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The Evolution of *Zinjanthropus boisei*

PAUL CONSTANTINO AND BERNARD WOOD

Many people assume that OH 5, the type specimen of *Paranthropus boisei,* collected in 1959, was the first evidence of that taxon to be found, but OH 3, recovered in 1955, predated the discovery of OH 5 by four years. Thus, *Paranthropus boisei* recently celebrated the equivalent of its fiftieth birthday. This review marks that milestone by examining the way our understanding of this taxon has changed during its fifty, or so, year history.

Several hominin taxa have been established longer or have a larger fossil record, but *Paranthropus boisei,* the hominin taxon that began life as *Zinjanthropus boisei,* is unusual for several reasons. First, much of its skull morphology is apparently derived[1–3] and highly distinctive (Table 1). Second, most of its hypodigm comes from sites with good stratigraphic and chronological control and can be dated with relative precision.[4,5] Third, the fossil record of *Paranthropus boisei* is almost exclusively cranial, consisting mostly of jaws and teeth. This means there are reasonably sized, relatively well-dated samples for some morphological regions like the mandible and the mandibular dentition. Researchers can thus trace the evolution of metrical and nonmetrical variables across hundreds of thousands of years. Finally, all these factors, together with the fifty, or so, years that have elapsed since its discovery, mean that it is possible to use *Paranthropus boisei* as an example of how our understanding of a hominin taxon changes over time. For example, to what extent has the increase in the size of the sample changed our perception of the taxon? Have important sample parameters changed significantly as the hypodigm has increased in size? To what extent can we disentangle the influence of an enlarged fossil record from the benefits that have accrued from advances in analytical methods? Thus, this review not only summarizes what we know of the evolutionary history of *Paranthropus boisei,* but also traces the evolution of our understanding of its evolutionary history.

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HISTORY OF DISCOVERY

The first evidence of a megadont hominin (that is, a hominin with very large postcanine tooth crowns relative to its estimated body size) from East Africa was found at Olduvai Gorge in 1955 (Fig. 1).[6,7] Labeled OH 3, for "Olduvai Hominid 3," it was a specimen consisting of two teeth, a deciduous canine and a large deciduous molar crown (Fig. 2). The huge size of the teeth made them unique among East African hominins known at the time. The taxonomy of OH 3 therefore remained uncertain until the 1959 recovery of a well-preserved subadult cranium with similar teeth (OH 5) that was assigned to *Zinjanthropus boisei* (Fig. 3).[8]

No mandibles to match the OH 5 cranium have been found at Olduvai Gorge, but the recovery in 1964 of a well-preserved, robust-bodied, adult mandible with megadont postcanine tooth crowns (Peninj 1) from a site on the western shore of Tanzania's Lake Natron seemed to provide evidence of the type of mandible that would be compatible with OH 5.[9] Three years later, another hominin mandible with postcanine megadontia was recovered from the Omo Shungura Formation in southern Ethiopia (Omo 18.18).[10] Since 1967, many additional mandibles and isolated teeth similar to these megadont fossils have been collected from these same sediments.[11–14]

Beginning in 1968, a series of *P. boisei* fossils was uncovered near what was then known as East Rudolf (now called Koobi Fora) in northern Kenya. This series included the recovery in 1969 of a well-preserved but edentulous adult cranium (KNM-ER 406) and the recovery in 1970 of an adult hemicranium preserving the majority of the vault, the right side of the face,

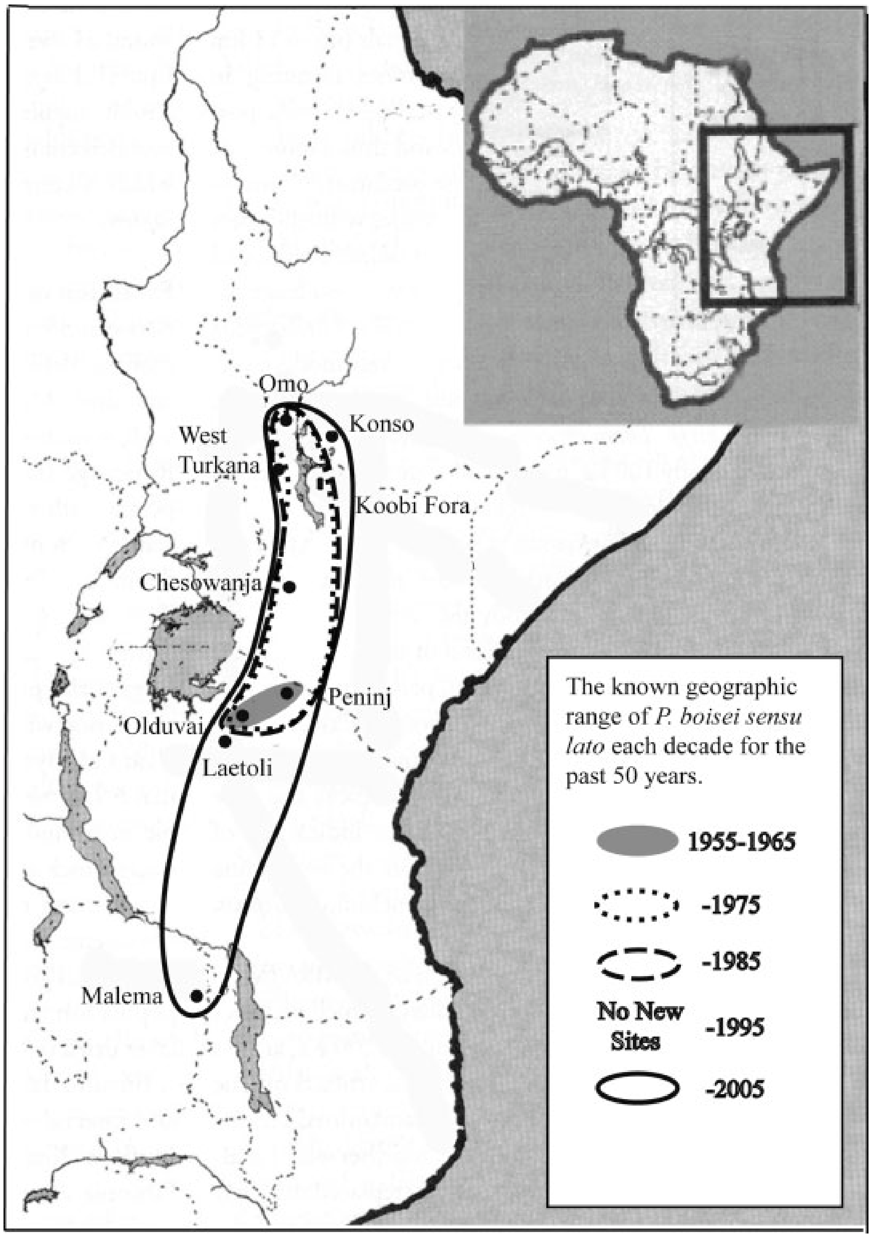

Figure 1. Map of *P. boisei* sites in East Africa highlighting the change in its known geographic range over the past five decades. The only new site discovered between 1975 and 1985 was West Turkana; no new sites were discovered between 1985 and 1995. The last decade has seen a significant increase in the range of *P. boisei* due mainly to the discovery of Malema in Malawi, but also Konso in Ethiopia. Adapted from Delson and coworkers.[99]

and part of the right side of the cranial base (KNM-ER 732) (Fig. 4). Several mandibular specimens have also been found at Koobi Fora and elsewhere, so that numerically it is the best-sampled region of the *P. boisei* skeleton (Fig. 5).[1] About the same time that many of the Koobi Fora fossils were being discovered, the Chemoigut Formation at Chesowanja, Kenya also provided evidence of *P. boisei,* most notably in the form of a cranium discovered in 1970 that preserved the right side of the face and the anterior part of the cranial base (KNM-CH 1).[15]

The intensive prospecting in the Omo Shungura Formation and at Koobi Fora in the late 1960s and early 1970s resulted in the rate of discovery of *P. boisei* fossils reaching its peak in the second decade (1966–1975) of the taxon's history (Fig. 6). After that time, cranial remains belonging to *P. boisei* continued to be recovered from Koobi Fora and began to be found at West Turkana.[1,4,16–18] Two noteworthy *P. boisei*-like specimens from West Turkana, a mandible (KNM-WT 16005) and a cranium (KNM-WT 17000), were recovered in sediments dating to ca. 2.5 Ma.[16,19] Along with Omo 18.18 and others, these specimens have been suggested as possible representatives of a second megadont taxon in East Africa, *Paranthropus aethiopicus,* which was geologically older than *P. boisei*. They therefore have particular relevance to the debate about the origin and subsequent evolution of megadont archaic hominins. Additional evidence of *P. boisei* has come from sites elsewhere in East Africa, most notably in 1993, when a well-preserved skull of *P. boisei* (KGA 10-525) was recovered in Ethiopia at Konso (formerly called Konso Gardula).[20] This skull was not only the geologically youngest known specimen of *P. boisei,* at 1.4 Ma, but also increased the geographical range of the taxon. Moreover, this was the first time that cranial and mandibular evidence from the same individual had been found in proximity, affirming the presumed associations between the "robust" crania and large jaws made by previous researchers. Also, in 1999, a *P. boisei*-like maxilla was recovered from Malema, Malawi, thus substantially expanding the southern extent of *P. boisei's* range by more than 1,000 km.[21]

FOSSIL EVIDENCE

Cranial

More than 111 craniodental specimens are now attributed to *P. boisei sensu stricto;* an additional 56 are assigned to *P. aethiopicus.* Only the most complete and well-preserved of these are reviewed here.

