 304, were also later assigned to *P. boisei* (Gowlett et al., 1981).

The rate of discovery of *P. boisei* reached its peak in the second decade (1966–1975) of the taxon's history. Since that period of initial intensive prospecting in the Omo Shungura Formation and at Koobi Fora, further sub-ca. 2 myr-old cranial remains belonging to *P. boisei* have been found at Koobi Fora (e.g., KNM-ER 13750 and KNM-ER 23000) and some belonging to *P. boisei* or *P. aethiopicus* have been found on the opposite side of the lake at West Turkana (e.g., KNM-WT 16005, KNM-WT 17000, and KNM-WT 17400) (Leakey and Walker, 1988; Feibel et al., 1989; Wood, 1991; Brown et al., 1993; Prat et al., 2003) (see Fig. 3). Evidence for *P. boisei* has also come from sites elsewhere in East Africa, most notably in 1993 when KGA 10-525, a well-preserved skull of *P. boisei*, was recovered at Konso (then called Konso Gardula) in Ethiopia (Suwa et al., 1997). The recovery of a *P. boisei*-like maxilla from Malema, Malawi was significant from a biogeographical standpoint since it greatly increased the southern extent of *P. boisei*'s known range (Kullmer et al., 1999).

GEOGRAPHIC AND TEMPORAL RANGE

Paranthropus boisei sensu lato is currently known from eight sites in East Africa, or nine if one includes an unpublished *P. aethiopicus* maxilla recovered from Laetoli in 2001 (Harrison, 2002) (Fig. 1). These sites extend from the Omo River and Konso in southern Ethiopia

(~5° North) to Malema in northern Malawi (~10° South). The discovery of the Malema maxilla more than doubled the north–south range of *P. boisei* to over 2,000 km, for prior to its recovery the most southerly site known to contain remains of *P. boisei* was Olduvai Gorge. Konso and Malema are also the most easterly (~37° East) and westerly (~33° East) sites, respectively.

Presently, the oldest known evidence of *P. boisei s.l.* comes from the Omo ca. 2.6 Ma (Brown and Lajoie, 1972; Feibel et al., 1989) and from West Turkana ca. 2.5 Ma (Walker et al., 1986) (see Fig. 4). Although not yet officially published, the maxilla from Laetoli is also likely to be among the oldest *Paranthropus* specimens as the Ndolanya Beds in which it was found are believed to be between 2.5 and 2.7 Ma (Harrison, 2002). The *P. boisei* maxilla from Malema is estimated to be between 2.3 and 2.5 Ma based on faunal correlations with the Omo (Kullmer et al., 1999) and is currently the only possible evidence of *P. boisei sensu stricto* prior to ca. 2.3 Ma.

The geologically youngest known members of *P. boisei* are from Konso in Ethiopia (Suwa et al., 1997). These ca. 1.4 Ma fossils are slightly younger than specimens from Koobi Fora dated between 1.49 and 1.50 Ma. Since there are no major East African hominin sites dated between ca. 1.4 and 1.0 Ma, we do not know for how long *P. boisei* persisted in that interval, but the lack of evidence in more recent sediments suggests that it went extinct at some point before 1.0 Ma. It is also possible that *P. boisei s.l.* evolved earlier in East Africa since sites dating to between ca. 2.5 and ca. 3.0 Ma are rare. However, the lack of *P. boisei s. l.* specimens in the older sediments of the Omo and the lower Lomekwi Member at West Turkana suggest that their first appearance date of 2.7–2.5 Ma is likely to be close to the origin of the taxon.

HYPODIGM

There are three ways any taxon, hominin or otherwise, can be morphologically distinctive. The first is to have evidence of what in cladistic jargon is called *autapomorphic* morphology. This means that members of the taxon possess derived features whose morphology is not shared with any other closely related taxon. A caveat about aut-
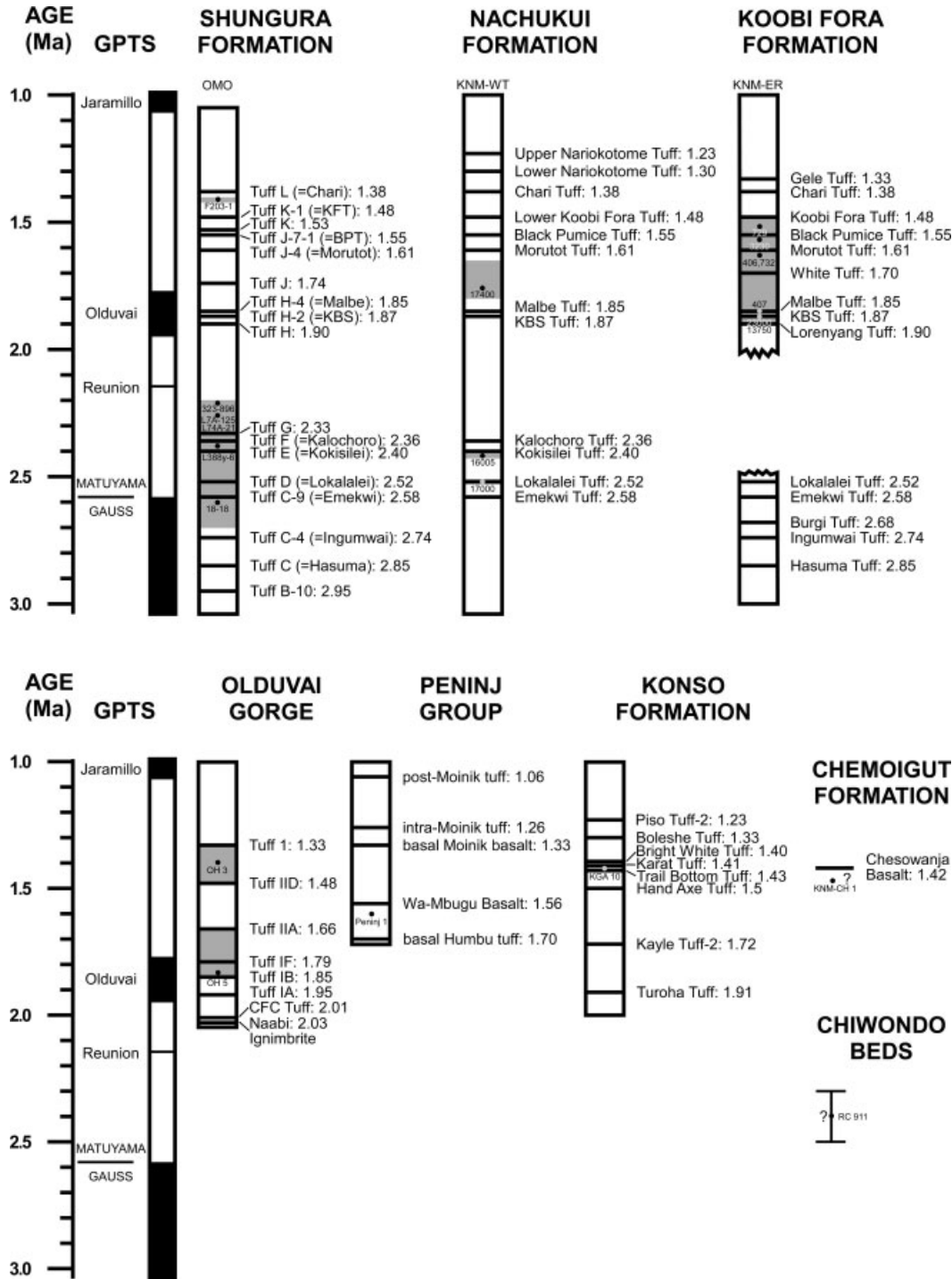
Fig. 4. Stratigraphic location of the *P. boisei* hypodigm. Shaded areas indicate levels where *P. boisei* fossils have been found. The specific positions of key specimens mentioned in the text are shown. All ages are approximate. The oldest known specimens of *P. aethiopicus* are from the Omo and are dated to ca. 2.6 Ma while the oldest fossils of *P. boisei sensu stricto* are from Malema and are approximately 2.3 Ma based on faunal correlations with the Omo. The specimens from Konso at ca. 1.4 Ma are the youngest known for *P. boisei*. References: Turkana Basin (Brown et al., 1985; Feibel et al., 1989; McDougall et al., 1992; McDougall and Brown, 2006), Olduvai Gorge (Walter et al., 1991; Manega, 1993; Tamrat et al., 1995; Hay and Kyser, 2001; Blumenschine et al., 2003), Peninj (Isaac and Curtis, 1974; Manega, 1993), Konso (Katoh et al., 2000; McDougall and Brown 2006), Chemoigut (Hooker and Miller, 1979; Bromage et al., 1995; Kullmer et al., 1999).

apomorphies must be emphasized. When a morphological feature is cited as being autapomorphic for *P. boisei*, this does not mean researchers are claiming that the same feature will never be found in a small proportion of individuals belonging to another taxon. For example, the distinctive shape of the nasal bones (being broadest superiorly and narrowing inferiorly) seen in *P. boisei* and in other *Paranthropus* taxa is also seen in a small percent-

age of some extant hominoids (Eckhardt, 1987). However, the modest incidence of a feature in extant taxa does not invalidate the significance of its occurrence in the nearly all of the specimens assigned to *P. boisei* that have that region preserved. In the case of *P. boisei*, examples of autapomorphic features include the extensively overlapping parietotemporal suture (Rak, 1978), mandibular premolar crowns with a particularly large and elaborate talonid (Suwa, 1988), and first mandibular molar crowns in which additional cusps are confined to the talonid (Wood and Abbott, 1983).

The second way a taxon can be distinctive is by possessing a *distinctive expression* of a shared, or symplesiomorphic morphology. Thus, while postcanine megadontia is probably symplesiomorphic for a *Paranthropus* clade (if such exists), the extreme expression of postcanine megadontia in *P. boisei* is distinctive.

The third category of morphological distinction is a distinctive combination of shared, or symplesiomorphic morphology (Wood, 1988). For example, *P. boisei* is the only hominin to combine a massive, wide, flat, face with a megadont postcanine dentition, molarized mandibular premolars, and a modest (mean ca. 450–500 cm^3) endocranial volume. Other hominin taxa have one, or more, of these attributes, but it is only in *P. boisei* that the most derived states of all of these characters are combined.

The individual fossils that make up the hypodigm of *P. boisei* are listed in Table 1. The characteristic and distinctive morphology of *P. boisei sensu stricto* is summarized in the Appendix, and examples are shown in Figure 5.

Cranial

Similarities between OH 5 and KNM-ER 406 were noted at the time of the latter's announcement (Leakey, 1970). Despite certain differences between these two large, presumed male crania including the pattern of ectocranial cresting and the degree of prognathism of the lower face (Wood, 1991), most researchers have concluded that these and other differences are best interpreted as evidence of intraspecific and not interspecific variation (Howell, 1978; Wood, 1991). The morphology of two partial crania from Koobi Fora, KNM-ER 13750 and 23000, and of the skull from Konso, KGA-10-525, is also consistent with the observation that whereas some aspects of cranial morphology such as the topography of the ectocranial crests and the face vary within the presumed male morph of *P. boisei*, other regions (e.g., the cranial base) are relatively, but not entirely, invariant (Brown et al., 1993; Wood et al., 1994).

The calvaria KNM-ER 407 and the partial hemicranium KNM-ER 732 differ in both size and shape from presumed male *P. boisei* crania such as OH 5 and KNM-ER 406. Indeed, the contrast in morphology between KNM-ER 406 and 407 was considered to be so great that the initial taxonomic assessment of the latter placed it in "… either a gracile species of *Australopithecus* or else a very early representative of *Homo* …" (Leakey, 1970, p. 224). In contrast, the initial taxonomic assessment of KNM-ER 732 suggested that "it seems likely that the two specimens (KNM-ER 406 and 732) represent the two sexes of the same species" (Leakey, 1971, p. 244) (see Fig. 6). The microstructure of the exposed enamel of the only preserved tooth crown of KNM-ER 732 is *P. boisei*-like (Beynon and Wood, 1986) and the relative size of the postcanine dentition as judged from the proportions

of the alveolar process is at, or just below, the range for *P. boisei* (Wood, 1991). In addition, the arrangement of the cranial base of KNM-ER 732 and KNM-ER 407, especially the relatively anterior position of the foramen magnum and the more coronally-orientated petrous temporal bones, resembles the arrangement of the external cranial base seen in OH 5 and KNM-ER 406 (Dean and Wood, 1982; Wood, 1991).

Because the *P. boisei* hypodigm at the time comprised crania whose ectocranial morphology was analogous to that of large male members of *Gorilla* and *Pongo*, and because both KNM-ER 407 and 732 possessed morphological features that were regarded as diagnostic of *P. boisei* despite their smaller size, many researchers subscribed to the view that these crania were smaller-bodied, presumably female, representatives of *P. boisei*, thereby providing evidence of sexual dimorphism within that taxon (e.g., Robinson, 1972; Howell, 1978; Wood, 1985, 1991; Wood et al., 1991). Erosion has damaged the frontal and zygomatic regions of the Koobi Fora cranium KNM-WT 17400 (Leakey and Walker, 1988), but the remaining osseous and dental morphology leaves little doubt that this subadult specimen represents a further example of the small, presumably female, morph of *P. boisei*.