Similarities between the type specimen (OH 5, Fig. 3) and the large, crested cranium from Koobi Fora (KNM-ER 406, Fig. 4) were noted at

TABLE 1. Some Characteristic and Distinctive Features of *Paranthropus boisei sensu stricto*

Cranium
- Orthognathic facial profile
- Broad mid-face with anteriorly positioned and laterally flaring zygomatic bones
- High degree of postorbital constriction
- Overlap of parietotemporal sutures with marked *striae parietales*
- Polymorphic pattern of sagittal and nuchal cresting in presumed males
- Anteriorly positioned, heart-shaped foramen magnum

Mandible
- Deep and wide corpus with a rounded base
- Substantial superior and inferior transverse tori at the symphysis
- Tall and wide ramus

Dentition
- Very small anterior teeth relative to the posterior teeth
- Very large posterior teeth relative to skull size
- Maxillary premolars having large crowns with a relatively large paracone; 2 or 3 roots
- Maxillary molars, $M^1 < M^2 = M^3$; large crowns with high incidence of a Carabelli's cusp; 3 roots
- Mandibular premolars, P_4 crown base area is ca. 140% that of P_3; talonid area is positively allometric relative to total crown area; 2 plate-like roots
- Mandibular molars-$M_1 < M_2 < M_3$; expanded talonid; usually > 6 cusps; usually at least one C6; unlikely to have a C7; 2 plate-like roots
- ``Hyper-thick'' enamel with relatively little enamel decussation on postcanine crowns

the time of the latter's announcement.[22] Most researchers have concluded that the differences between these two large, presumed male crania are best interpreted as evidence of intraspecific and not interspecific variation.[1] The morphology of two other partial crania from Koobi Fora (KNM-ER 13750 and 23000) and of the skull from Konso is also sufficiently similar to that of OH5 and KNM-ER 406 to suggest that all five crania belong to *P. boisei.* Some aspects of their morphology, such as the topography of the ectocranial crests and the face, vary within the presumed male morph of *P. boisei,* while other regions, such as the cranial base, are relatively invariant.[17,23,24]

A calvarium (KNM-ER 407) and a partial hemicranium (KNM-ER 732) differ in both size and shape from the presumed male *P. boisei* crania. In the case of KNM-ER 407, the contrast in morphology was considered to be so great that its initial taxonomic assessment concluded it was "either a gracile species of *Australopithecus* or else a very early representative of *Homo* ...."[22] In contrast it was suggested that KNM-ER 406 and 732 "represent the two sexes of the same species."[25] Most researchers now agree with this assessment, interpreting these crania as smaller-bodied, presumably female representatives of *P. boisei,*[1,26,27] thus providing evidence of substantial cranial sexual dimorphism within this taxon (Fig. 4). Another cranium recovered from Koobi Fora (KNM-WT 17400) has lost some of the diagnostic morphology of the face, but what remains of its osseous and dental morphology leaves little doubt that this specimen represents another example of the small, presumably female morph of *P. boisei.*

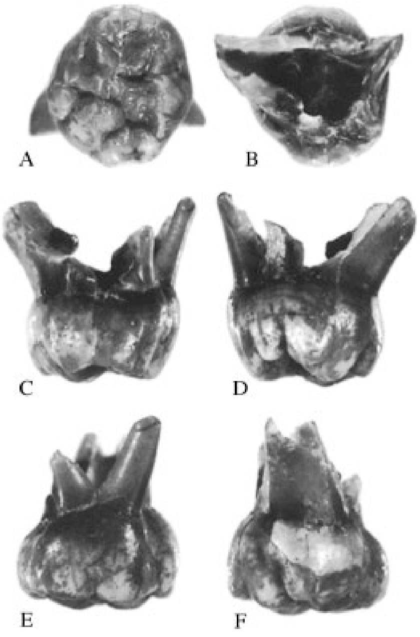

Figure 2. The first evidence of *Paranthropus boisei.* The deciduous right M^2 of OH 3 in occlusal (A), alveolar (B), mesial (C), distal (D), buccal (E), and lingual (F) views. From Tobias.[100]

Postcranial

The only sure way for researchers to know what the postcranial hypodigm of a hominin taxon looks like is to find diagnostic craniodental remains together with elements of the postcranial skeleton. Unfortunately, there is no compelling evidence of an associated skeleton for *P. boisei* (but see Grausz and coworkers[28]). Thus, the problem researchers have faced at Olduvai Gorge, Koobi Fora, and elsewhere is how to tell which of the unassociated hominin postcranial fossils should be assigned to *P. boisei* and

Figure 3. Early photo of OH 5 in lateral view shortly after its reconstruction. The mandible was created based on the known morphology of the cranium. Its size and shape were later affirmed by the discovery of the Peninj mandible at Lake Natron, which closely resembles the one created for OH 5. Photo by Bob Campbell.

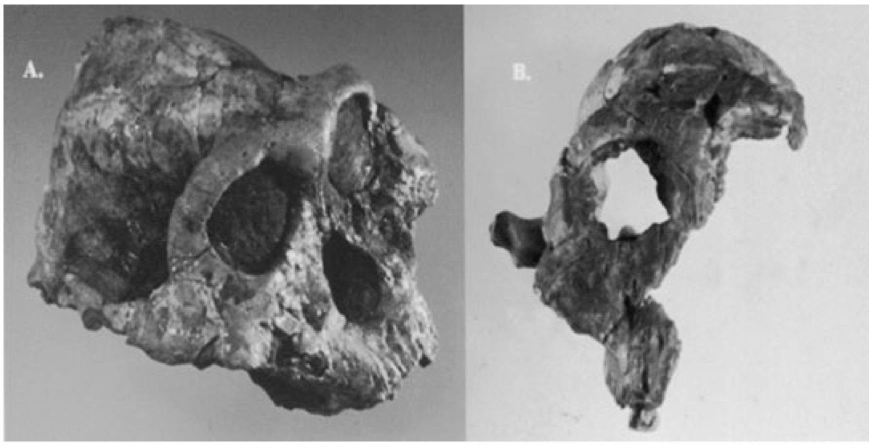

Figure 4. Right anterosuperior view of the presumed male cranium KNM-ER 406 (A) and anterior view of the presumed female cranium KNM-ER 732 (B).

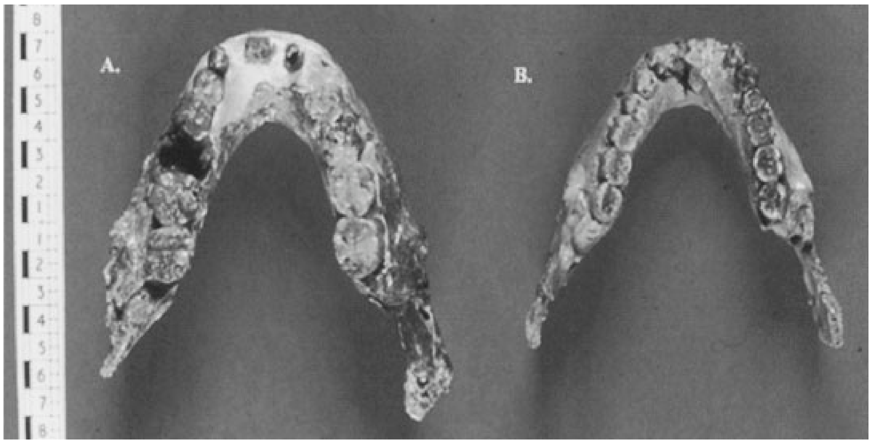

Figure 5. Occlusal views of KNM-ER 729 (A) and KNM-ER 992 (B) casts. KNM-ER 729 has been attributed to *P. boisei.* Easily visible are its huge molar teeth, molarized premolars, and thick corpus. KNM-ER 992 is the type specimen of *Homo ergaster.* Although its postcanine teeth are larger than those of modern humans, they are clearly much smaller than those of *P. boisei.*

which should be assigned to the contemporaneous species *Homo habilis*.