Postcranial

Because the diagnoses of almost all fossil hominin taxa are based on craniodental material, the usual way that researchers identify the postcranial hypodigm of a hominin taxon is by finding an associated skeleton that includes diagnostic craniodental remains together with elements of the postcranial skeleton. But, as yet, there is no sign of a well-authenticated *P. boisei* skeleton. The only uncontroversial associated skeletons from Bed I and Lower Bed II at Olduvai are OH 7 (Leakey et al., 1964) and OH 62 (Johanson et al., 1987). The former is the type specimen of *Homo habilis*, and even though the craniodental evidence of OH 62 is very fragmentary, enough is preserved to be sure that cranially the affinities of OH 62 are with *H. habilis* and not with *P. boisei*. Thus, first at Olduvai Gorge and later at sites in the Omo region including Koobi Fora, the problem researchers have faced is how to tell which of the unassociated hominin postcranial fossils should be assigned to *P. boisei*, and which should be assigned to early *Homo* as *H. habilis*? As we will see, some of the initial allocations of isolated hominin postcranial fossils at both sites were made on the basis of three assumptions. The first was that a taxon with large postcanine tooth crowns and a large mandibular corpus must also have been large-bodied. The second assumption was that any hominin postcranial specimen that was not like later *Homo* belonged to *P. boisei* (e.g., Walker, 1973). The third assumption was that any postcranial fossils found "in close proximity and derived from the same fossiliferous horizon" as *P. boisei* cranial fossils should be assigned to the same taxon (Howell, 1978, p. 179).

Potential* P. boisei *postcranial fossils from Olduvai Gorge. Among the unassociated hominin postcranial fossils recovered from Bed I and Bed II at Olduvai were a partial foot (OH 8), a hallucial terminal phalanx (OH 10), a proximal femur (OH 20), a tibia and fibula (OH 35), and an ulna (OH 36). Of these only OH 20 (the

TABLE 1. Provisional list of the craniodental hypodigm of P. boisei sensu stricto *and* sensu lato

Specimen #	Age	Morphology represented	Specimen #	Age	Morphology represented
	Omo, Ethiopia		**Omo 33-9**	2.36	Rt mandibular M3
Omo F22-1a	2.33–2.36	Rt mandibular M2	**Omo 33-62**	2.36	Mandibular premolar or rt maxillary M3 fragment
Omo F22-1b	2.33–2.36	Rt mandibular M3			
Omo F203-1	1.40–1.45	Rt mandibular M3	**Omo 33-63**	2.36	Rt maxillary M1
Omo L7A-125	2.19–2.27	Mandible	**Omo 33-65**	2.36	Lt mandibular M3 germ
Omo L10-21	2.36–2.40	Rt mandibular M3 fragment	**Omo 33-506**	2.36	Rt maxillary P3
			Omo 33-507	2.36	Rt mandibular P4 or lt maxillary M3
Omo L26-59	2.36–2.40	Lt maxillary M2 or M3			
Omo L28-58	2.33–2.36	Rt maxillary M2 (or M1)	**Omo 33-508**	2.36	Lt mandibular P4
Omo L28-126	2.33–2.36	Lt premolar crown fragment	**Omo 33-6172**	2.36	Rt mandibular M3
			Omo 44-1410	2.36–2.40	Rt maxillary P4 fragment
Omo L40-19	2.36–2.40	Rt ulna			
Omo L50-2	2.40–2.52	Lt maxillary M2 (or M1)	**Omo 44-2466**	2.36–2.40	Lt mandible fragment
Omo L51-79	2.52–2.58	Rt mandibular P4	Omo 47-46	2.19–2.27	Worn rt mandibular M2
Omo L55-33	2.58–2.75	Lt mandibular fragment	Omo 47-1500	2.10	Right mandibular M2
Omo L62-17	2.58–2.75	Rt mandibular M2	**Omo 57-41**	2.38	Mandible
Omo L64-2	2.40–2.52	Lt deciduous mandibular P4	**Omo 57-42**	2.36–2.40	Mandibular M1
			Omo 57-147	2.36–2.40	Lt mandibular P4 or maxillary M3 fragment
Omo L74A-21	2.19–2.27	Rt mandible			
Omo L157-35	2.33–2.36	Lt mandibular M2	**Omo 57-148**	2.36–2.40	Rt mandibular premolar fragment
Omo L209-17	2.33–2.36	Rt mandibular M2 fragment			
Omo L209-18	2.33–2.36	Lt mandibular M fragment	Omo 76-37	2.27–2.33	Lt mandibular M3, buccal half
Omo L238-35	2.33–2.36	Rt maxillary M2	**Omo 76r-11**	2.33–2.36	Rt mandibular M3 fragment
Omo L296-1	2.40–2.52	Rt mandibular M3			
Omo L338X-32	2.36–2.40	Lt maxillary M3	**Omo 84-100**	2.60	Right mandibular M3
Omo L338X-33	2.36–2.40	Rt maxillary P4 fragment	Omo 141-2	2.27–2.33	Maxillary M1 or M2
			Omo 323-896	2.19–2.27	Partial cranium
Omo L338X-34	2.36–2.40	Lt maxillary M1 or M2		Koobi Fora, Kenya	
Omo L338X-35	2.36–2.40	Rt maxillary P3			
Omo L338X-39	2.36–2.40	Lt mandibular M3 crown	KNM-ER 403	1.67	Rt mandible fragment
Omo L338X-40	2.36–2.40	Lt mandibular P4	KNM-ER 404	1.49–1.55	Rt mandible fragment
Omo L338y-6	2.36–2.40	Parieto-occipital portion of cranium	KNM-ER 405	1.87	Palate/maxilla fragments
			KNM-ER 406	1.56–1.60	Edentulous cranium
Omo L338y-89	2.36–2.40	Lt maxillary P3 fragment	KNM-ER 407	1.85	Calvaria
Omo L398-14	2.36	Rt mandibular dm1, dm2 or M1	KNM-ER 725	1.49–1.55	Lt mandibular body
			KNM-ER 726	1.55–1.65	Lt mandibular body
Omo L398-120	2.36	Rt mandibular P3	KNM-ER 727	1.56–1.60	Rt mandibular fragment
Omo L398-264	2.36	Rt mandibular M3 fragment	KNM-ER 728	1.49–1.55	Rt mandibular body
			KNM-ER 729	1.49–1.55	Mandible
Omo L398-266	2.36	Rt mandibular M3	KNM-ER 732	1.56–1.60	Partial cranium
Omo L398-630	2.36	Rt mandibular M3	KNM-ER 733	1.49–1.55	Skull fragments
Omo L398-847	2.36	Lt mandibular M3 fragment	KNM-ER 801	1.56–1.60	Mandible fragment
			KNM-ER 802	1.56–1.60	Isolated teeth
Omo L398-1223	2.36	Rt mandibular P4 fragment	KNM-ER 805	1.49–1.55	Mandible fragment
			KNM-ER 810	1.77	Mandible fragment
Omo L398-2608	2.36	Rt maxillary M3 fragment	KNM-ER 812	1.77	Mandible fragment
			KNM-ER 814	1.77	Vault fragments
Omo L420-15	2.33–2.36	Lt mandibular P4	KNM-ER 816	1.77	Lt maxillary canine
Omo L427-7	1.8–2.0	Rt mandible	KNM-ER 818	1.55–1.65	Mandible fragment
Omo L465-111	2.33–2.36	Lt mandibular P3 fragment	KNM-ER 1170	1.56–1.60	Vault fragments
			KNM-ER 1171	1.56–1.60	Isolated teeth
Omo L465-112	2.33–2.36	Lt mandibular M2 fragment	KNM-ER 1467	1.49–1.55	Isolated tooth
			KNM-ER 1468	1.55–1.65	Mandible fragment
Omo L628-1	2.27–2.33	Lt maxillary P4	KNM-ER 1469	1.87–1.90	Mandible fragment
Omo L628-2	2.27–2.33	Rt mandibular M3	KNM-ER 1477	1.85–1.90	Mandible, no rami
Omo L628-3	2.27–2.33	Lt mandibular M3	KNM-ER 1479	1.87	Isolated teeth
Omo L628-4	2.27–2.33	Lt mandibular P4	KNM-ER 1500	1.87–1.90	Partial skeleton
Omo L628-5	2.27–2.33	Rt mandibular P4	KNM-ER 1509	1.56–1.60	Isolated teeth
Omo L628-9	2.27–2.33	Lt mandibular M1	KNM-ER 1803	1.87–1.90	Mandible fragment
Omo L704-2	2.40–2.52	Lt deciduous mandibular P3	KNM-ER 1804	1.77	Mandible fragment
			KNM-ER 1806	1.85	Mandible fragments
Omo L726-11	2.19–2.27	Rt maxillary P4	KNM-ER 1816	1.56–1.60	Mandible fragments
Omo L797-1	2.19–2.27	Lt mandibular P4 fragment	KNM-ER 1818	1.56–1.60	Isolated tooth
			KNM-ER 1819	1.60–1.70	Isolated tooth
Omo L860-2	2.33–2.36	Mandible fragment	KNM-ER 1820	1.67–1.70	Mandible fragments
Omo 18-18	2.58–2.75	Edentulous mandible	KNM-ER 2607	1.60–1.87	Isolated tooth
Omo 18-31	2.6?	Mandibular P3	KNM-ER 3229	1.85	Mandible fragment
			KNM-ER 3230	1.56–1.60	Mandible, no rami

TABLE 1. (Continued)

Specimen #	Age	Morphology represented	Specimen #	Age	Morphology represented
KNM-ER 3729	1.87–1.90	Mandible fragment		Konso, Ethiopia	
KNM-ER 3731	1.87–1.90	Mandible fragments	KGA 10-506	1.41–1.43	Lt palate w/ dentition
KNM-ER 3737	1.56–1.60	Isolated teeth	KGA 10-525	1.41–1.43	Partial skull
KNM-ER 3885	1.77–1.79	Isolated tooth	KGA 10-565	1.41–1.43	Rt maxillary M1
KNM-ER 3886	1.77	Isolated tooth	KGA 10-570	1.41–1.43	Mandible (juvenile)
KNM-ER 3887	1.50–1.65	Isolated tooth	KGA 10-900	1.41–1.43	Molar fragments
KNM-ER 3889	1.49	Mandible frag	KGA 10-1455	1.41–1.43	Lt parietal
KNM-ER 3890	1.56–1.60	Isolated tooth	KGA 10-1720	1.41–1.43	Lt mandibular M3
KNM-ER 3952	1.87	Isolated teeth	KGA 10-2705	1.41–1.43	Rt mandibular M2
KNM-ER 3954	1.60–1.87	Mandible fragments	KGA 10-2741	1.41–1.43	Molar fragments
KNM-ER 5429	1.56–1.60	Mandible fragment		Chesowanja, Kenya	
KNM-ER 5679	1.56–1.60	Isolated tooth	KNM-CH 1	>1.42	Hemi-face and anterior cranial base
KNM-ER 5877	1.49–1.55	Mandible fragment			
KNM-ER 6080	1.55–1.65	Isolated tooth	KNM-CH 302	>1.42	Molar tooth fragments
KNM-ER 6082	1.55–1.65	Isolated tooth	KNM-CH 304	>1.42	Cranial fragments (5)
KNM-ER 6128	1.77	Isolated tooth		Olduvai Gorge, Tanzania	
KNM-ER 13750	1.87	Cranium w/ endocast	OH 3	1.40–1.45	Isolated molar
KNM-ER 15930	1.77	Lt mandible	OH 5	1.79–1.85	Cranium
KNM-ER 15940	1.77	Lt & Rt M2 or M3 germs	OH 20	1.66–1.79	Proximal end of lt femur
KNM-ER 15950	1.49–1.55	Mandibular Lt M3, heavily weathered	OH 26	1.66–1.79	Unerupted maxillary molar
KNM-ER 16841	1.60–1.87	Edentulous mand	OH 30	1.66–1.79	Deciduous and permanent teeth
KNM-ER 17760	1.77	Lt maxillary I2	OH 36	1.40–1.45	Nearly complete ulna
KNM-ER 23000	1.87	Cranium	OH 38	1.40–1.45	Rt mandibular M2 and two incisors
KNM-ER 25520	1.80–1.90	Rt mandibular corpus			
	West Turkana, Kenya		OH 46	1.79–1.85	Premolar or molar crown fragment
KNM-WT 16005	2.36–2.46	Partial mandible		Peninj (Lake Natron), Tanzania	
KNM-WT 17000	2.47–2.57	Cranium and endocast	NMT-W64-160	1.56–1.70	Mandible
KNM-WT 17396	1.65–1.79	Lt mandibular M3 (possibly M2)		Laetoli, Tanzania	
KNM-WT 17400	1.67–1.87	Anterior cranium and endocast	**EP 1500/01**	2.5–2.7	Edentulous maxilla
				Malema, Malawi	
KNM-WT 18600	1.65–1.79	Lt maxillary P3	RC 911	2.3–2.5	Maxilla fragment
KNM-WT 37100	1.65–1.79	Lt mandibular M3			
KNM-WT 37744	1.65–1.79	Lt maxillary canine			
KNM-WT 37747	1.65–1.79	Lt maxillary M1			
KNM-WT 37748	1.65–1.79	Rt maxillary M3			

P. boisei sensu lato includes specimens attributed to both *P. boisei sensu stricto* and *P. aethiopicus*. Specimens that have been attributed to *P. aethiopicus* are in bold type (based on Arambourg and Coppens, 1968; Kimbel et al., 1988; Suwa et al., 1996).

proximal end of an adult left femur that lacks the head and the tips of the trochanters) has been explicitly assigned to *P. boisei* (Day, 1969; Leakey, 1978) (Fig. 7). The OH 20 proximal femur was found in 1959 on the surface at the excavation that was then being conducted at locality HWK in Lower Bed II at Olduvai Gorge. It was not immediately identified as a hominin femur, but when Napier (1964) reported on three australopith proximal femora from southern Africa, one from Sterkfontein (Sts 14), and two from Swartkrans (he referred to them as SK 82 and 83, but the latter is evidently what is now referred to as SK 97), it soon became apparent that the HWK proximal femur belonged to a hominin and it was given the field number OH 20.

A detailed analysis of OH 20 suggested that the features it shares with the two femora attributed to *P. robustus* (SK 82 and 97) include a relatively broad, anteroposteriorly flattened and long neck, a vertical and not laterally expanded greater trochanter, a posteriorly-positioned lesser trochanter, a deep trochanteric fossa, and a groove on the posterior aspect of the neck for the tendon of obturator externus (Day, 1969). These shared features prompted Day (1969) to suggest that "it would

seem reasonable to allocate the new femoral fragment to *Australopithecus cf. boisei*" (p. 232). Other postcranial skeletal elements were for various reasons interpreted as being modern human-like (e.g., Day and Napier, 1964; Day and Wood, 1968) and so had been assigned to *H. habilis*. Since, no one then knew what a *H. habilis* femur looked like, so it seemed logical to link the *P. robustus*-like proximal femur, OH 20, with *P. boisei*, and to link what were then interpreted as the more modern human-like Olduvai Beds I and II postcranial specimens (e.g., OH 8 and 10) with *H. habilis*.

The discovery in 1971 of KNM-ER 813, a modern human-like talus from Koobi Fora (Wood, 1974b), weakened the case for assuming the OH 8 foot belonged to *H. habilis* because the latter foot included a talus that looked more like TM 1517, a *P. robustus* talus (Wood, 1974a; Gebo and Schwartz, 2006) (see Fig. 8). Wood (1974a) had also argued that the logic that had led OH 8 and OH 10 (a terminal hallucial phalanx) to be interpreted as being modern human-like (Day and Napier, 1964, 1966; Day and Wood, 1968; Day, 1967, 1974) may have been flawed (see also Oxnard, 1972). In that case, OH 8 and 10 (and possibly OH 35 also if that proves to
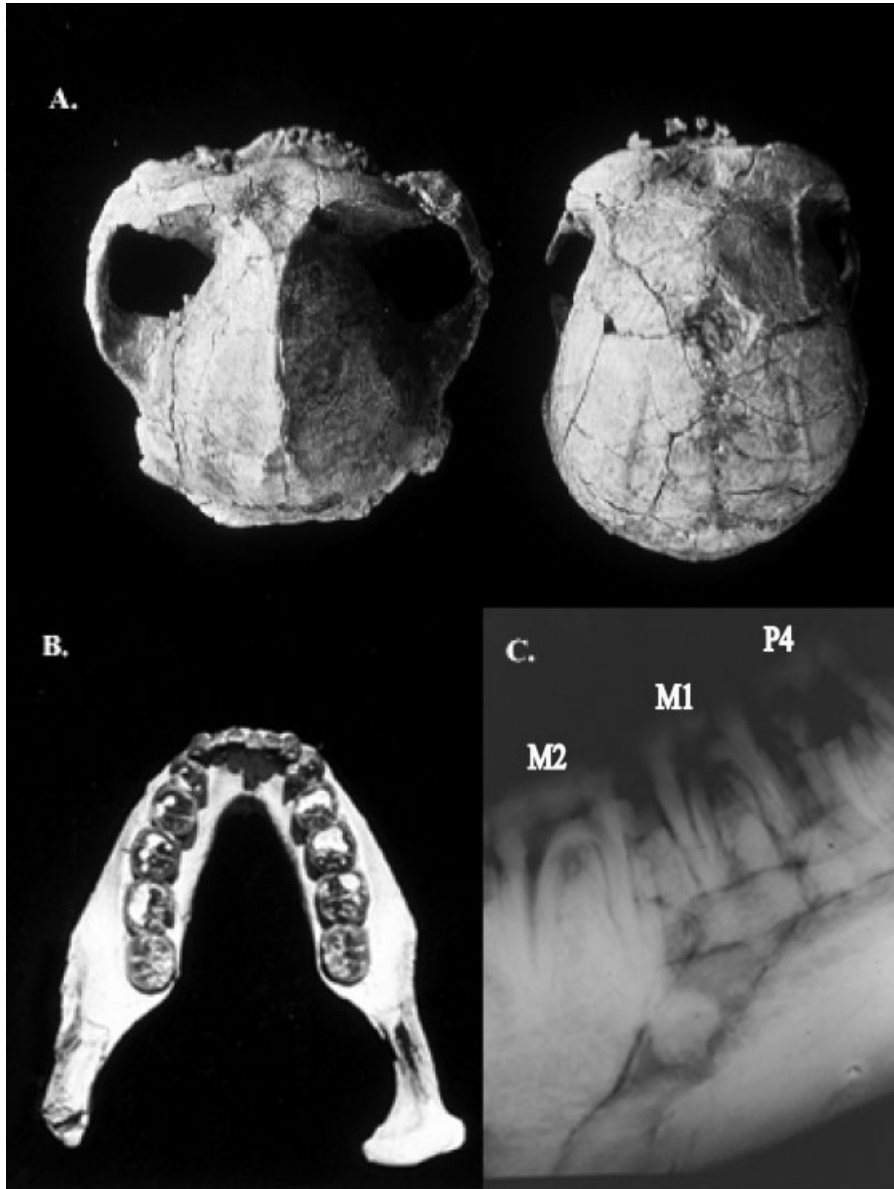
Fig. 5. Examples of the derived morphology of *P. boisei*. (**A**) KNM-ER 406 (left) next to KNM-ER 3733 highlights the broad zygomatic arches, facial orthognathy, postorbital constriction, and ectocranial crests of *P. boisei*. (**B**) The Peninj mandible shows the broad corpus and the large postcanine:anterior tooth size ratio in *P. boisei*. (**C**) A radiograph of the KNM-ER 729 mandible shows the molariform roots of the lower P_4. Note that the P_4 roots are longer than those of the M_1.

make up an associated skeleton with OH 8) would have as much claim to be attributed to *P. boisei* as they have to *H. habilis*, and recently Gebo and Schwartz (2006) suggested the similarities between OH 8 and TM 1517 point to the former probably belonging to *P. boisei*. The only other relevant individual Olduvai postcranial fossil to be analyzed in any detail is the OH 36 ulna, and although Aiello et al. (1999) suggested "OH 36 has a greater claim to be assigned to *Paranthropus boisei*" (p. 89) than the Omo Loc 40-19 or KNM-BK 66 ulnae, they recommended that for the time being OH 36 be regarded as Hominini gen. et sp. indet. McHenry et al. (2007) also suggest that it would be "reasonable to assign (OH 36) to *P. boisei*" (p. 217), and they support the attribution of Omo L40-19 to *P. aethiopicus*.

P. boisei *postcranial remains from Koobi Fora?*. At approximately the same time as the reassessments of the Olduvai hominin pedal postcranial fossils were tak-

ing place, Richard Leakey (1971) and his team had begun to recover hominin postcranial remains from Koobi Fora. Most were femoral specimens and provisional comparisons suggested that they could be divided into those that were more like the femora of modern humans (e.g., KNM-ER 737), and those (e.g., KNM-ER 738) that were "not unlike other femoral fragments that have been collected elsewhere and assigned to *Australopithecus*" (Leakey, 1971, p. 243). A year later, two other femora, KNM-ER 815 and 993, were likened to "the similar fragment from Olduvai (Old. Hom. 20)" (Leakey, 1972, p. 266), and in 1973 KNM-ER 738 and 1503 were added to the list of proximal femora from Koobi Fora that shared "this constellation of anatomical features" (Day, 1973, p. 36–37). For this reason, these hominin femora from Koobi Fora were attributed to *Australopithecus* and not to *Homo* (Walker, 1973).

However, these attributions to *Australopithecus* (and by inference to *Australopithecus* cf. *boisei*, the name
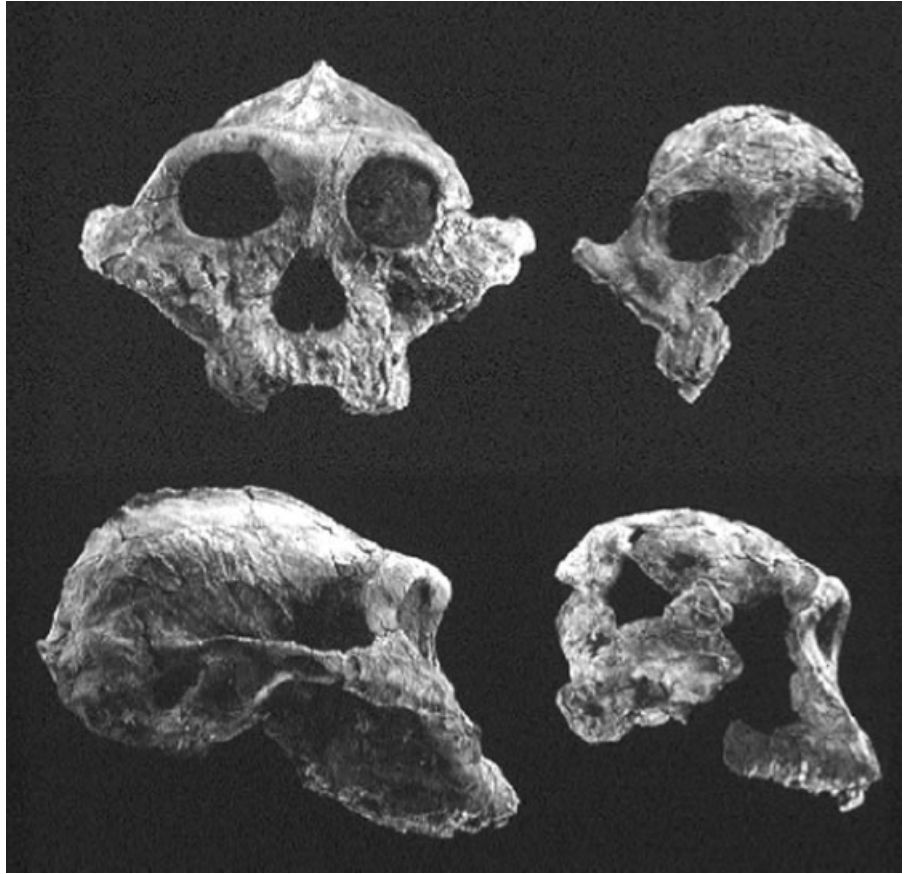
Fig. 6. Possible sexual dimorphism in *P. boisei*. The specimen shown in anterior and lateral views on the left, KNM-ER 406, is a presumed male while KNM-ER 732 on the right is a presumed female.
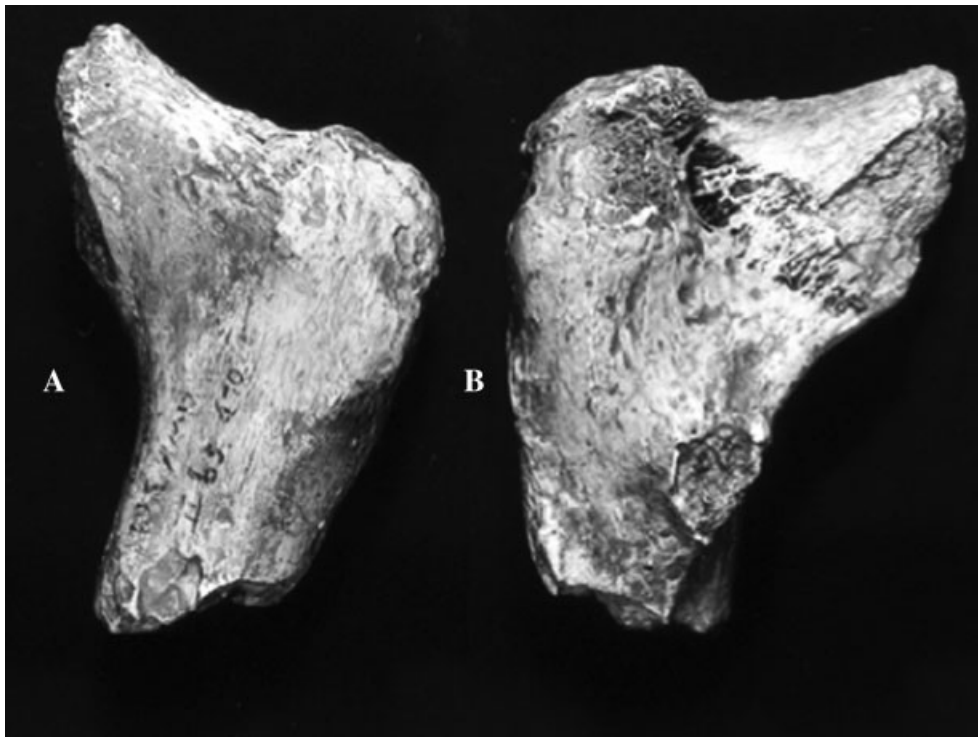

Fig. 7. The proximal femur OH 20 seen in anterior (**A**) and posterior (**B**) views. Adapted from original images belonging to Michael Day.

used by these authors for the taxon we refer to as *P. boisei*) depended on the untested assumption that the femora of *H. habilis* were recognizably more modern human-like than the femora of *P. boisei*. The discovery of OH 62 (Johanson et al., 1987) seemed to challenge the conventional wisdom of the time that the femoral mor-

phology of early *Homo* and *Australopithecus* was distinct. Although the postcranial skeleton of OH 62 is poorly preserved and its interpretation remains controversial (e.g., Richmond et al., 2002; Reno et al., 2005), its femoral morphology is evidently similar enough to femora from Olduvai and Koobi Fora that had been assigned to *Australopithecus* and thence to *P. boisei* (Johanson et al., 1987) to make these latter attributions suspect.