The only unassociated hominin postcranial fossil recovered at Olduvai Gorge to be explicitly assigned to *P. boisei* is a proximal femoral fragment (OH 20, Fig. 7).[29] A detailed analysis of OH 20 suggested that it shares a suite of features with two proximal femora attributed to *P. robustus* (SK 82 and 97). These features prompted Day[29] to remark that "it would seem reasonable to allocate the new femoral fragment to *Australopithecus cf. boisei*" (Note that *Australopithecus boisei* is the same taxon as *Paranthropus boisei.* The reason for the continued disagreement about whether to attribute these fossils to *Australopithecus* or *Paranthropus* will be discussed later). At that time, no one knew what an *H. habilis* femur looked like, so it seemed logical to link a *P. robustus*-like proximal femur with *P. boisei,* as well as to link what were then interpreted as the more modern human-like Olduvai Bed I and II postcranial specimens (for example, OH 8 and 10) with *H. habilis*.

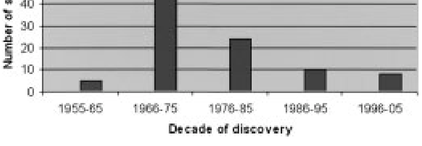

Figure 6. The number of *P. boisei* specimens discovered each decade for the past 50 years. The large number of specimens discovered between 1965 and 1975 was mostly due to the beginning of field work at Koobi Fora and the Omo.

The discovery of a modern human-like ankle bone (the talus KNM-ER 813) at Koobi Fora[30] weakened the case for assuming that the OH 8 foot belonged to *H. habilis,* since the OH 8 talus more closely resembles a talus assigned to *P. robustus* (TM 1517).[31,32] Wood[31] argued that the logic that had led to the interpretation of Olduvai foot fossils (OH 8 and 10) as modern human-like was flawed and suggested that they have as much claim to be attributed to *P. boisei* as they have to *H. habilis*.

At approximately the same time that these reassessments of the Oldu-

Figure 7. The proximal left femur OH 20 in anterior (A) and posterior (B) views.

vai hominin postcranial fossils were taking place, Richard Leakey and his team had begun to recover hominin postcranial remains from Koobi Fora. Most were femoral specimens; provisional comparisons suggested that they could be divided into those that were more like the femora of modern humans and those that were "not unlike other femoral fragments that have been collected elsewhere and assigned to *Australopithecus*."[25] However, the attributions of the more primitive specimens to *Australopithecus* and, by inference, to *Australopithecus cf. boisei,* depended on the untested assumption that the femora of *H. habilis* were recognizably more modern human-like than were the femora of *P. boisei.* The subsequent discovery of an *H. habilis* partial skeleton (OH 62) challenged this assumption. The partial skeleton is poorly preserved and its interpretation remains controversial. Nevertheless, its femoral morphology is evidently similar enough to that of femora from Olduvai and Koobi Fora that had been assigned to *Australopithecus* and thence to *P. boisei*[33] to make these latter attributions suspect. Consequently, there is no current way of telling to which taxon or taxa the "*Australopithecus*-like" hominin postcranial evidence from Olduvai and Koobi Fora belongs. For the time being, it would be prudent to regard this fossil evidence as Hominini gen. et sp. indet.

Attempts to identify the postcranial skeleton of *P. boisei* at sites other than Olduvai and Koobi Fora have been *ad hoc,* and none has been particularly convincing. So where does that leave us? In short, we are 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,* exhibits similar 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.

SYSTEMATICS

Upon the discovery of OH 5, Louis Leakey[8] drew attention to twenty differences between this cranium and crania already attributed to *Australopithecus* and *Paranthropus,* which at the time were only known from southern Africa. The following year Robinson[34] went through Leakey's claimed "major differences" and, to the former's satisfaction, refuted the vast majority. Robinson suggested that the genus name *Zinjanthropus* be abandoned and proposed that OH 5 be included within the existing genus *Paranthropus.*

How Many Species?

There are currently three main debates about the taxonomy of *P. boisei.* The first focuses on whether there are sufficient differences between *P. boisei* and *P. aethiopicus* to justify retaining *P. aethiopicus* as a separate species. The second asks whether recent discoveries have blurred the distinction between *P. boisei* and the megadont taxon from southern Africa, *Paranthropus robustus.* The third debate concerns whether the differences in size and shape subsumed within *P. boisei* are consistent with a sexually dimorphic early hominin taxon or whether they are an indication that even *P. boisei sensu stricto* subsumes more than one taxon.

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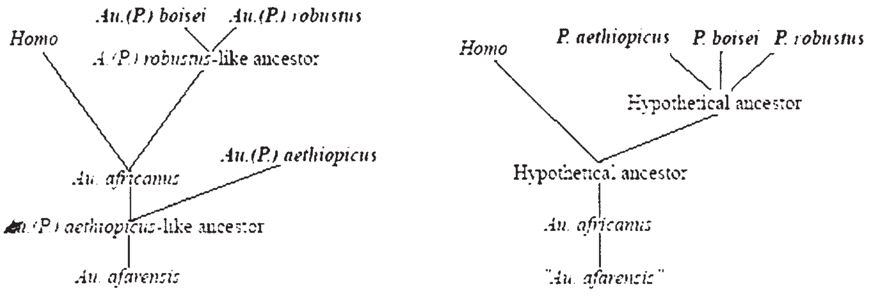
If the hypodigm of *P. boisei* is restricted to the post-2.3 Ma fossil record, then the name *P. boisei sensu stricto* should be retained for the main hypodigm and *P. aethiopicus* should be used as the species name for the earlier fossil evidence. However, if the *P. boisei* hypodigm is judged to include the pre-2.3 Ma fossils, among them Omo 18.18, L338y-6, and KNM-WT 17000, then *P. aethiopicus* becomes a junior synonym of *P. boisei sensu lato*. The point at issue is whether the differences between KNM-WT 17000 and the < 2.3 Ma crania belonging to the *P. boisei sensu stricto* hypodigm (for example, OH 5, KNM-ER 406) justify a specific distinction for the West Turkana cranium and the early megadont jaws and teeth attributed to *P. aethiopicus.*[10] Two studies have looked at this problem in detail. Suwa[35] concluded that there are differences in mandibular premolar cusp morphology between the pre-2.3 Ma and the post-2.3 Ma megadont fossil evidence, with the later material having larger and more elaborate talonids. Wood, Wood, and Konigsberg[23] found that several features of the mandible and the mandibular dentition (other than the premolar morphology referred to by Suwa[35]) also change at ca. 2.3 Ma. These authors supported the interpretation that the early stage of the *Paranthropus* lineage in East Africa should be recognized as a different species. The main differences between the two East African *Paranthropus* species are the greater facial prognathism, larger incisors, flatter cranial base, smaller mandibular corpus, and shorter postcanine tooth row of *P. aethiopicus.*[23]

Tobias[36] cogently made the case for distinguishing between *P. boisei* and *P. robustus* and, until recently, the enlargement of the two hypodigms had not materially altered that assessment. However, the discovery of a megadont hominin skull (KGA 10-525) at Konso prompted Suwa and coworkers[20] to suggest that some aspects of its morphology are common to both *P. boisei* and *P. robustus.* This, together with the recovery of additional cranial material from Koobi Fora (for example, KNM-ER 23000)[17] and the publication of the detailed analysis of a cranium from the Omo (Omo 323–896)[14] prompted at least one commentator to suggest that *Paranthropus* taxonomy should be reassessed.[37] In addition, the recovery of a large, "*P. boisei* size" molar from Gondolin[38] suggests that it would be worthwhile to consider whether the recent discoveries in



Phylogeny of Skelton & McHenry (1992) **Phylogeny of Strait, Grine, and Moniz (1997)**

Figure 8. Adaptations of two proposed phylogenies for Plio-Pleistocene hominin evolution with the ``robust'' australopiths highlighted in bold. The phylogeny by Skelton and McHenry[48] shows the ``robust'' australopiths as a polyphyletic group descended from two different ancestors, with many of the morphological features that are shared between *Au. (P.) aethiopicus* and the *Au. (P.)boisei/Au. P. robustus* clade having evolved through parallel or convergent evolution. The phylogeny by Strait, Grine, and Moniz[46] shows the ``robust'' australopiths as monophyletic (all evolving from the same recent common ancestor). The length of the lines is arbitrary and not meant to be reflective of time. In the phylogeny by Strait, Grine, and Moniz,[46] ``*Au. afarensis*'' is in quotes because the authors designated a new taxon name for members of this group. ``*Au. afarensis*'' is retained here for clarity of comparison with the Skelton and McHenry phylogeny. Also for ease of comparison, additional taxa such as *Kenyanthropus platyops* and *Au. garhi* are not included.

southern Africa at this site and at Drimolen[39] may have closed the morphological gap between *P. robustus* and *P. boisei*. However, recent studies addressing these issues have found no support for taxonomic revision based on the current evidence. Wood and Lieberman[24] concluded that "the Konso specimens fit within the population parameters of *P. boisei* predicted by the 'pre-Konso' hypodigm. When Constantino and Wood[40] compared the regional hypodigms of *Paranthropus* before and after 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 increased rather than decreased.

As for whether the *P. boisei* hypodigm samples more than one hominin taxon, it has been suggested that the degree of size variation in the mandibular hypodigm of *P. boisei* is exceptional.[41,42] 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 larger individuals, while erosion of surface bone has reduced the size of the corpus of some of the smaller individuals in the hypodigm.[1,43] Apart from these extrinsic causes of differences in overall size, the size and shape of the mandibular corpus of *P. boisei* is remarkably stable through geological time[23] (see Fig. 2E), with both small and large mandibles in the sample retaining their characteristically robust corpus and rounded base.[1,23]

Is *Paranthropus* Monophyletic?

Regardless of whether one or two *Paranthropus* species are recognized in East Africa, dental metrical evidence still indicates that *P. boisei* is distinct from *P. robustus*.[40] But did the East and southern African megadont 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. 8)?

In 1988 Wood[44] reviewed fifteen hominin cladistic studies, all of which concluded that the two regional variants of *Paranthropus* are sister taxa. An independent review published in the same year also found that one of the few reliable parts of the hominin cladogram is the *Paranthropus* clade.[45] The major cladistic study by Strait, Grine, and Moniz[46] also found that the most parsimonious cladograms support *Paranthropus* monophyly. As part of their comprehensive morphological analysis of the cranial remains of *Au. afarensis,* Kimbel, Rak, and Johanson[3] also found consistent support for a "robust" australopith clade.

Given the near unanimity of the conclusions of these studies, what reasons are there to continue to scrutinize the hypothesis of "robust" monophyly? First, the average confidence interval for hominin cladistic analyses of ca. 0.65 means that approximately 35% of the characters used in the analyses must have been independently acquired; that is, they are homoplasies. If these homoplasies are concentrated in one anatomical region such as the skull, and if that region has a major influence on the shape of the cladograms, then an analysis of the preserved morphology may not result in an accurate reconstruction of evolutionary relationships. Second, many of the characters that link *Paranthropus* taxa are related to the masticatory system. For example, when Wood and Chamberlain[47] 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 regions all reflect masticatory adaptations and are thus 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. Skelton and McHenry[48] reached a comparable conclusion. Evidence from other groups of mammals (see, for example, Maglio[49] and Vrba[50,51]) also suggests that the masticatory system might be the equivalent of a "homoplasy ghetto." It should be noted, however, that even when Strait, Grine, and Moniz[46] excluded masticatory characters from one of their cladistic analyses they still found strong support for a *Paranthropus* clade.

A third argument for questioning *Paranthropus* monophyly is that a study that used Patterson's[52] similarity and ontogenetic criteria to test the hypothesis of *Paranthropus* monophyly[44] with respect to mandibular molar cusp morphology and mandibular premolar root form produced mixed results in terms of supporting or falsifying the hypothesis. In a further examination of *Paranthropus* postcanine cusp morphology, Suwa, Wood, and White[53] noted that "the individual cups involved in the talonid expansion are not always the same," with the hypoconid and the entoconid contributing more to talonid expansion in *P. boisei* and *P. robustus,* respectively. This suggests that the derived dental morphology in the two *Paranthropus* taxa may not have the same developmental basis.

The question of *Paranthropus* monophyly is therefore unresolved. Future research will have to determine whether the shared skull morphology of East and southern African *Paranthropus* is due to common ancestry or convergent evolution. If one is sanguine that hard-tissue morphology is capable of recovering phylogenetic relationships established on the basis of independent genetic evidence, then *Paranthropus* monophyly must be the hypothesis of choice. But if one is more skeptical about its ability to do so, then what others interpret as overwhelming evidence for *Paranthropus* monophyly looks less compelling. This has taxonomic implications since the genus name *Paranthropus* is only appropriate if these taxa form a monophyletic group. Otherwise, they cannot be included in their own separate genus and should be included as members of the genus *Australopithecus.* Because the majority of phylogenetic analyses currently support *Paranthropus* monophyly, we suggest that until the evidence demonstrates otherwise, the genus name *Paranthropus* should be used to recognize the strong possibility that megadont taxa in both regions form an adaptively distinctive and monophyletic group.

What about the evolutionary relationships between *Paranthropus* and nonrobust taxa? A recent attempt to use morphological evidence to reevaluate the phylogenetic relationships of *Au. afarensis* has revealed several similarities in cranial morphology between that taxon and *P. boisei sensu lato,*[3] but failed to support a direct phyletic link between these hominins. Interestingly, another hominin with postcanine megadontia, *Australopithecus garhi,* has been recovered from ca. 2.5 Ma sediments in the Middle Awash of Ethiopia.[54] While it does not seem to be a member of the *Paranthropus* clade based on other aspects of its craniofacial morphology, it is too early to know how it is related to other hominins. Finally, most researchers accept that the derived morphology shared between *Paranthropus* and *Homo,* such as cranial base flexion, either evolved independently in the two lineages or was inherited from an as-yet undiscovered recent common ancestor of the *Paranthropus* and *Homo* clades. The distinctness of other aspects of their morphology leaves little doubt that *H. habilis* and *P. boisei* are at least separate species, probably belonging to different genera. Thus, the existing fossil evidence suggests that the genus *Paranthropus* went extinct without contributing to the evolution of later hominins.

CONTEXT

Geographical and Temporal Range

Paranthropus boisei sensu lato (*P. boisei sensu stricto* plus *P. aethiopicus*) is currently known from eight sites in East Africa and spans a geological age range of ca. 2.6–1.4 Ma (Figs. 1 and 9). With the exception of the Omo, no major East African sites are known to have fossiliferous deposits dated to between ca. 1.4 and 1.0 Ma or between 3.0 and 2.5 Ma. Therefore, it could be argued that there is a gap of half a million years on each side of the temporal range of *P. boisei sensu lato.* We do not know how far into those gaps *Paranthropus* fossils extend, but the apparent absence of *Paranthropus* fossils in the older Omo sediments suggests that the currently accepted temporal range of ca. 1.2 Ma is likely to be close to the true temporal range.

Paleohabitat

There have been various interpretations of the habitat preferences of *Paranthropus* in East Africa. Shipman and Harris[55] concluded that *P. boisei sensu lato* probably preferred closed and wet habitats, while Reed[56] suggested that these hominins lived in more open environments such as edaphic grasslands. Some *P. boisei* sites not included in these analyses, such as Peninj and Chesowanja, do not have detailed paleoenvironmental data available for the relevant stratigraphic levels, but habitats have been reconstructed at the more recently discovered sites of Konso and Malema. The nine Konso specimens are associated with a "predominantly dry grassland fauna"[20] close to a paleolake,[57] with no *P. boisei* fossils coming from the more mesic (moderately wet) localities. The faunal assemblage found with the *P. boisei* maxillary fragment[21] at Malema is sparse and highly biased, but it is dominated by open-habitat mammals including alcelaphines, antilopines, *Hipparion,* and the pig *Notochoerus scotti,* suggesting that *P. boisei* was preserved in a relatively open environment at that site as well. The results of earlier work[58] also indicate the proximity of a large paleolake at Malema. Thus, at both Konso and Malema, the evidence supports the assertion that *P. boisei* favored open habitats near permanent water, as advocated by Reed.[56]

BEHAVIOR

Given the lack of postcranial bones that can be confidently attributed to *P. boisei,* there is not much that can be said of this taxon's dexterity, posture, or locomotion except that data on the relative position of the foramen magnum[67,68] indicate that the habitual posture of *P. boisei* was similar to that of modern humans. This section will therefore focus on the evidence we have regarding diet and the function of the masticatory system, followed by a brief discussion of attempts to infer social structure from morphology.