More than 20 Koobi Fora hominin postcranial specimens have been assigned to *Australopithecus* (Leakey, 1972, 1973), yet in a wide-ranging review of the early hominin postcranial skeleton, McHenry (1994) attributes just five Koobi Fora hominin specimens to *A. boisei*, namely the associated skeleton KNM-ER 1500 and the isolated limb bones KNM-ER 1464, 1823, 1824, 1825. What is the evidence for these attributions and how reliable are they?

KNM-ER 1500. Some researchers have suggested that KNM-ER 1500 (an associated partial skeleton recovered from the Upper Burgi Member in Area 130 at Koobi Fora in 1972) has the potential to help identify the postcranial elements of *P. boisei*. It was initially referred to *Australopithecus* presumably on the basis of its preserved femoral morphology (Leakey, 1973). It was suggested that KNM-ER 1500 (which contained fragments from most of the elements of the right and left upper and lower limbs, plus some unidentified fragments) provided "important new evidence on limb proportions in addition to morphological
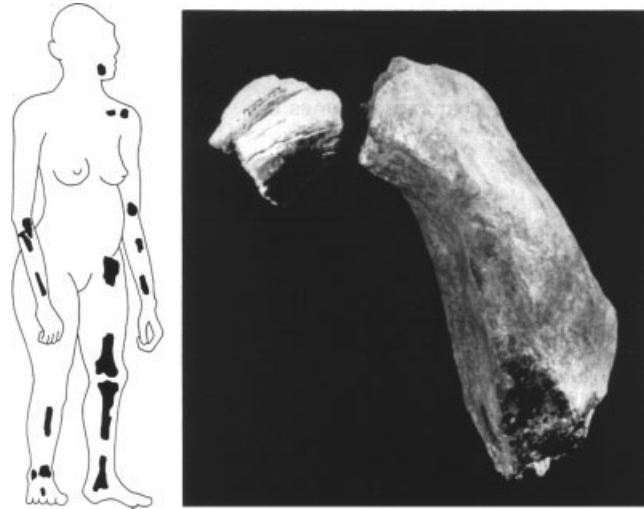
details of australopithecine postcranial bones" (Leakey, 1973, p. 171). Subsequently, one of the fragments, labeled "Q," was identified as being from the base of the right side of the mandibular corpus in the region of the submandibular fossa. Grausz et al. (1988) suggested that its thickness and the presence of a "blunt marginal crest" made it "easily identifiable" (p. 127) as a "female *A. boisei*" mandible (p. 130) (Fig. 9), and other researchers have accepted this attribution (e.g., Ruff et al., 1999).

However, Wood (1991) was much less certain the small piece of mandible could be confidently assigned to *P. boisei*. He suggested that its morphology could also be duplicated "in mandibles attributed to *Homo sp. indet.*" (subsequently called *Homo rudolfensis*) (p. 182). In any event, even if KNM-ER 1500 can for some other reason be tied to *P. boisei*, Grausz et al. (1988) point out that "the postcranial skeleton of female *A. boisei* is very similar to that of female *A. afarensis* and *A. africanus*" (p. 131–2). They also suggest that their comparisons of KNM-ER 1500 with the *Homo habilis* specimens OH 8 and OH 35 indicate that "either OH 8 and OH 35 should be attributed to *A. boisei* …" "or the lower limb skeleton of *H. habilis* and *A. boisei* cannot be easily distinguished" (Grausz et al., 1988, p. 132).

KNM-ER 1464, 1823, 1824, 1825. The rest of the postcrania attributed by McHenry (1994) to *P. boisei* all come from a single level in Area 6A at Ileret, Koobi Fora. The logic behind their taxonomic assignment is similar to that used to try and identify postcranial fossils in Member 1 at Swartkrans (Susman, 1988). It suggests that if all the craniodental fossils found at a fossil locality can be confidently assigned to one taxon, then it is a reasonable hypothesis that any hominin postcranial fossils found at the same locality will belong to the same taxon.

In Area 6A at Koobi Fora, 14 fossil hominin specimens have been recovered from the KBS Member. The first of these was the mandible KNM-ER 801 (Leakey, 1972). This is a typical, robust, *P. boisei* right mandibular corpus with a small I_2 and large M_2 and M_3 crowns with dis-

tal (C_6) accessory cusps (Wood, 1991). A left M_2 found at the site shows substantially less wear than the right M_2 so the former is now regarded as a separate specimen, KNM-ER 5679, from a second individual. A fragmented cranium, KNM-ER 1170, and several sets of isolated teeth, KNM-ER 802, 1171, 1816, and 3737, were recovered from the sieving operation at the site of KNM-ER 801 and all were judged to show distinctive morphology only seen in *P. boisei* (e.g., *striae parietales* on KNM-ER 1170 and the distinctive *P. boisei* crown morphology and enamel microstructure on the dental evidence (Wood, 1991)). In 1972, a right talus KNM-ER 1464 (Leakey, 1973) was found "eroding out of the sediment at the site of KNM-ER 801" (Leakey and Leakey, 1978, p. 127) and subsequently KNM-ER 1823, the proximal end of a third metatarsal, KNM-ER 1824, a distal humeral fragment, and KNM-ER 1825, part of an atlas, were "recovered while sieving for (further) fragments of KNM-ER 801" (Leakey and Leakey, 1978, p. 166). In addition to the dental evidence suggesting that at least two individuals are represented in the hominins from Area 6A, McHenry (1991a) pointed out that the discrepancy between sizes of the small KNM-ER 1823 metatarsal and the larger KNM-ER 1464 talus and KNM-ER 1825 atlas also indicates the presence of at least two individuals.

The craniodental components of the hominin collection from the KBS Member of Area 6A all display distinctive *P. boisei* morphology, so it is a reasonable assumption that the postcranial elements might also belong to that taxon. Unfortunately, however, distinctive and otherwise commonly preserved hominin postcranial elements such as the proximal ends of the femur and tibia are not found in the Area 6A sample. The best-preserved postcranial element is the KNM-ER 1464 talus which was recently included in a morphometric analysis of fossil hominin tali (Gebo and Schwartz, 2006). The authors concluded that the KNM-ER 1464 talus differed from a cluster of tali consisting of TM 1517, OH 8, and KNM-ER 1476. Because this cluster includes the only known *P. robustus* talus (TM 1517), Gebo and Schwartz (2006) concluded that the two East African tali within the cluster (OH 8 and KNM-ER 1476) most likely also belong to *P. boisei*. In contrast, the affinities of the KNM-ER 1464 talus are enigmatic. In some aspects of its morphology it resembles OH 8 and TM 1517 (grooved trochlea, a laterally-projecting fibular facet, a wide head, and a weakly curved medial border to the trochlea), yet in others (large size and short head and neck relative to the trochlea) it resembles the tali of later *Homo*. Thus, even if there are contextual grounds for linking KNM-ER 1464 with *P. boisei*, it departs morphologically from what is inferred to be the derived *P. boisei* talar morphology.

Other areas with only P. boisei fossils. Areas 10, 11, and 119 at Koobi Fora are additional locations where the only hominin fossils known are *P. boisei* craniodental remains along with individual, isolated, postcranial elements. However, these areas contain a total of only 4, 3, and 4 specimens, respectively. Therefore, attribution of the postcrania to *P. boisei* on contextual association alone is dubious. Nevertheless, the lone postcranial elements in both Areas 10 and 11 (KNM-ER 815 and 1465, respectively) are proximal femora with long, antero-posteriorly compressed necks (Leakey and Leakey, 1978). This morphology, along with a small femoral head, are features that have been attributed to *Australopithecus* femora, (Lovejoy and Heiple, 1972) and indeed both

specimens were allocated to *P. boisei* by Howell (1978). The lone postcranial element from Area 119 is a left talus, KNM-ER 5428, which could be compared with the KNM-ER 1464 talus from Area 6A to determine if these two tali are likely to have come from the same species. At the Tanzanian site of Laetoli, the first recorded hominins from the Ndolanya Beds (~2.5–2.7 Ma) are a *P. aethiopicus* maxilla (EP 1500/01) and a proximal tibia (EP 1000/98), but there is no evidence that the two are associated (Harrison, 2002).

The bulk of the evidence therefore suggests that there is currently no way of telling to which taxon the "*Australopithecus*-like" hominin postcranial evidence from Olduvai (Beds I and II), Koobi Fora (Okote, KBS, and Upper Burgi Members), and Laetoli (Ndolanya Beds) belongs. For the time being it would be prudent to regard this fossil evidence as Hominini gen. et sp. indet.

Potential P. boisei postcranial fossils from the Omo Shungura formation. Attempts to identify the postcranial skeleton of *P. boisei* at sites other than Olduvai and Koobi Fora have been *ad hoc*. Howell and Wood (1974) reported on Omo Loc 40-19, a right ulna recovered in 1971 from Member E of the Shungura Formation, and suggested that it was sufficiently different from a modern human ulna to "be referred to *Australopithecus boisei*" (p. 176). This and other comparable attributions were partly influenced by overall size, but when McHenry (1991b) cast doubt on the assumption that *P. boisei* was larger-bodied than other australopiths, it no longer made sense to stress the overall size of a limb element as a criterion for attribution to *P. boisei*. In any event, a subsequent comparative study (Aiello et al., 1999) concluded the Omo Loc 40-19 ulna was as modern human-like as KNM-BK 66, an ulna well outside the temporal range of *P. boisei*. This raises the possibility that the Omo Loc 40-19 ulna belongs to early *Homo* and not *P. boisei*. Deloison (1986) described Omo 33-74-895 (presumably the author intended to refer to Omo 33-74-894), a calcaneus from Tuff F of the Shungura Formation, and suggested that it might belong to *P. boisei*. Deloison listed ways in which the calcaneus is similar to modern human calcanei, but also cited ways in which it differed from them. Gebo and Schwartz (2006) have subsequently emphasized its similarities to modern human calcanei.

So where does the search for *P. boisei* postcrania in the Turkana Basin leave us? In short, badly in need of an associated skeleton that includes cranial elements diagnostic of *P. boisei*. Finding archaic-looking femora is not enough because at least one other synchronic East African hominin, *H. habilis*, has a similar femoral morphology. It may be that some of the hominin postcranial specimens assigned to *H. habilis* actually belong to *P. boisei*, but for the time being we have no way of telling. We suggest it is better to accept that for various reasons no postcranial remains can be confidently assigned to *P. boisei* than to continue with the present confusion.

TAXONOMY

There are three main debates concerning the taxonomy of *P. boisei*. The first is whether recent discoveries in East and southern Africa have blurred the distinction between *P. boisei* and *P. robustus*. The second is whether *P. boisei* should subsume *P. aethiopicus*, or are there sufficient differences between the two East African hypodigms to justify retaining *P. aethiopicus* as a separate species? The third debate concerns the significance of

the size and shape differences subsumed within *P. boisei*. Are they consistent with a single sexually dimorphic early hominin taxon, or should they be interpreted as indicating that even the *P. boisei sensu stricto* hypodigm subsumes more than one taxon?

Is *P. boisei* a valid taxon?

The case for distinguishing between *P. robustus* and *P. boisei* was cogently made by Tobias (1967) and until recently the enlargement of the two hypodigms had not materially altered that assessment. However, the discoveries of megadont hominins at Konso prompted Suwa et al. (1997) to suggest that some of the morphology seen in the KGA 10-525 skull, such as a zygomaticomaxillary fossa and a median maxillary torus, are features that had not been noted in crania belonging to *P. boisei*, but which were known from the *P. robustus* hypodigm. Thus, the new Konso evidence, together with the recovery of KNM-ER 23000 from Koobi Fora (Brown et al., 1993) and the detailed analysis of Omo 323-896 (Alemseged et al., 2002), prompted at least one commentator to suggest that *Paranthropus* taxonomy should be reassessed (Delson, 1997). The large size of the molar tooth from Gondolin also suggests it would be worthwhile considering whether the recent discoveries in southern Africa at Gondolin (Menter et al., 1999) and Drimolen (Keyser, 2000; Keyser et al., 2000) may have helped close the morphological gap between *P. robustus* and *P. boisei*.

The short answer to both of these possibilities is apparently "no." Wood and Lieberman (2001) concluded the Konso specimens are not distinctive and actually do "fit within the population parameters of *P. boisei* predicted by the "pre-Konso" hypodigm" (p. 20), and when Constantino and Wood (2004) compared the regional hypodigms of *Paranthropus* before and after the addition of the new material from Drimolen and Gondolin, they found that the number of significant metrical differences between the postcanine dentition from East and southern Africa actually increased rather than decreased.

Is *P. aethiopicus* a valid taxon?

Nearly all researchers accept there are differences between KNM-WT 17000 and the <2.3 myr-old crania belonging to the *P. boisei sensu stricto* hypodigm (Walker et al., 1986; Kimbel et al., 1988). The point at issue is whether the differences justify a specific distinction for the West Turkana cranium and other early megadont jaws and teeth attributed to *P. aethiopicus* (Arambourg and Coppens, 1968). Two studies have looked at this problem in detail. Suwa (1988) concluded that there were differences in mandibular premolar cusp morphology between the pre-2.3 myr-old and the post-2.3 myr-old megadont fossil evidence, with the later material having larger and more elaborate talonids. Wood et al. (1994) found that several other features of the mandible and the mandibular dentition (such as the height of the mandibular symphysis and mandibular corpus at M_1, and the P_4 crown area) also change ca. 2.3 Ma, and they supported the interpretation that the "early" and the "late" stages of the *Paranthropus* lineage in East Africa should be recognized as different species, with the "early" taxon taking the name *Paranthropus aethiopicus* (Arambourg and Coppens, 1968). However, if they are recognized as separate species, then because they are apparently time successive, the nature of the differences

between them is consistent with their being chronospecies within an evolving lineage. Nonetheless, other scenarios are not necessarily any less parsimonious (Kimbel et al., 1988). The cranial differences between the two East African *Paranthropus* species include the more prognathic face, larger incisors (inferred), less flexed cranial base, smaller mandibular corpus, and shorter postcanine tooth row of *P. aethiopicus*. No postcranial evidence has thus far been assigned to *P. aethiopicus*, but a proximal tibia recovered from the same Laetoli Beds as a probable *P. aethiopicus* maxilla (Harrison, 2002) may one day prove to be part of this hypodigm.

Does *P. boisei* subsume more than one taxon?

It has been suggested that the degree of size variation in the mandibular hypodigm of *P. boisei* is exceptional, indicating that the hypodigm may sample more than one hominin taxon (Dean, 1988; Groves, 1989). However, much of this 'excessive' variation can be explained by post mortem cracks that fill with matrix and artificially inflate the size of the mandibular corpus of the larger individuals, and erosion of surface bone that has reduced the size of the corpus of some of the smaller individuals in the hypodigm (Wood, 1991; Silverman et al., 2001). Apart from these extrinsic causes for differences in overall size, the size and shape of the mandibular corpus of *P. boisei* is remarkably stable through geological time (Wood et al., 1994, p. 129, Fig. 2E), and both small and large mandibles in the sample retain their characteristically robust (i.e., relatively broad for its height) corpus and rounded base (Wood, 1991; Wood et al., 1994). In addition, Wood et al. (1991) demonstrated that the pattern of intraspecific cranial (as opposed to dental) variation within *P. boisei* was similar to that seen in closely-related extant taxa, and Wood and Lieberman (2001) showed (but not necessarily to the satisfaction of all researchers) that the pattern of cranial regional variability (the tendency of regions within the cranium to vary) was consistent with the hypothesis that regions that are subjected to high levels of masticatory-related strain, such as the face and mandible, tend to vary more than regions such as the cranial base and cranial vault which are subjected to lower levels of strain.

PHYLOGENETIC RELATIONSHIPS

No matter whether one or two *Paranthropus* species are recognized in East Africa, dental metrical evidence still indicates that *P. boisei sensu stricto* or *P. boisei sensu lato* are distinct from *P. robustus* (Constantino and Wood, 2004). But did the East and southern African "robust" taxa evolve from a recent common ancestor exclusive to themselves and thus form a monophyletic group, or did the various regional *Paranthropus* taxa evolve independently (Fig. 10)? This is not a trivial question for if the two forms evolved from a recent common ancestor, then because the less derived "robust" form (*P. robustus*) is apparently more recent than the more derived form (*P. boisei*) this would either imply several reversals in cranial morphology, or that *P. robustus* existed for several hundred thousand years prior to its current first appearance datum. Alternatively, if the two regional variants arose independently, then it would be a striking case of homoplasy with both lineages exhibiting a morphological trend towards masticatory hypertrophy and extreme postcanine megadontia.
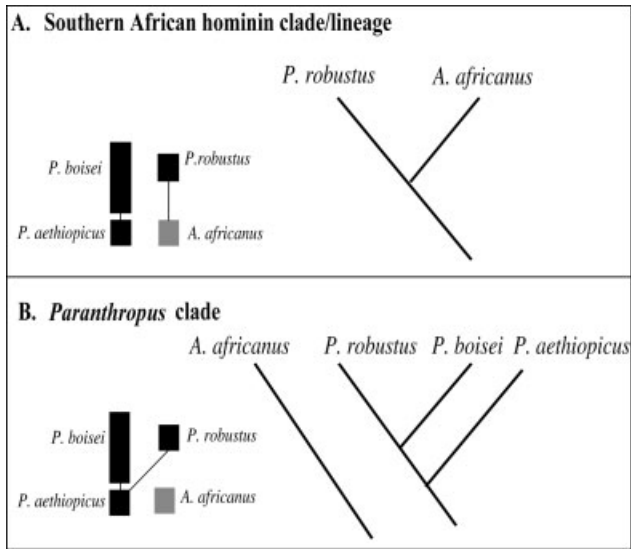
Fig. 10. Two proposed hypotheses for *Paranthropus* phylogenetics. The first hypothesis (**A**) posits that *P. robustus* evolved from *A. africanus* thus highlighting the similarities in morphology and geography between these two taxa. In this scheme, many of the morphological features shared between *P. robustus* and the *P. aethiopicus/P. boisei* lineage would have evolved through parallel or convergent evolution. The second hypothesis (**B**) highlights the morphological similarity among the three *Paranthropus* taxa and suggests they form a monophyletic group. Note that in the first hypothesis, the genus name *Paranthropus* would not be valid for these taxa since they do not form a clade and hence cannot be grouped into a common genus to the exclusion of other australopiths. Additional hypotheses have been suggested such as that of Skelton and McHenry (1992) which views the "robust" australopiths as a polyphyletic group with *P. aethiopicus* separate from a *P. boisei/P. robustus* clade.

The case for *Paranthropus* monophyly

Several different studies have found support for *Paranthropus* monophyly. Wood (1988) reviewed 15 hominin cladistic studies that had treated the East and southern African "robust" taxa as separate operational taxonomic units (OTUs). All of these studies concluded the two regional variants were sister taxa, but as some of the studies had used the same data sets, this series of results is not as impressive as it appears. Corruccini (1994) also reviewed the results of early hominin cladistic analyses, and concluded that one of the few reliable parts of the hominin cladogram is the *Paranthropus* clade. The major hominin cladistic study by Strait et al. (1997) used 60 traits derived from five previous studies, but they also adjusted some of the character states on the basis of their own observations. They subjected these traits to eight parsimony analyses "that differed with respect to the number of characters examined and the manner in which the characters were treated" (Strait et al., 1997, p. 17), and in all eight analyses the "robust" taxa form a single clade. In an even more comprehensive study, Strait and Grine (2004) used 109 nonmetric traits, 89 traits based on linear measurements, and two different out-groups, and found the three "robust" taxa consistently formed an independent clade. In the same year, Kimbel et al. (2004) published the results of a cladistic analysis based on 82 characters generated when they undertook their comprehensive morphological analysis of the cranial remains of *A. afarensis*. The three "robust"

australopith taxa were among the eight early hominin OTUs in their study and they combined observations on *Pan* and *Gorilla* for their outgroup. Like the studies that preceded it, Kimbel et al. (2004) also found consistent support for a "robust" australopith clade.

The case against *Paranthropus* monophyly

With all of these studies supporting a recent common origin for the *Paranthropus* taxa, what reasons are there to continue to scrutinize the hypothesis of *Paranthropus* monophyly? First, the discoverers of KNM-WT 17000 suggested that previous assumptions about the morphoclines within *Paranthropus* needed to be revised and that KNM-WT 17000 (and additional specimens reported at the same time) were evidence that early hominin phylogeny "will prove to be more complex" than had been stated (Walker et al., 1986, p. 522). Second, if consistency indices (CI) are any guide to homoplasy, the ca. 0.65 average CI for hominin cladistic analyses means that approximately 35% of the characters used in the analyses must have been independently acquired (i.e., they are homoplasies). If these homoplasies are concentrated in one anatomical region, and if this region forms a substantial part of the hypodigms of early hominins such as *P. boisei*, then the preserved morphology may not reflect the true evolutionary relationships of the megadont australopiths.

The third reason to reexamine the hypothesis of megadont australopith monophyly is that many, but by no means all, of the characters that link *Paranthropus* taxa in the same clade are related to the masticatory system. For example, when Wood and Chamberlain (1986) organized characters according to anatomical region, they found that support for a *Paranthropus* clade relied heavily on characters from the face, palate, and mandible. These are all regions that reflect masticatory adaptations and thus are likely to be functionally integrated. Therefore, the characters derived from those regions are potentially "non-independent," and if so, should not be coded as individual characters in a cladistic analysis. A comparable conclusion was reached by Skelton and McHenry (1992) who found they could generate a most parsimonious hominin cladogram that included a *Paranthropus* clade, but only when they limited their characters to those drawn from the face, mandible, and dentition. There is also some comparative evidence from other groups of mammals (e.g., Maglio, 1975; Vrba, 1979, 1984) to suggest that the masticatory system might be the equivalent of a "homoplasy ghetto." It should be noted, however, that Strait et al. (1997) excluded masticatory characters from one of their cladistic analyses and still found strong support for a *Paranthropus* clade.

Nevertheless, homoplasy in traits related to the masticatory apparatus appears to be prevalent in the hominin fossil record. For example, the faces of *Kenyanthropus platyops* and *P. boisei* are both orthognathic relative to earlier hominins, but whereas the former has relatively small postcanine teeth the latter shows extreme postcanine megadontia. Similarly, *Australopithecus garhi* has a modest-sized face but very large postcanine teeth. Since neither *K. platyops* nor *A. garhi* are believed to be very closely related to *P. boisei*, the cited similarities among these taxa must be due to convergent or parallel evolution. Although this does not directly address homoplasy within the *Paranthropus* clade, it lends support to the idea that homoplasy may be common in traits related to the hominin masticatory system.
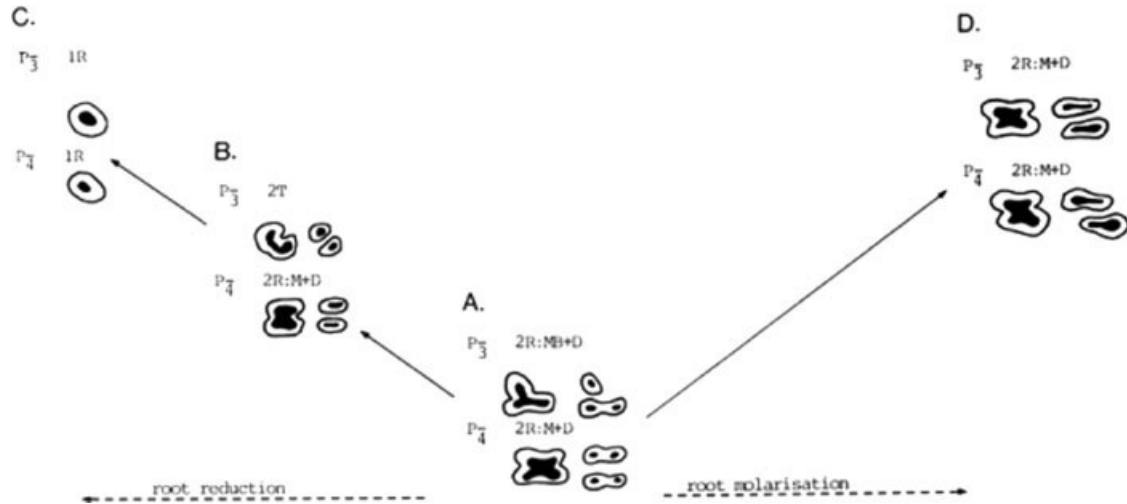
Fig. 11. Proposed evolutionary trends in mandibular premolar root form in fossil hominins (taken from Wood et al., 1988). For those teeth with more than one root, two sections are given. The left-hand corner of each pair is taken immediately above the bifurcation: the right-hand section is taken below it. (**A**) The inferred primitive condition of premolar roots for a hominin ancestor. This is the arrangement for the majority of the Hadar specimens. (**B**) Ontogenetic evidence suggests that Tomes' root form for P_3, and single root canals for the P_4 roots, are a stage between the inferred primitive condition and the derived condition of single-rooted premolars seen in modern humans. The majority of the small sample of *A. africanus* have this root form. (**C**) Derived condition of root reduction in both P_3 and P_4 seen in *Homo sapiens*. (**D**) Derived condition of root elaboration seen in *P. boisei*. 1R = single root; 2T = the second root is a Tomes' root; 2R:M+D = two roots: molariform plate-like mesial and distal roots; 2R: MB+D = two roots: a mesiobuccal root and a molariform plate-like distal root.

Tests of *Paranthropus* monophyly

The results of one of the few studies that specifically set out to test the hypothesis of *Paranthropus* monophyly were mixed in terms of supporting or falsifying the hypothesis (Wood, 1988). The two tests used were based on Patterson's (1982) similarity and ontogenetic criteria, respectively. The logic used in the first test is the null hypothesis that any shape differences between two closely related sister taxa should be predictable from allometric relationships common to the two taxa. Thus, in the case of the taxa within *Paranthropus*, the null hypothesis would predict that for any character state morphocline the apparently more derived East African megadont taxon should be a scaled variant of the less derived southern African taxon. When this proposition was tested using 10 morphoclines based on mandibular postcanine crown morphology, only two of these were consistent with the hypothesis. In a subsequent paper, Suwa et al. (1994) took the examination of postcanine cusp morphology a stage further and noted that "the individual cups involved in the talonid expansion are not always the same" (p. 423) with the hypoconid contributing more to the expansion in *P. boisei*, whereas the entoconid made the greatest contribution in *P. robustus*. This is further evidence that the derived dental morphology seen in the two *Paranthropus* taxa may not necessarily have the same developmental basis.

The logic of the second test (Wood, 1988) was that if *P. boisei* and *P. robustus* are sister taxa with *P. boisei* being generally more derived than *P. robustus*, then the morphology of *P. robustus* should be closer to the primitive state of a character state morphocline. The root system of the P_3 is one of the few systems where the morphoclines have been worked out in any detail (Wood et al., 1988), and the predominant P_3 root forms of *P. robustus* (2T) and *P. boisei* (2R: M and D) (see the legend for Fig. 11 for an explanation of these terms) suggests that these taxa are not on the same morphocline (Fig. 11). The P_3

roots of *P. robustus* are on the trend towards root reduction relative to the inferred primitive condition, whereas the P_3 roots of *P. boisei* are more complex than those of the inferred primitive condition, and are on a separate morphocline (Wood et al., 1988).