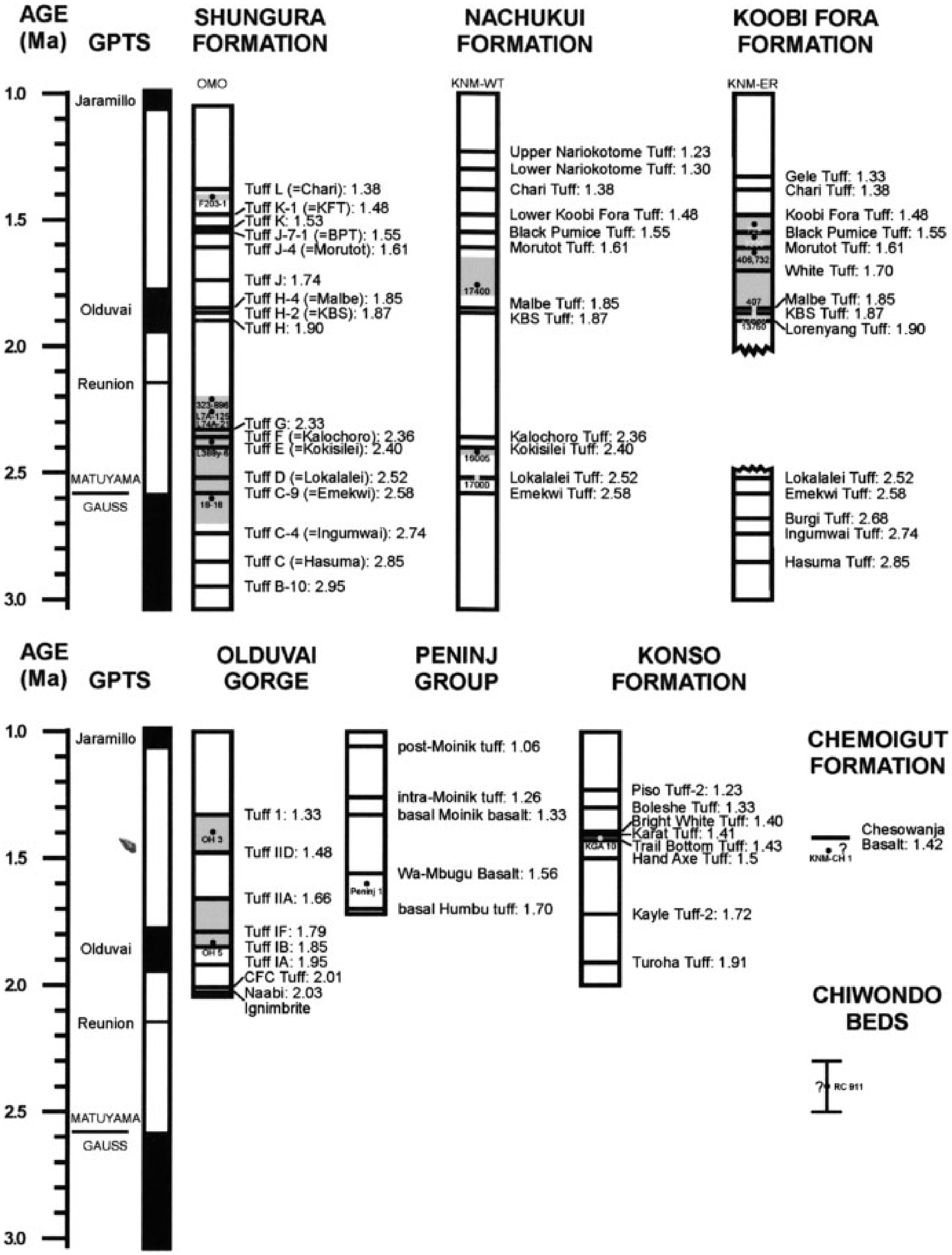


Figure 9. Stratigraphic location of the *P. boisei* hypodigm. Shaded areas indicate levels where *P. boisei* fossils have been found. The specific positions of key specimens mentioned in the text are shown. The oldest known specimens of *P. aethiopicus* are from the Omo and are dated to ca. 2.6 Ma, while 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 are the youngest known for *P. boisei,* at ca. 1.4 M.

Diet

There has not been much success in determining the diet of *P. boisei.* This is somewhat surprising considering the predominance of cranial, gnathic, and dental evidence in its hypodigm, the likely role diet played in the evolution of its derived masticatory morphology, and the potential for diet to provide information regarding the divergence between *Paranthropus* and early *Homo.* We will review what has been done to understand *P. boisei*'s diet in terms

BOX 1: Was *Paranthropus boisei* a maker and user of stone tools?

When the OH 5 cranium was discovered at FLK I, it was assumed to be the manufacturer of the stone tools found on the "living floor."[8] However, the career of *P. boisei* as the maker of the Oldowan stone tools ended just five years later, when Louis 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. He 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."[59] This conclusion was reached not because any evidence suggested that *P. boisei* could *not* be the toolmaker, but because *H. habilis,* with its larger brain and apparently modern human-like hand bones, seemed a more likely toolmaker than did *P. boisei.*

Since 1964, virtually all researchers have come to agree that *H. habilis* made stone tools. Most of these researchers have relegated *P. boisei* to the sidelines of cultural evolution. However, a few have entertained the possibility that members of more than one hominin lineage may have had the ability to manufacture simple stone tools.[60–64] The truth is that there is no direct evidence linking *any* of these early hominin species with stone tools. No hand bones can be confidently assigned to either *P. aethiopicus* or *P. boisei,* so we do not know whether these taxa were dexterous enough to make or use stone tools. Hand bones tentatively attributed to *P. robustus* in southern Africa reportedly indicate that these hominins were capable of a human-like precision grip.[65] Both stone and bone tools have been found in loose association with *P. robustus* at Swartkrans[61] and Sterkfontein.[66] However, even if these anatomical and archeological associations prove to be sound, it is unclear what the implications would be for *P. boisei.* Thus far, there is no firm evidence that *P. boisei* made and used stone tools, but there is also no firm evidence that members of this taxon were incapable of doing so.

of dental morphology, masticatory biomechanics, dental microwear, and chemical analyses of bones and teeth.

Dental morphology

The small incisors of *P. boisei* appear to indicate a diet that did not require a significant amount of incisal preparation such as one consisting of leaves or berries.[69] Therefore, if *P. boisei* was eating fruit, then the fruit either lacked thick husks or fleshy pulp or was small enough to need little preparation before mastication with the postcanine teeth. However, the possibility that foods were being prepared outside of the mouth must be considered (see Box 1).

The very large, bunodont postcanine tooth crowns of *P. boisei* may have been an adaptation to disperse high occlusal loads or simply to increase the surface area over which food could be processed at any one time. Lucas, Corlett, and Luke,[70] showed that the ratio of the area of M1 to M3 (both upper and lower) in primates was inversely related to the amount of leaves consumed and suggested that the low M1:M3 ratio of *Paranthropus* indicates that they were "probably consuming small mouthfuls of leaves and seeds." However, the low shearing crests[71] and rounded cusps of these teeth suggest that a diet high in fibrous leaves or grasses was unlikely. Nevertheless, it is still possible that seeds and plant underground storage organs such as tubers, bulbs, roots, and rhizomes made up a significant proportion of *P. boisei*'s diet.[72,73]

All post-4 Ma hominins have relatively thick enamel but, as with postcanine crown area, *P. boisei* was even more derived along this morphocline than were other hominins; its enamel has been described as "hyper-thick"[74] (p. 33). The functional role of thick enamel is still unclear, but it has been suggested that it is part of a strategy to resist wear and/or withstand high occlusal loads caused by abrasive or hard foods. Gantt and Rafter[75] suggested that the hyper-thick enamel of *P. boisei* was linked with "increased crushing and grinding and adaptation to savanna habitat." While few would disagree with this statement, there is still no consensus as to what it was that *P. boisei* was "crushing and grinding."

Masticatory biomechanics

The cranial attachments for the masseter muscles are more anteriorly positioned in *P. boisei* than they are in other early hominins[76] and, to judge from the size of the ectocranial crests, zygomatic bones, and other muscle attachment areas, *P. boisei* probably had larger masticatory muscles as well (Fig. 10).[77] However, it is unclear whether these larger masticatory muscles would have resulted in higher

Figure 10. KNM-ER 406 (A) and KNM-ER 3733 (B) in superior view. The large and laterally flaring zygomatic arches of KNM-ER 406 can be seen clearly. Coupled with the shorter anteroposterior length of the cranium, this gives *P. boisei* a much more circular cranial circumference when viewed from this angle. Also apparent in this photograph are the high degree of postorbital constriction and sagittal crest development in *P. boisei,* both related to its smaller relative brain size. One can also see evidence of the convergence in facial orthognathy between *P. boisei* and *Homo.*

occlusal forces. As Demes and Creel[78] have pointed out (and as Walker[79] pointed out earlier for *P. robustus*), *P. boisei* would have been able to generate exceptionally high bite forces relative to those of other hominins, but the occlusal forces at the molars would not have been exceptional if they were distributed over the entire occlusal surface. Only if *P. boisei* was feeding on limited numbers of small objects at any one time would increased force on any single object result.

Since, under certain circumstances, *P. boisei* could *generate* significantly higher bite forces than could other hominins, it is not surprising that they also appear to have had the ability to *withstand* high bite forces. Hylander[80] has suggested that the thick mandibular symphysis and the deep, thick mandibular corpus of *P. boisei*, which is approximately three times larger than would be expected in a generalized hominoid of the same body mass,[81] allowed these creatures to resist high stresses caused by masticating very hard or tough food items.