Other studies have also addressed the question of *Paranthropus* monophyly. Turner and Wood (1993a) assessed the probability of monophyly in the megadont australopiths by examining the biogeographic patterns of African Plio-Pleistocene large mammals. Their results show that during the time range of *Paranthropus*, faunal dispersal between the two regions seems to have been frequent and several monophyletic groups had representatives in each of the areas. This lends credibility to the hypothesis of *Paranthropus* monophyly, but does not refute a polyphyletic origin for this group. In their second "test" of the *Paranthropus* monophyly hypothesis, Turner and Wood (1993b) assumed that the distinctive masticatory system of *Paranthropus* was an adaptation to enable the increased consumption of tough food items in response to greater environmental aridity. They found that similar trends were detectable in the craniodental anatomy of other terrestrial fauna from this time period, and parallels in lineage turnover suggest that a large-scale response to environmental cues was occurring. This second study by Turner and Wood does not contradict the first, but it does show that there are comparative precedents for two regional hominin lineages (i.e., the East and southern African) to have independently evolved similar masticatory adaptations in response to changing environmental conditions.

The question of *Paranthropus* monophyly is therefore unresolved and future research will have to determine whether the shared skull morphology of East and southern African *Paranthropus* is due to recent common ancestry or convergent evolution. What is clear is that the balance of the present cladistic evidence is in favor of monophyly. If one is sanguine that hard-tissue mor-

phology is capable of recovering phylogenetic relationships established on the basis of independent genetic evidence (e.g., Strait and Grine, 2004), then *Paranthropus* monophyly must be the hypothesis of choice. But if one is more skeptical about its ability to do so (e.g., Collard and Wood, 2000), then what many researchers interpret as overwhelming evidence for *Paranthropus* monophyly looks less compelling.

Relationships between *Paranthropus* and other early hominin taxa

What then of the relationships between *Paranthropus* and other hominin species? Recent attempts to use morphological evidence to reevaluate the phylogenetic relationships of *A. afarensis* have highlighted several similarities between that taxon and *P. boisei*, but found no evidence for a direct phyletic link (Kimbel et al., 2004; Rak and Kimbel, 2006). Also, as mentioned earlier, a third hominin with postcanine megadontia, *A. garhi*, has been recovered from ca. 2.5 myr-old sediments in the Middle Awash of Ethiopia (Asfaw et al., 1999). In the absence of details of this material, it is too early to tell how it is related to the taxa we have included in *Paranthropus*, but what is known indicates that it is probably not very closely related. Most researchers accept that the derived morphology shared between *Paranthropus* and *Homo*, such as increased cranial base flexion (Dean, 1986), evolved independently in the two lineages. The overlap in temporal and geographical ranges precludes one genus from evolving from the other, and the distinctness of other aspects of their morphology leaves little doubt that *H. habilis* and *P. boisei* are at least separate species, and very likely different genera.

PALEOHABITAT

Attempts to determine the habitat preferences of *Paranthropus* in East Africa have reached different conclusions. Shipman and Harris (1988) examined the bovid remains from four sites (Olduvai, Koobi Fora, West Turkana, and Omo) and found that *P. boisei sensu lato* "probably preferred closed over open habitats and favored wetter rather than drier closed habitats" (p. 376). This is a different picture from the one for *Paranthropus* in southern Africa where the same authors suggested that the *P. robustus*-bearing cave sites sampled only open/arid habitats. Reed (1997) compared ecomorphological data from modern mammal assemblages with similar data from fossil assemblages in both East and southern Africa. She concluded that *P. aethiopicus* from West Turkana and Omo existed in "bushland to open woodland" and always in the presence of some degree of edaphic grasslands (i.e., grasslands in waterlogged soils). This is similar to the habitat she reconstructed for *Australopithecus*. *Paranthropus boisei* from Koobi Fora was found to be in more open habitats, but again in association with edaphic grasslands. Earlier reconstructions of these localities as "deltaic" (Behrensmeyer, 1978) or "lake margin" (Shipman and Harris, 1988) are consistent with this interpretation. Reed's conclusions differ from those of Shipman and Harris in not associating *P. boisei* with closed habitats. Instead, *P. boisei* is seen as living in more open environments near perpetual water sources.

Evidence from other *P. boisei* sites may help determine which of these paleohabitat reconstructions is more likely to be correct. Unfortunately, detailed paleoenvironmental reconstructions have not been forthcoming for either Peninj or Chesowanja. Dominguez-Rodrigo et al. (2001) performed a pollen analysis at Peninj, but it was confined to the Upper Sands of the Humbu Formation and the Peninj mandible comes from the older Basal Sands. Chesowanja has a published faunal list, but it is unclear to what degree the fauna is associated with the hominin specimens, except that all the faunal evidence comes from the Chemoigut Formation. Nevertheless, Bishop et al. (1978) suggest that Chesowanja featured a bushed grassland habitat, with riverine and lacustrine elements.

Since Reed's (1997) study, remains of *P. boisei* have been described from two additional sites, Konso and Malema. The nine Konso specimens were all found at the same locality associated with what Suwa et al. (1997) called a "predominantly dry grassland fauna" (p. 489) consisting of an alcelaphine-dominated assemblage of over 2400 mammalian specimens including equids and two species of the pig *Metridiochoerus*. There is clear evidence of a paleolake nearby (Nagaoka et al., 2005), but *P. boisei* fossils are reportedly absent from the more mesic Konso localities, despite a combined sample of over 4,000 specimens (Suwa et al., 1997). Evidence about *P. boisei* in Malawi is confined to just one fossil, a maxillary fragment with a damaged M^1 and fragmentary M^2 (Kullmer et al., 1999). The faunal assemblage found with it is sparse and highly biased for it includes neither carnivores nor small mammals. However, it is dominated by open-habitat mammals including alcelaphines, antilopines, *Hipparion*, and the pig *Notochoerus scotti* suggesting that, as at Konso, *P. boisei* was preserved in a relatively open environment. The results of earlier work (Schrenk et al., 1995) indicate that, also like Konso, a large paleolake was in the vicinity of the Malema site. Thus, the balance of paleoenvironmental evidence from these newer sites suggests that *P. boisei* favored open habitats near water, although the small size and apparent biases in Malema's limited fossil assemblage need to be kept in mind.

There is no evidence of any temporal trend in the ecological preferences of *P. boisei*, since Konso (ca. 1.4 Ma) and Malema (ca. 2.5 Ma) are at the opposite ends of *P. boisei's* temporal range, yet both indicate a preference for a more open habitat. We suggest that the most reasonable interpretation of the paleohabitat evidence from Konso and Malema, combined with Bishop et al.'s (1978) reading of the habitat at Chesowanja and the evidence from the large-scale analyses referred to above, is that *P. boisei* was one of the first hominin taxa to exploit open habitats. Because of the inherent taphonomic problems associated with paleoenvironmental reconstructions of this sort (White, 1988), it is difficult to say to what degree *P. boisei* preferred these habitats, but a review of the evidence shows that, except for the reconstructions of Shipman and Harris (1988) all *P. boisei* localities have been interpreted as containing grassland and/or open woodland (see Table 3 in Wood and Strait, 2004). It is also possible that a broad ecological tolerance allowed *P. boisei* to continue to occupy closed habitats as well. Regardless, the evidence seems clear that *P. boisei* exploited open habitats and thus apparently provides yet another parallel with the evolution of our genus.

BEHAVIOR
Dexterity and tool use

Inferences about the dexterity of fossil hominin taxa come from either paleontological or archeological evi-

dence. The former involves using the shapes of individual hand bones or the form of the joints between the hand bones to make predictions about the capacity to grip and manipulate objects (e.g., Marzke and Shackley, 1986; Marzke and Marzke, 2000; Tocheri et al., 2003). The latter requires evidence that a particular tool kit can be unambiguously related to a particular hominin taxon.

Functional morphology of hand bones. There are no hand bones that can be confidently assigned to either *P. boisei* or *P. aethiopicus*. In southern Africa some hand bones were initially believed to be associated with TM 1517, the type specimen of *P. robustus* from Kromdraai, but these were later determined to be those of a baboon (Krantz, 1960). Subsequently, hand bones from Member 1 at Swartkrans have been attributed to *P. robustus* on the basis that approximately 95% of the craniodental remains from that member belong to this taxon, and also because of reported differences between the Swartkrans hand bones and those known to belong to *Homo* (Susman, 1988). These latter hand fossils reportedly indicate that *P. robustus* was capable of a modern human-like precision grip (Susman, 1988).

Archeological evidence. When the OH 5 cranium was discovered at FLK I it was dubbed "the oldest yet discovered maker of stone tools" (Leakey, 1959, p. 493), and it was assumed that it was the manufacturer of the stone tools found on the "living floor" (e.g., Clark, 1963 cited by Tobias, 1967). However, the career of *P. boisei* as the maker of the Oldowan stone tools was a brief one. For, just 5 years later, Leakey was forced to consider the implications of the subsequent discovery of *Homo habilis* fossils in association with the Oldowan culture at three other localities at Olduvai and concluded that "while it is possible that *Zinjanthropus* and *Homo habilis* both made stone tools, it is probable that the latter was the more advanced tool maker and that the *Zinjanthropus* skull represents an intruder (or a victim) on a *Homo habilis* living site" (Leakey et al., 1964, p. 9). So, in just 5 years *P. boisei* had gone from a stone tool maker to a hapless victim. This "about face" was made not because any evidence suggested that *P. boisei* could not be the toolmaker (as mentioned, no securely associated hand bones of *P. boisei* were known at the time or have been found since), but because *H. habilis* with its larger brain and apparently modern-human like hand bones seemed more likely than *P. boisei* to possess such a modern human-like behavioral trait.

Since 1964, most researchers have been willing to accept *H. habilis* as the toolmaker and thus have relegated *P. boisei* to the sidelines of cultural evolution. However, some researchers (Isaac, 1984; Brain et al., 1988; Clark, 1990; Susman, 1991; Wood, 1997) have entertained the possibility that members of more than one hominin lineage may have had the ability to manufacture simple stone tools. Included among these researchers is Mary Leakey who conceded that "the australopithecines may well have made simple tools" (Leakey, 1966, p. 466). Nonetheless she remained convinced that Oldowan tools were the work of *Homo*.

Both stone and bone tools have been found in Member 3 of Swartkrans where the only hominin fossil evidence is of *P. robustus* (Brain et al., 1988). Across the Blauuwbank Valley at the site of Sterkfontein, flake-based tools have been recovered from the Member 5 Oldowan Infill and the only hominins known from that part of the cave

have been assigned to *P. robustus* (Kuman and Clarke, 2000). These patterns, along with the suggestion that the Swartkrans bone tools were used to dig into termite mounds (Backwell and d'Errico, 2001), have reinvigorated the debate about the tool-using abilities of *Paranthropus*.

However, even if we could be confident about the taxonomic assignment of the Swartkrans hand bones, and of the ability of *P. robustus* to generate a precision-grip, it is unclear what the implications would be for *P. boisei*. It seems then, based on both morphological and archeological evidence, that the position is much the same as it was in 1964. There is no firm evidence that *P. boisei* made and used stone tools, but there is also no firm evidence that they were incapable of doing so.

Diet

It is curious that although diet is almost universally cited as the reason for the morphological distinctiveness of *P. boisei*, there have been remarkably few studies that have focused on the diet of *P. boisei* (see contributions in Ungar, 2006). However, studies of dental morphology, masticatory biomechanics, dental microwear, and chemical analyses of bones and teeth have allowed researchers to make some inferences about *P. boisei*'s diet, and these are discussed.

Dental morphology. Correlations have been made between diet and tooth size and shape. For example, members of *P. boisei* had relatively small incisors and canines and relatively large postcanine teeth (Tobias, 1967, and see Wood, 1991 for a review of the metric evidence). Small incisors indicate a diet that does not require a significant amount of incisal preparation, such as one consisting of leaves or berries (Hylander, 1975). This suggests that if *P. boisei* was eating fruit, then the fruit either lacked thick husks or fleshy pulp, or it was small enough to need no preparation prior to ingestion. The small size of the canines supports this interpretation since these teeth do not appear to be adapted for use in food preparation. However, the possibility that foods were being prepared outside of the mouth must be considered.

The very large, bunodont, postcanine tooth crowns of *P. boisei* may have been an adaptation to disperse high occlusal loads, or to simply increase the surface area over which food could be processed at any one time. Lucas et al. (1986) showed that the ratio of the area of M1 to M3 was inversely related to the amount of leaves consumed, and suggested that the low M1/M3 ratio of *Paranthropus* indicates they were "probably consuming small mouthfuls of leaves and seeds" (p. 269). While their low shearing crests (*sensu* Kay, 1975) and rounded cusps suggest that a diet high in fibrous leaves or grasses was unlikely, it is still possible that seeds and underground storage organs such as tubers, bulbs, roots, and rhizomes made up a significant proportion of *P. boisei*'s diet (Hatley and Kappelman, 1980; Laden and Wrangham, 2005; Yeakel et al., 2007).

All post-4 Ma hominins have relatively thick enamel, but as with postcanine crown area, *P. boisei* is the most derived hominin along this morphocline so that its enamel is described as "hyper-thick" (Grine and Martin, 1988, p. 33). It has been suggested that hyper-thick enamel is part of a strategy to resist wear and/or protect the enamel from cracking under the influence of high occlusal loads (Kay, 1981; Grine and Martin, 1988;

Dumont, 1995). Gantt and Rafter (1998) suggested that the hyper-thick enamel of *P. boisei* was "due to increased crushing and grinding and adaptation to savanna habitat" (p. 195). While few would disagree with this statement, there is still no consensus as to what *P. boisei* was "crushing and grinding." Lucas et al. (in review) suggest that thick enamel protects the teeth of mammals against excessive wear caused by small, hard objects, while it resists fracture of the enamel cap that results from contact with large, hard objects. If it was possible to examine *P. boisei* postcanine teeth with well–preserved microwear, it should be possible to tell whether the thick enamel was functioning more to protect against small, hard, objects—in which case there should be evidence of abrasive microwear—or large, hard objects—whose ingestion would not necessarily be linked with surface damage to the enamel.