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 nondiet-related microwear due to erosion, weathering, and trampling.[82] Although the analysis of dental microwear has proven to be a valuable technique for understanding diet in the megadont hominins from southern Africa,[83,84] it is unclear what these results say, if anything, about the diet of *P. boisei*.

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*. One of the only chemical studies that included *P. boisei* was by Boaz and Hampel,[85] who found that *P. boisei* had lower Sr:Ca ratios than did early *Homo*. This is broadly consistent with later analyses of *P. robustus* from Swartkrans[86] and suggests that *Paranthropus* may have been consuming more meat than did the earliest members of our own genus. However, the results of the Boaz and Hampel study need to be interpreted with caution due to the small samples used for early *Homo*.

Social Structure

Plavcan[87] has been at the forefront of efforts to predict the social structure of extinct taxa through comparisons of sexual dimorphism in body size and canine crown size. Unfortunately, we currently lack reliable ways of determining the sex of most early hominins but, as mentioned earlier, the pattern of craniodental size dimorphism apparent in *P. boisei* suggests the presence of distinctive male and female morphs. These morphs are somewhat unusual, however, in that they both possess relatively small canines, despite their evident craniodental and inferred body size differences. Therefore, even if we assume that the larger specimens are males and the smaller specimens are females, there are no modern higher primate analogues that show a comparable pattern of within-species variation.

Inferences could be made about the social structure of *P. boisei* by atomizing its morphology and then comparing the predictions from each of the components (canine crown height, canine crown buccolingual width, body size, and so on), but Plavcan[87] suggested that the relationships among these variables in living higher primates are "not strong enough to make detailed inferences about mating systems or behavior on the basis of dimorphism alone." In a later paper, Plavcan[88] cautions against assuming that any living hominoid is a suitable analogue for early hominins with respect to predicting social structure.

LIFE HISTORY

The stages through which an individual passes during its lifetime are collectively termed its life history. Knowledge of the pattern and timing of an organism's life history can reveal information about its strategies for survival and reproduction. Unfortunately, little is known about the life history of *P. boisei*. Here we discuss why neither life-history variables (ones directly related to life history) nor life-history-related variables (ones indirectly related to life history) are currently able to tell us much about life history in this taxon.

Life-History Variables

Age at weaning is an indicator of relative offspring dependence and maternal investment. Because lactation suppresses ovulation in great apes and humans, it is also a determinant of interbirth interval. Among living primates, weaning appears to coincide with M_1 eruption,[89] but within the hominin clade some evidence suggests that weaning may predate M_1 emergence.[90] This is certainly the case for modern human groups who wean infants at about the age of 2.5 years, whereas the first permanent mandibular molar does not erupt until children are approximately 6 years old. Determination of age at weaning in fossil hominins has thus been based on an assessment of the degree and timing of the deciduous dental attrition associated with dietary supplementation. Aiello, Montgomery, and Dean[91] 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 *Au. afarensis*. However, these authors acknowledged that this difference could be related to either an earlier age at weaning or to differences in diet.

Life-History-Related Variables

Body size

There are strong correlations between body size and life-history variables such as gestation length, weaning age, age at first reproduction, interbirth interval, and maximum life span across subfamilies of primates.[92] Researchers who have used cranial

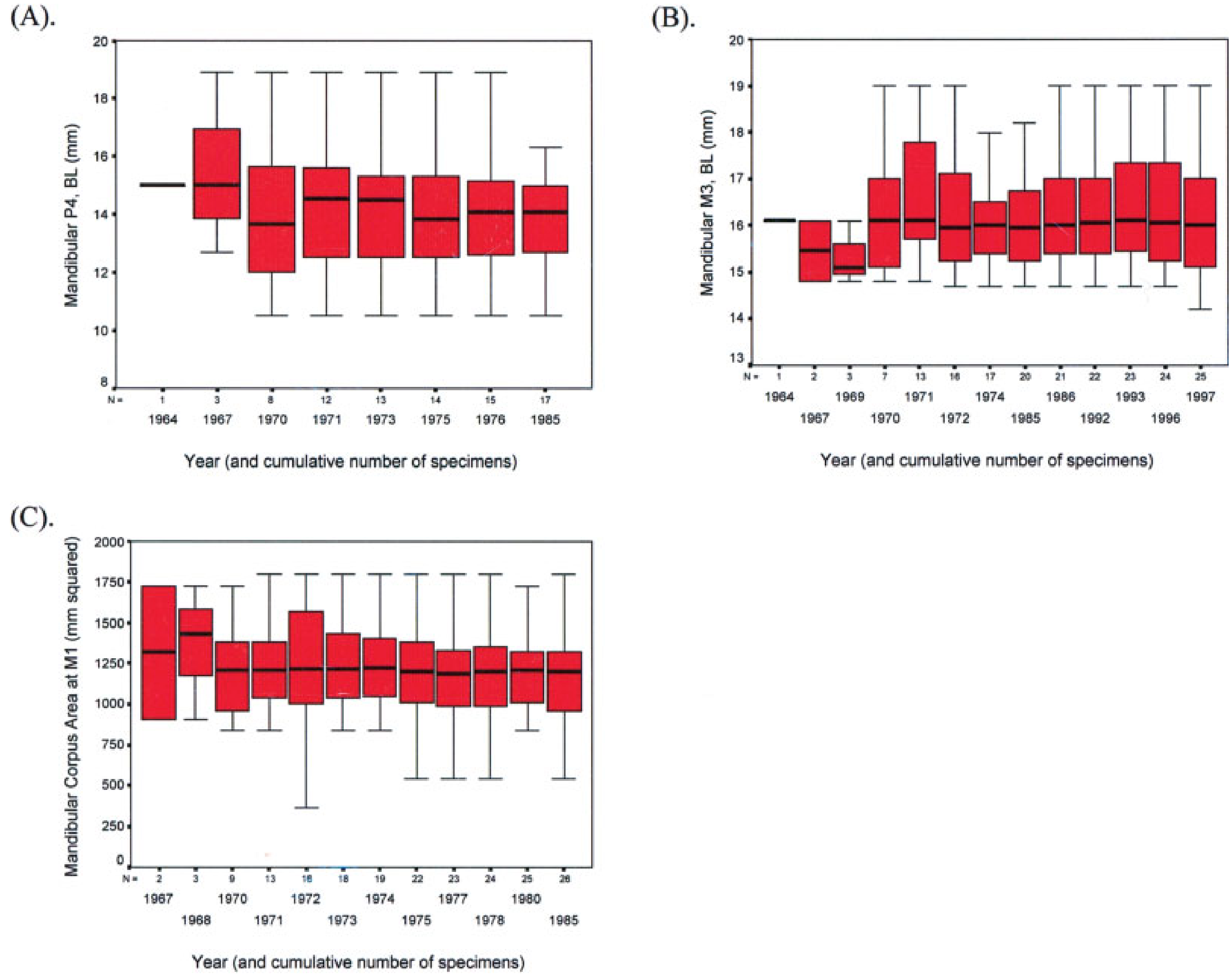


Figure 11. The effect of additional specimens on three *P. boisei* dentognathic variables including (A) P_4 buccolingual breadth, (B) M_3 buccolingual breadth, and (C) mandibular corpus area (h × w) at M_1. Variables were chosen based on the number of available fossil specimens. For the three variables selected, the median values stabilize after approximately 7 to 15 specimens have been assessed. The dark horizontal line across each box is the median value; the box itself represents the interquartile range (middle 50%); the lines (whiskers) show the complete range (excluding outliers). (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

variables as proxies for body mass[93,94] have concluded that the estimated body mass of *P. boisei* is similar to that of archaic hominin taxa in the genus *Australopithecus*. Thus, differences in body mass cannot be used to account for any differences in predictions about the life history of *P. boisei* and other archaic hominins.

Brain size

Brain mass has also been shown to be highly correlated with many life-history variables.[92] Brain mass can be derived from brain volume, and brain volume can be derived from endocranial volume if allowance is made for the space occupied by the endocranial vasculature and the intracranial extracerebral cerebrospinal fluid. The mean of the ten endocranial volumes in the *P. boisei* sample is 481 cm^3, with a range of 400–545 cm^3. This range substantially overlaps with that of extant nonhominin higher primates and that of archaic hominins, including *H. habilis sensu stricto*.[95] Like body size, therefore, brain size is not very useful in elucidating life-history differences between *P. boisei* and closely related taxa.