Biomechanics. To judge from the size of the ectocranial crests and the inframtemporal fossa, *P. boisei* probably had larger masticatory muscles than other early hominin taxa (Tobias, 1963). However, it is unclear whether these larger masticatory muscles would have necessarily resulted in higher occlusal forces. As Demes and Creel (1988) have pointed out (and as Walker, 1981 pointed out earlier for *P. robustus*) *P. boisei* would have been able to generate higher bite forces than other hominins, but the occlusal forces at the molars would not have been exceptional if they were distributed over the entire area of the occlusal surface. Only if *P. boisei* was feeding on small objects in limited numbers at any one time would increased force on any single object result. As will be discussed later, a diet of small, hard objects is precisely what studies of microwear predict for *P. robustus*.

In addition to having larger jaw muscles, the cranial attachments for the masseter muscle are more anteriorly positioned in *P. boisei* than they are in other early hominins (Rak, 1988). Also, compared to the extant great apes and *A. afarensis*, most of the crania assigned to *P. boisei* reveal evidence of greater emphasis on the anterior, as opposed to the posterior, fibers of the temporalis as evidenced by greater anterior development of the sagittal crest (Kimbel et al., 2004). Combined with the more orthognathic face, this suggests that *P. boisei* featured an increase in the mechanical advantage (output force relative to input force) of the major jaw muscles.

Since under certain circumstances *P. boisei* individuals could generate significantly higher bite forces than other hominins, it is not surprising that they also appear to have had gnathic adaptations to withstand high masticatory stresses. Hylander (1988) determined that "the vertical depth and transverse thickness of the mandibular corpus ... were unusually large" in *P. boisei* and suggested these were structural adaptations to "counter powerful parasagittal bending moments" and "powerful twisting moments," respectively (p. 77). The transverse thickness of *P. boisei*'s mandibular symphyses was also unusually large and this, along with the increased transverse thickness of the corpus, would have been effective at countering stresses due to wishboning (lateral bending in the transverse plane). According to Hylander, these results imply that *P. boisei* was adapted to resist high stresses caused by masticating very hard or tough food items. The interpretation of *P. boisei*'s mandibular corpus dimensions as "unusually large" was corroborated by Wood and Aiello (1998) who found that *P. boisei* had significantly larger mandibles than either an extant

hominoid or a generalized extant simian with a similar body mass, and they suggested that any attempt to determine the diet of *P. boisei* would need to consider the reasons for this extra-large mandibular corpus. CT scans of the compact bone distribution within the mandibular corpus of *P. robustus* indicate that they likely featured a significant transverse component to their chewing cycles (Daegling, 1989). Unfortunately, no similar studies have been performed on specimens of *P. boisei*, but DuBrul's (1977, 1992) interpretation of the TMJ morphology of OH 5 also indicated a significant transverse chewing component.

Dental microwear. Thus far no study of *P. boisei* dental microwear has been reported in the literature. This is due, at least in part, to the fact that most *P. boisei* fossils are found on the surface, and surface specimens typically exhibit a substantial proportion of non-diet-related microwear due to erosion, weathering, and trampling (Walker, pers. comm.). However, the analysis of dental microwear has proved to be a valuable technique for understanding diet in the megadont hominins from southern Africa, and in the light of the probable close evolutionary relationship between *P. robustus* and *P. boisei* it will be briefly reviewed here.

On the basis of comparisons between *P. robustus* and *A. africanus*, *P. robustus* molars generally feature a higher incidence of pitting suggesting these creatures likely ate harder, and perhaps smaller, objects than did the more gracile australopiths (Grine, 1981, 1986; Grine and Kay, 1988). In addition, lower densities of microwear on the incisors of *P. robustus* relative to *A. africanus* suggests that the incisors of *P. robustus* were not used to process as many different types of food items as were those of *A. africanus*, nor did they process foods that were as abrasive or large (Ungar and Grine, 1991). Recent work using scanning confocal microscopy and scale-sensitive fractal analysis supports the hypothesis that *P. robustus* ate harder and more brittle food items than did *A. africanus*, but it also suggests that both taxa had variable diets that overlapped significantly (Scott et al., 2005).

Chemical analysis. The chemical analysis of bones and teeth is another method that has significantly increased our understanding of hominin diet, but as with dental microwear analysis, it has not yet been used in an in-depth study of the diet of *P. boisei*. The results of Sr/Ca ratios and $^{13}C/^{12}C$ isotope ratios when applied to *P. robustus* have indicated an omnivorous diet that included both C_3 and C_4 foods (Sillen, 1992; Lee-Thorp et al., 1994; Sponheimer et al., 2005) with evidence of significant seasonal, interannual, and individual variability (Sponheimer et al., 2006). Although these results cannot be simplistically translated to the diet of *P. boisei*, they at least show that the derived masticatory apparatus of *P. robustus* was not greatly limiting its dietary breadth. One of the only chemical studies that included *P. boisei* was by Boaz and Hampel (1978) who found that *P. boisei* had lower Sr/Ca ratios than early *Homo*. This is broadly consistent with later analyses of *P. robustus* from Swartkrans (Sillen et al., 1995) and suggests that *Paranthropus* may have been consuming more meat than the earliest members of our own genus. However, the results need to be interpreted with caution due to the small sample sizes for *Homo*.

Posture and locomotion

Given the uncertainty about its postcranial hypodigm, it would not be sensible to speculate about what postcranial fossil evidence can tell us about the posture and locomotion of *P. boisei*. However, comparative studies of the *P. boisei* crania that include evidence about the relative position of the foramen magnum (Dean and Wood, 1981, 1982) suggest that the habitual posture of *P. boisei* was similar to that of premodern *Homo* and modern humans.

Social structure

Plavcan and colleagues (Plavcan and Van Schaik, 1997; Plavcan, 2000, 2002, 2003) have been at the forefront of efforts to use correlations between size and shape sexual dimorphism and social structure in living higher primate taxa to make predictions about the social structure of extinct hominins. They have mostly concentrated their efforts on predicting the social structure of extinct taxa through comparisons of body size/mass and canine crown dimorphism (e.g., Plavcan and Van Schaik, 1997). What can be reliably inferred about the levels of body mass and canine sexual dimorphism in *P. boisei*?

For at least the time being we lack reliable ways of determining the sex of most early hominins, so the extent of sexual dimorphism in *P. boisei* has to be inferred in other ways. There is substantial morphometric variation within the *P. boisei* hypodigm (Wood, 1991). Researchers who have compared this variation with the degree and pattern of intraspecific and interspecific variation within living higher primate taxa have concluded that variation within the *P. boisei* hypodigm is consistent with high levels of intraspecific variation (Aiello and Wood, 1994; Silverman et al., 2001), or is more consistent with intraspecific than with interspecific variation (Wood, 1991; Wood et al., 1991). For the purposes of reconstructing social structure, we will assume the *P. boisei* hypodigm exhibits substantial levels of intraspecific cranial size and shape variation (Wood, 1991) and substantial levels of intraspecific mandible (Wood and Aiello, 1998) and body size (Aiello and Wood, 1994; Kappelman, 1996) variation. Canines are relatively rare in the *P. boisei* hypodigm, but examination of the few that exist suggests that *P. boisei* is characterized by modest levels of canine crown size variation and little or no canine crown shape variation (Wood, 1991). Even if we assume that a substantial component of the intraspecific variation within *P. boisei* is sex-related, there are no modern higher primate analogues that show a similar pattern of within species variation (i.e., substantial body mass dimorphism combined with modest canine size dimorphism). Thus, inferences have to be made about the social structure of *P. boisei* by atomizing its morphology and then comparing the predictions from each of the relevant components (i.e., canine crown height, canine crown buccolingual width, body size, etc.).

The initial predictions derived from estimates of canine and body mass sexual dimorphism embraced a range of social structures including monogamous polyandry, single-male/multi-female and multi-male social structures (Plavcan and Van Schaik, 1997). Plavcan's later conclusions were more cautious and indicated that the relationships among these variables in the living higher primates are "not strong enough to make detailed inferences about mating systems or behavior on the ba-

sis of dimorphism alone" (Plavcan, 2000, p. 342), and in an even more recent paper, Plavcan (2003) cautions against assuming that any living hominoid is a suitable analogue for early hominins with respect to predicting social structure.

LIFE HISTORY

Most of the current evidence of extinct hominin life history is indirect (Skinner and Wood, 2006). However, determination of age at weaning in fossil hominins is one possible exception. It has been based on an assessment of the degree and timing of the attrition of the deciduous dentition associated with dietary supplementation. Aiello et al. (1991) showed that specimens of *P. boisei* and *P. robustus*, judged to be between 2.5 and 3.5 years of age, exhibit high levels of deciduous dental attrition compared to specimens of *A. afarensis*, but these authors concluded that this could be related to earlier age at weaning and/or to dietary differences. Other variables, such as body mass and brain size, have been shown empirically to either influence life history or to be correlated with certain life history traits (e.g., Sacher, 1975; Martin, 1981, 1983; Hofman, 1984; Smith, 1989, 1992; Smith and Tompkins, 1995; Smith et al., 1995; Godfrey et al., 2003), but since *Paranthropus* appears to overlap significantly both with other archaic hominins and with extant higher primates in both body mass and brain size, these variables provide no reason to suggest that *P. boisei* differed greatly from these other taxa in aspects of its life history.

Much of the remaining evidence related to hominin life history comes from ontogenetic studies of the dentition. In some respects, dental development in *P. boisei* resembles that of modern humans (e.g., incisor crown formation and eruption sequence), while in others it resembles chimpanzees (e.g., rate of root formation), and in yet others dental development in *P. boisei* is unique. For example, the premolar and molar crowns of *P. boisei* take the same time, or less, to form than those of modern humans and chimps, despite the fact that *P. boisei* crowns are more than twice the size of modern human and chimp crowns. This is due to a combination of more enamel secretion per day by ameloblasts and a faster rate of ameloblast activation (Beynon and Wood, 1987). More information is needed before we can determine whether these differences are due to selection operating on life history, diet, or a combination of the two, but the dental evidence appears to indicate that the ontogeny, and thus the life history of *P. boisei*, was neither modern human-like nor chimpanzee-like.

CONCLUSIONS AND PROSPECTS

This review shows that over the past half century considerable advances have been made in the task of understanding the paleobiology of *P. boisei*. Additions to the cranial hypodigm have provided the majority of those advances, with the balance coming from new and improved analytical methods. Nonetheless, even with a relatively good fossil record of the cranium and dentition some important inferences (e.g., diet) about *P. boisei* still elude us. But this is not an atypical experience of researchers who seek to learn about the adaptive regime of an extinct taxon.

How near to the present day mark were the initial interpretations of *P. boisei* made by Leakey (1959) and Tobias (1967)? Two of Leakey's judgments appear to have been supported by the much enlarged hypodigm. First, no one since Robinson (1960b) has seriously doubted the wisdom of establishing a new taxon for the fossils belonging to *P. boisei*. Second, although there is little enthusiasm for recognizing *P. boisei* and its ilk at the level of a separate "subfamily *Australopithecinae*" (Leakey, 1959, p. 491), few would question that *P. boisei* belongs in the same general grade as hominin taxa presently included in the genera *Australopithecus* and *Kenyanthropus*, albeit as the most derived member of that inclusive grade. Leakey's judgments about phylogenetic relationships have fared less well, for the enlargement of the hypodigm has effectively falsified Louis Leakey's claim that what was then called *Z. boisei* "differs from both *Australopithecus* and *Paranthropus* much more than these two genera differ from each other" (Leakey, 1959, p. 491). As we have seen in the section on phylogenetic relationships, the vast majority of phylogenetic analyses link *P. boisei* with *P. robustus* to the exclusion of *A. africanus*. As for Tobias' groundbreaking monograph on the OH 5 cranium (Tobias, 1967), several of the conclusions reached in that publication have been vindicated. For example, Tobias agreed with Robinson in recognizing the close affinity between *P. boisei* and *P. robustus*. In doing so he identified *P. boisei* as "one extreme in the diverse spectrum" of hominins, an extreme that he realized was to eventually become extinct.

What are the priorities in terms of improving our understanding of the paleobiology of *P. boisei*? The first priority is a simple one. It is to find at least one, and preferably several, taxonomically unambiguous associated skeletons. This would help the task of working out which limbs go with which heads at Olduvai and Koobi Fora. The second priority would be a way of extracting more information about the functional morphology of the hominin masticatory system and thus about the diet of *P. boisei*. Third, we need to establish more firmly the evolutionary relationships between *P. boisei* and the other megadont archaic hominin taxa. The fourth priority is to tease out which aspects of dental growth and development are diet-related, and which carry a signal about life history. Finally, we have to find more effective ways of establishing whether, and to what extent, *P. boisei*, was a cultural animal. Was its cultural repertoire a substantial advance on that of a modern chimpanzee? Did its cultural ability differ from that of the other less megadont archaic hominins?

This review of 50 years of research into a single taxon illustrates how analytical advances and an increase in the quantity and quality of its hypodigm have combined to advance our understanding of its paleobiology. The rate of discovery of *P. boisei* fossils is on the decline (Constantino and Wood, 2007), probably because of changes in research priorities within paleoanthropology. Nevertheless, there is much to learn about this distinctive and derived taxon. But for this we require both additional fossil evidence and further technical advances in the way we extract information from that evidence.