Dental ontogeny

In some respects, such as incisor crown formation and eruption sequence, dental development in *P. boisei* resembles that of modern humans, while in others, such as the rate of root formation, it resembles that of chimpanzees. In still other respects, dental development in *P. boisei* is unique (for example, enamel formation in the postcanine teeth). The premolar and molar crowns of *P. boisei* take the same time, or less, to form than do those of modern humans and chimps, despite the fact that *P. boisei* crowns are approximately twice the size of 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.[96] We need more information before we can determine whether these differences are due to selection operating on life history, on diet, or on a combination of the two.

TRACKING MORPHOLOGICAL VARIABLES OVER TIME

Most contributions to the paleoanthropological literature either focus on the latest tranche of fossil discoveries or look in depth at the fossil evidence from a single site or from a particular region or body part. Relatively few studies focus attention on the accumulated hypodigm of a single early hominin taxon.[3,97]

Mandibular and dental remains are particularly well represented in the hypodigm of *P. boisei* and for some parameters the sample sizes ($N > 20$) are respectable, at least by paleontological standards. For some variables, therefore, it is possible to investigate how much the sample parameters of *P. boisei* have changed as the sample sizes have increased. We track the parameters of three such variables (Fig. 11). These variables have been chosen at random to the extent that they happen to be the ones represented by the largest number of specimens. The parameters of all three variables are remarkably consistent, and other variables with smaller hypodigms show comparable patterns. The two largest samples are for M_3 buccolingual breadth and mandibular corpus area at M_1. There is very little change in the sample parameters once the hypodigm reaches $N =$ ca. 10. These data contradict the notion that paleoanthropological samples are generally too small to support claims of morphological distinctiveness. Richard Smith has provided a chastening demonstration that this is the case for very small samples,[98] but our *post-hoc* investigation of one early hominin taxon should encourage field researchers and funding agencies to recognize that even relatively modest-sized samples can provide useful information about the original population from which the fossil sample was drawn. Larger samples are still important, however. As this review has highlighted, larger samples of *P. boisei* fossils have increased our understanding about morphological character combinations, the geographic and temporal range of the taxon, and variation in nonmetrical traits such as the patterns of ectocranial cresting.

The premolar and molar crowns of *P. boisei* take the same time, or less, to form than do those of modern humans and chimps, despite the fact that *P. boisei* crowns are approximately twice the size of 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.

CONCLUSIONS AND PROSPECTS

Half a century of collection and analysis has vindicated some of the initial assessments of the taxonomy of *P. boisei* by Leakey[8] and Tobias.[36] For example, two judgments of Leakey[8] appear to have been supported by the new evidence. First, only Robinson[34] has seriously doubted the wisdom of establishing a new taxon for the *P. boisei* hypodigm. Second, although support for recognizing *P. boisei* and its ilk at the level of a separate "sub-family Australopithecinae"[8] has waned, few would demur from the judgment that *P. boisei* belongs to the same general grade of archaic hominins as do taxa presently included in the genera *Australopithecus* and *Kenyanthropus,* albeit as the most derived member of that grade grouping. Two judgments about the phylogenetic relationships of *P. boisei* have fared less well. First, the enlargement of the hypodigm has effectively falsified Louis Leakey's claim that OH 5 "differs from both *Australopithecus* and *Paranthropus* much more than these two genera differ from each other."[8] Because phylogenetic analyses seldom, if ever, put *H. habilis sensu stricto* and *P. boisei* in the same clade, Phillip Tobias'[36] suggestion that it is "unlikely" that *P. boisei* and *H. habilis* "were genetically isolated" (p. 244) can be refuted.

This review highlights how much remains to be learned about most aspects of *P. boisei*'s paleobiology, including its diet, life history, tool use, temporal and geographical range, phylogenetic relationships, and even what it looked like from the neck down. So how can we improve our understanding of the paleobiology of *P. boisei*? The first priority is to find at least one, and preferably several, taxonomically unambiguous associated skeletons. This would help researchers work out which limbs go with which heads at Olduvai and Koobi Fora. The second priority is to extract more information about the functional morphology of *P. boisei*'s masticatory system, and thus about its diet, from the fossil record. Third, we need to clarify the evolutionary relationships between *P. boisei* and the other "robust" taxa. Fourth on the list would be a way of teasing out what aspects of dental growth and development are diet-related and what aspects carry a signal about life history. Finally, and perhaps the trickiest of all, is the task of finding ways of establishing whether, and to what extent, *P. boisei* was a cultural animal. Did its cultural repertoire go beyond that of a modern chimpanzee? If so, how did its culture differ from that of the other less megadont archaic hominins?

The rate of discovery is on the decline for *P. boisei* fossils (Fig. 6), probably due mainly to changes in research priorities within paleoanthropology. Nevertheless, there is much to learn about this intriguing taxon, and we need both additional fossils and new analytical methods and strategies in order to move forward.

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REFERENCES

1 Wood BA. 1991. Koobi Fora research project, vol. 4. Hominid cranial remains. Koobi Fora Research Project, series ed. Leakey RE. Oxford: Clarendon Press.

2 Strait DS, Grine FE. 2004. Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. J Hum Evol 47:399–452.

3 Kimbel WH, Rak Y, Johanson DC. 2004. The skull of *Australopithecus afarensis*. Oxford: Oxford University Press.

4 Feibel CS, Brown FH, McDougall I. 1989. Stratigraphic context of fossil hominids from the Omo group deposits: Northern Turkana Basin, Kenya and Ethiopia. Am J Phys Anthropol 78:595–622.

5 McDougall I, Brown FH. 2006. Precise ^{40}Ar/^{39}Ar geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. J Geol Soc London 163:205–220.

6 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. The Illustrated London News 232:1104–1105.

7 Leakey LSB. 1958. Recent discoveries at Olduvai Gorge, Tanganyika. Nature 181:1099–1103.

8 Leakey LSB. 1959. A new fossil skull from Olduvai. Nature 184:491–493.

9 Leakey LSB, Leakey MD. 1964. Recent discoveries of fossil hominids in Tanganyika, at Olduvai and near Lake Natron. Nature 202:5–7.

10 Arambourg C, Coppens Y. 1968. Decouverte d'un australopithecien nouveau dans les Gisements de L'Omo (Ethiopie). S Afr J Sci 64:58–59.

11 Coppens Y. 1978. Evolution of the hominids and of their environment during the Plio-Pleistocene in the lower Omo Valley, Ethiopia. In: Bishop WW, editor. Geological background to fossil man. Edinburgh: Scottish Academic Press. p 499–506.

12 Coppens Y. 1980. The differences between *Australopithecus* and *Homo;* preliminary conclusions from the Omo research expedition's studies, ed. Konigsson LK. Oxford, Pergamon.

13 Coppens Y, Sakka M. 1983. Un nouveau crane d'australopitheque. Evolutive Morphogenese du Cranie et Anthropogenese. Paris, CNRS. p 185–194.

14 Alemseged ZY, Coppens Y, Geraads D. 2002. Hominid cranium from Omo: description and taxonomy of Omo-323-1976-896. Am J Phys Anthropol 117:103–112.

15 Gowlett JAJ, Harris JWK, Walton D, Wood BA. 1981. Early archaeological sites, hominid remains and traces of fire from Chesowanja, Kenya. Nature 294:125–129.

16 Leakey REF, Walker A. 1988. New *Australopithecus boisei* specimens from East and West Lake Turkana, Kenya. Am J Phys Anthropol 76:1–24.

17 Brown B, Walker A, Ward CV, Leakey RE. 1993. New *Australopithecus boisei* calvaria from East Lake Turkana, Kenya. Am J Phys Anthropol 91:137–159.

18 Prat S, Brugal J-P, Roche H, Texier P-J. 2003. Nouvelles découvertes de dents d'hominidés dans le membre Kaitio de la formation de Nachukui (1, 65-1, 9 Ma), Ouest du lac Turkana (Kenya). CR Palevol 2:685–693.

19 Walker AC, Leakey RE, Harris JM, Brown FH. 1986. 2.5 Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. Nature 322:517–522.

20 Suwa G, et al. 1997. The first skull of *Australopithecus boisei*. Nature 389:489–492.

21 Kullmer O, Sandrock O, Abel R, Schrenk F, Bromage TG, Juwayeyi YM. 1999. The first *Paranthropus* from the Malawi Rift. J Hum Evol 37:121–127.

22 Leakey REF. 1970. New hominid remains and early artefacts from North Kenya. Nature 226:223–224.

23 Wood BA, Wood CW, Konigsberg LW. 1994. *Paranthropus boisei*: an example of evolutionary stasis? Am J Phys Anthropol 95:117–136.

24 Wood B, Lieberman DE. 2001. Craniodental variation in *Paranthropus boisei*: a developmental and functional perspective. Am J Phys Anthropol 116:13–25.