ACKNOWLEDGMENTS

APPENDIX

TABLE A1. Characteristic and distinctive features of Paranthropus boisei sensu stricto

Part 1: Cranium		
Cranium-wide	Relative size of the components	Distinctive combination of an absolutely (presumed males) and relatively (both presumed males and females) large and supranasally orthognathic viscerocranium, a wide midface, and a modest-sized neurocranium (Bilsborough and Wood, 1988).
Vault	Shape, thickness and sutures	Relatively long and narrow parietals, low and wide occipital, absolutely thin vault bones, and extensive overlap of the parietotemporal suture with marked *striae parietales* (Rak, 1978; Rak and Howell, 1978), even in smaller (presumed female) crania.
	Ectocranial structures	Substantial polymorphism in sagittal cresting patterns in the larger (presumed male) crania (Walker and Leakey, 1988; Brown et al., 1993; Wood et al., 1994). Some individuals have the greatest height of the crests anteriorly (e.g., OH 5) whereas some specimens have crests that are highest posteriorly (e.g., KGA-10-525). There is a "bare area" (Dart, 1948) on the occiput and a compound temporonuchal crest in some large (presumed male) crania.
Endocranium	Endocranial volume and mass	The *P. boisei* mean value of 488 cm^3/490 g ($N = 10$; range 400 (KMN-WT 17400)–545 (KGA-10-525) cm^3—details of the sample are given in (Skinner and Wood, 2006)). The estimated endocranial volume and mass of *P. boisei* is most likely insignificantly larger than for *P. aethiopicus* for which there is only one data point (KNM-WT 17000 = 410 cm^3/407 g). The *P. boisei* sample mean is also not significantly different ($P = 0.36$) from the *P. robustus* sample, even though the latter taxon includes individuals with larger brains resulting in a higher (533 cm^3/535 g) mean brain volume and mass. There is a slight temporal increase in brain size within the *P. boisei* hypodigm (Elton et al., 2001).

(continued)

TABLE A1. (Continued)

	Gross endocranial morphology	Some *P. boisei* endocasts show evidence of a posteriorly-positioned lunate sulcus, but they retain an ape-like, beak-shaped, frontal lobe, and rounded temporal poles. Four or five *P. boisei* endocasts (KGA-10-525, KNM-ER 23000, KNM-WT 13750, OH 5 and possibly Omo L338Y-6) have slight L.O.R.F. petalial patterns (Holloway et al., 2004). For all other *P. boisei* endocasts, it is either not possible to determine whether a petalia exists, or this information has not been reported. In KNM-WT 17400, the Broca's cap region is larger on the left than on the right side, but it is not clear whether this is due to distortion (Holloway et al., 2004). The temporal lobe of KNM-WT 17400 is African ape-like in its size and shape (Falk et al., 2000). In KGA-10-525, KNM-ER 23000, and Omo L338Y-6 convolutional details in the occipital region are sufficiently well-preserved to suggest a reduction in the relative size of the primary visual cortex. Three *P. boisei* endocasts, KNM-ER 23000, KNM-WT 17400 and OH 5, have a pointed frontal lobe, a morphology they share with *P. aethiopicus* and the great apes, and which contrasts with the condition in *A. afarensis*, *A. africanus*, and modern humans (Falk et al., 2000).
	Venous sinuses and meningeal vessels	*Venous sinuses*–Tobias (1967) noted that OH 5 had an enlarged occipital marginal sinus system, a trait it shares on at least one side with most other scorable *P. boisei* specimens (i.e., KNM-CH 304, KNM-ER 23000 (Brown et al., 1993), KNM-ER 407, and KNM-ER 732). A probable exception to this trend is Omo L-338Y-6, for several authors have failed to confirm the presence of an enlarged O/M sinus system in this specimen (Rak and Howell, 1978; Holloway, 1981; Kimbel, 1984; Falk et al., 1995). The fossil KGA-10-525 has no O/M sinus system (Suwa et al., 1997; Holloway et al., 2004), nor any impressions for the transverse sinus (Suwa et al., 1997; White and Falk, 1999). *Meningeal vessels*—Saban (1983) found that some *P. boisei* crania (e.g., KNM-ER 407) had three major branches (anterior, middle, and posterior) of the middle meningeal vessels. Others (e.g., Omo 338y-6) had only simple anterior and posterior branches (Walker and Leakey, 1988; White and Falk, 1999).
Face	Overall size and shape	The face is both morphologically distinctive (see below and Rak, 1983; Bilsborough and Wood, 1988) and polymorphic (Wood et al., 1994; Suwa et al., 1997). Compared to the upper face, the mid-face is absolutely and relatively broad in both large and small crania.
	Upper face	Prominent glabella combined with a frontal trigone (Tobias, 1967).
	Midface	Broad, anteriosuperiorly-flaring malar region located anterior to the plane of the nasal cavity. The origin of the maxillary zygomatic process and the masseteric attachment are both anteriorly-located so that they are situated no further posteriorly than above the premolars (Rak, 1983).
	Lower face and palate	The combination of a lack of a distinct nasal sill and little or no eversion of the nasal margin that results in the distinctive "punched out" appearance of the nasal aperture, with the majority of individuals having nasal bones that are widest superiorly (Rak, 1983; Wood, 1991).
Base		The foramen magnum is heart-shaped (Tobias, 1967) and the long axis of the petrous is coronally-orientated (Dean and Wood, 1981; Dean and Wood, 1982; Dean, 1988). The cranial base of *P. boisei* is unusual in a hominin with only a modest brain size in that the foramen magnum is situated relatively far forward. Uniquely modified glenoid and mastoid morphologies including a deep mandibular fossa, lateral to medial twisting of the articular eminence, flattening of the tympanic plate, increased horizontal distance between porion and the tip of the mastoid process, and a maximum lateral projection of the mastoid that is more inferiorly positioned than in other hominins (Kimbel et al., 2004).

Part 2: Mandible

Corpus	Overall	Deep and wide corpus with a rounded base, a marked lateral prominence, a wide extra molar sulcus, vertical inner wall and more rounded "bulging" lateral wall.
	Alveolar process	Relatively little of the alveolar process is devoted to the anterior teeth, with a correspondingly greater proportion of the alveolar process devoted to the postcanine teeth.
Symphysis		The overall appearance of the external aspect is rounded, but some specimens have a weak but distinct mental eminence. Internally there is usually a long alveolar planum, with substantial superior and inferior transverse tori.
Ramus		Tall and wide, with both internal and external buttressing of the condyle.

Part 3: Dentition-microstructure

Enamel	First order process-related variables	Ameloblast daily secretion rate(s): Lower molars, the mean rate in the outer one third of the enamel in *P. boisei* ($N = 5$) of 7.12 μm/day contrasts with a slower rate of 5.22 μm/day at the equivalent location in *Homo habilis* and 5.2 μm/day in *H. sapiens* (Lacruz et al., in press). Prisms: Premolars, angle to EDJ (I) Mean = 55°; molars, angle to EDJ (I) Mean = 52° (Beynon and Wood, 1986). Periodicity, 7 ($N = 5$) (Lacruz et al., 2007). Striae of Retzius: Premolars, angle to EDJ (D) Mean = 28°; molars, angle to EDJ (D) Mean = 23° (Beynon and Wood, 1986); No tooth type specified, angle to EDJ (D) = 32° (Ramirez Rozzi, 1993). Hunter-Schreger bands: Premolars, curvature (HSBC) = 2/3; width (HSBW) = 54 mm; Molars, Curvature (HSBC) = 1/2; Width (HSBW) = 53 mm (Beynon and Wood, 1986).

TABLE A1. (Continued)

	Second order process-related variables	Daily extension rate: Crown, faster than in early *Homo*; Cervix, faster than in early *Homo* (Beynon and Wood, 1987). Crown formation time: Lower incisors, *P. boisei* is faster than *A. africanus* (Dean and Reid, 2001); Upper incisors, cuspal (i.e., appositional) = 0.46 y; cervical (i.e., imbricational) = 1.84 y; total = 2.3 y; Lower incisors, cuspal = 0.36 y; cervical = 1.84 y; total = 2.2 y; Upper canines, cuspal = 0.6 y; cervical = 2.46 y; total = 3.06 y; Lower canines, cuspal = 0.6 y; cervical = 2.25 y; total = 2.85 y; Premolars (P^4), cuspal = 1.36 y; cervical = 1.0 y; total = 2.4 y. (Beynon and Dean, 1988). Molars, cuspal = 1.4 y (early *Homo* = ca. 1.0 y); cervical = 0.72 y (early *Homo* = ca. 1.5 y); total = 2.12–2.5 y (early *Homo* = ca. 2.42–2.62 y) (Beynon and Wood, 1987).
	Pattern-related variables	Ratio of cuspal:cervical (i.e., imbricational) enamel: >10:1 (early *Homo* = 4:1) (Beynon and Wood, 1987). Enamel thickness: Premolars, OT (Corrected[2]) = 2.8 mm; CT (Corrected[2]) = 2.5 mm; LT (Corrected[2]) = 1.95 mm; Molars, OT (Corrected[2]) = 2.9 mm; CT (Corrected[2]) = 3.0 mm; LT (Corrected[2]) = 2.2 mm (Beynon and Wood, 1986).
Dentin		N/A
Dentition-macrostructure		
Deciduous	Relative size of dentition	The anterior deciduous tooth crowns are very small relative to the size of the crowns of the postcanine deciduous teeth (Wood, 1991: Ref. Table 30).
	Maxillary, anterior teeth, morphology	N/A
	Maxillary, molar crowns, size, and cusp morphology	dm^2, lingual cupsule interrupts the lingual groove; paracone projects mesiobuccally making the crown outline asymmetric; mesiodistal diameter exceeds the buccolingual diameter (Grine, 1985).
	Maxillary, molar roots, number and morphology	N/A
	Mandibular, anterior teeth	N/A
	Mandibular, molar crowns, size, and cusp morphology	dm_1, main buccal groove extends down to the EDJ (Grine, 1985); dm_2, five main cusps and a C6 (Wood, 1991: Ref. Table 30).
	Mandibular, molar roots, number, and morphology	N/A
Permanent	Relative size of dentition	The anterior tooth crowns and/or alveoli are very small relative to the size of the crowns of the postcanine teeth, *contra* their apparent relationship in *P. aethipicus* (Wood, 1991; Ref. Table 20–29). Their small size appears to be a "real" reduction in the sense that it runs counter to the allometric relationships seen in African apes (Wood and Stack, 1980). The crowns of the mandibular premolars, especially the P_4, are large relative to the anterior teeth, and the P_4 root system is especially molarized, so that its roots are either more substantial than, or subequal with, the roots of the M_1 (Wood et al., 1988).
	Maxillary, anterior teeth, morphology	Little or no distinctive crown morphology has been reported (Wood, 1991: Ref. Table 30).
	Maxillary, premolar crowns, size, and cusp morphology	Large crowns with a relatively large paracone; relatively little size discrepancy between P^3 and P^4 crown areas (Wood and Engleman, 1988).
	Maxillary, premolar roots, number, and morphology	P^3, two or three roots (Wood and Engleman, 1988). P^4, two or three roots (Wood and Engleman, 1988).
	Maxillary, molar crowns, size, and cusp morphology	Size order, $M_1 < M_2 = M_3$. M^{1-3}, large crowns with high incidence of a Carabelli complex (Wood and Engleman, 1988).
	Maxillary, molar roots, number, and morphology	Three roots (one mesio-buccal root, one distobuccal root, and one larger lingual root); little or no distinctive root morphology.
	Mandibular, anterior teeth, morphology	Very small crowns and little or no distinctive crown morphology has been reported (Wood and Stack, 1980; Wood, 1991: Ref. Table 25).
	Mandibular, premolar crowns, size, and cusp morphology	Size order, measured crown base area of P_4 is 145% of P_3 (Wood and Uytterschaut, 1987). P_3, normally three cusps; metaconid mesial relative to protoconid; positively allometric relationship between talonid area and overall crown area (Wood and Uytterschaut, 1987). P_4, always three, or more, cusps; metaconid mesial relative to protoconid; positively allometric relationship between talonid area and overall crown area (Wood and Uytterschaut, 1987; Suwa, 1988).
	Mandibular, premolar roots, number, and morphology	Root heights: relatively long distal roots (Wood et al., 1988). P_3, always two roots; the ratio of MB+D:M+D teeth is 1:2 (Wood et al., 1988). P_4, always two roots; the ratio of MB+D:M+D teeth is 0:15; distal root usually longer than the M_1 distal root (Wood et al., 1988).
	Mandibular, molar crowns, size, and cusp morphology	Size order, $M_1 < M_2 < M_3$. M_1, talonid expanded; >6 cusps; at least one C6; unlikely to have a C7; unlikely to have a protostylid (Wood and Abbott, 1983); steep-sided coronal profile (Wood et al., 1983). M_2, talonid expanded; >6 cusps; likely to have a C6; unlikely to have a C7; unlikely to have a protostylid (Wood and Abbott, 1983); steep-sided coronal profile (Wood et al., 1983). M_3, talonid expanded; usually >6 cusps; always one C6 and often two; very unlikely to have a C7; very unlikely to have a protostylid (Wood and Abbott, 1983); steep-sided coronal profile (Wood et al., 1983).
	Mandibular, molar roots, number, and morphology	M_1, always two roots; distal root inclined and robust. M_2, always two roots; relatively short and robust roots. M_3, always two roots; relatively short and robust roots (Wood et al., 1988).

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