25 Leakey REF. 1971. Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. Nature 231:241–245.

26 Robinson JT. 1972. The bearing of East Rudolf fossils on early hominid systematics. Nature 240:239–240.

27 Wood BA, Li Y, Willoughby C. 1991. Intraspecific variation and sexual dimorphism in cranial and dental variables among higher primates and their bearing on the hominid fossil record. J Anat 174:185–205.

28 Grausz HM, Leakey RE, Walker AC, Ward CV. 1988. Associated cranial and postcranial bones of *Australopithecus boisei*. In: Grine FE, editor. Evolutionary history of the "robust" Australopithecines. New York: Aldine de Gruyter. p 127–132.

29 Day MH. 1969. Femoral fragment of a robust australopithecine from the Olduvai Gorge, Tanzania. Nature 221:230–233.

30 Wood BA. 1974. Evidence on the locomotor pattern of *Homo* from Early Pleistocene of Kenya. Nature 251:135–136.

31 Wood BA. 1974. Olduvai Bed I post-cranial fossils: a reassessment. J Hum Evol 3:373–378.

32 Gebo DL, Schwartz GT. 2006. Foot bones from Omo: implications for hominin evolution. Am J Phys Anthropol 129:499–511.

33 Johanson DC, et al. 1987. New partial skeleton of *Homo habilis* from Olduvai gorge, Tanzania. Nature 327:205–209.

34 Robinson JT. 1960. The affinities of the new Olduvai australopithecine. Nature 186:456–458.

35 Suwa G. 1988. Evolution of the "robust" australopithecines in the Omo succession: evidence from mandibular premolar morphology. In: Grine FE, editor. Evolutionary history of the "robust" australopithecines. New York: Aldine de Gruyter. p 199–222.

36 Tobias PV. 1967. Olduvai Gorge, vol. 2. The cranium and maxillary dentition of *Australopithecus* (*Zinjanthropus*) *boisei*. Cambridge: Cambridge University Press.

37 Delson E. 1997. One skull does not a species make. Nature 389:445–446.

38 Menter CG, Kuykendall KL, Keyser AW, Conroy GC. 1999. First record of hominid teeth from the Plio-Pleistocene site of Gondolin, South Africa. J Hum Evol 37:299–307.

39 Keyser AW, Menter CG, Moggi-Cecchi J, Pickering TR, Berger LR. 2000. Drimolen: a new hominid-bearing site in Gauteng, South Africa. S Afr J Sci 96:193–197.

40 Constantino P, Wood B. 2004. *Paranthropus* paleobiology. Miscelánea en homenaje a Emiliano Aguirre. Madrid: Museo Arqueolócico Regional. p 136–151.

41 Dean MC. 1988. Growth of teeth and development of dentition in *Paranthropus*. In: Grine FE, editor. Evolutionary History of the "Robust" Australopithecines. New York, Aldine de Gruyter. p 43–53.

42 Groves CP. 1989. A theory of human and primate evolution. Oxford: Clarendon Press.

43 Silverman N, Richmond B, Wood B. 2001. Testing the taxonomic integrity of *Paranthropus boisei sensu stricto*. Am J Phys Anthropol 115:167–178.

44 Wood BA. 1988. Are "robust" australopithecines a monophyletic group? In: Grine FE, editor. Evolutionary history of the "robust" Australopithecines. New York: Aldine de Gruyter. p 269–284.

45 Corruccini RS. 1994. How certain are hominoid phylogenies? The role of confidence intervals in cladistics. In: Corruccini RS, Ciochon RL, editors. Integrative paths to the past: paleoanthropological advances in honor of F. Clark Howell. Englewood Cliffs: Prentice Hall. p 167–183.

46 Strait DS, Grine FE, Moniz MA. 1997. A reappraisal of early hominid phylogeny. J Hum Evol 32:17–82.

47 Wood BA, Chamberlain AT. 1986. *Australopithecus:* grade or clade? In: Wood B, Martin L, Andrews P, editors. Major topics in primate and human evolution. Cambridge: Cambridge University Press. p 220–248.

48 Skelton RR, McHenry HM. 1992. Evolutionary relationships among early hominids. J Hum Evol 23:309–349.

49 Maglio VJ. 1975. Origin and evolution of the Elephantidae. Trans Am Philos Soc 63:1–149.

50 Vrba ES. 1979. Phylogenetic analysis and classification of fossil and recent Alcelaphini (Mammalia: Bovidae). Biol J Linnaean Soc 11:207–228.

51 Vrba ES. 1984. Evolutionary pattern and process in the sister-group Alcelaphini-Aepycerotini (Mammalia: Bovidae). In: Eldredge N, Stanley SM, editors. Living fossils. New York: Springer-Verlag. p 62–79.

52 Patterson C. 1982. Morphological characters and homology. In: Joysey KA, Friday AE, editors. Problems of phylogenetic reconstruction. London: Academic Press. p 21–74.

53 Suwa G, Wood BA, White TD. 1994. Further analysis of mandibular molar crown and cusp areas in Pliocene and Early Pleistocene hominids. Am J Phys Anthropol 93:407–426.

54 Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. 1999. *Australopithecus garhi:* a new species of early hominid from Ethiopia. Science 284:629–635.

55 Shipman P, Harris JM. 1988. Habitat preference and paleoecology of *Australopithecus boisei* in eastern Africa. In: Grine FE, editor. Evolutionary history of the "robust" Australopithecines. New York: Aldine de Gruyter. p 343–381.

56 Reed KE. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J Hum Evol 32:289–322.

57 Nagaoka S, Katoh S, Wolde Gabriel G, Sato H, NaKaya H, Beyene Y, Suwa G. 2005. Lithostratigraphy and sedimentary environments of the hominid-bearing Pliocene-Pleistocene Konso Formation in the southern Main Ethiopian Rift, Ethiopia. Palaeogeogr Palaeocl 216: 333–357.

58 Schrenk F, Bromage TG, Gorthner A, Sandrock O. 1995. Paleoecology of the Malawi Rift: vertebrate and invertebrate faunal contexts of the Chiwondo Beds, northern Malawi. J Hum Evol 28:59–70.

59 Leakey LSB, Tobias PV, Napier JR. 1964. A new species of the genus *Homo* from Olduvai Gorge. Nature 202:7–9.

60 Isaac GL. 1984. The archaeology of human origins: studies of the Lower Pleistocene in East Africa 1971–1981. Advances in World Archaeol 3:1–87.

61 Brain CK, Churcher CS, Clark JD, Grine FE, Shipman P, Susman RL, Turner A, Watson V. 1988. New evidence of early hominids, their culture and environment from the Swartkrans cave, South Africa. S Afr J Sci 84:828–835.

62 Clark JD. 1990. The earliest cultural evidences of hominids in southern and south central Africa. In: Sperber G, editor. New York: Wiley-Liss. p 1–15.

63 Susman RL. 1991. Who made the Oldowan tools? Fossil evidence for tool behavior in Plio-Pleistocene hominids. J Anthropol Res 47:129–151.

64 Wood BA. 1997. The oldest whodunnit in the world. Nature 385:292–293.

65 Susman RL. 1988. Hand of *Paranthropus robustus* from Member 1, Swartkrans: fossil evidence for tool behaviour. Science 240:781–784.

66 Kuman K, Clarke RJ. 2000. Stratigraphy, artifact industries and hominid associations for Sterkfontein, Member 5. J Hum Evol 38:827–847.

67 Dean MC, Wood BA. 1981. Metrical analysis of the basicranium of extant hominoids and *Australopithecus*. Am J Phys Anthropol 54:63–71.

68 Dean MC, Wood BA. 1982. Basicranial anatomy of Plio-Pleistocene hominids from East and South Africa. Am J Phys Anthropol 59:157–174.

69 Hylander WL. 1975. Incisor size and diet in anthropoids with special reference to Cercopithecidae. Science 189:1095–1098.

70 Lucas PW, Corlett RT, Luke DA. 1986. Postcanine tooth size and diet in anthropoid primates. Z Morphol Anthropol 76:253–276.

71 Kay RF. 1975. The functional adaptations of primate molar teeth. Am J Phys Anthropol 43:195–216.

72 Hatley T, Kappelman J. 1980. Bears, pigs, and Plio-Pleistocene hominids: a case for the exploitation of belowground food resources. Hum Ecol 8:371–387.

73 Laden G, Wrangham R. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. J Hum Evol 49:482–498.

74 Grine FE, Martin LB. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine FE, editor. Evolutionary history of the "robust" australopithecines. New York: Aldine de Gruyter. p 3–42.

75 Gantt DG, Rafter JA. 1998. Evolutionary and functional significance of hominoid tooth enamel. Connect Tissue Res 39:195–206.

76 Rak Y. 1988. On variation in the masticatory system of *Australopithecus boisei*. In: Grine FE, editor. Evolutionary history of the "robust" Australopithecines. New York: Aldine de Gruyter. p 193–198.

77 Tobias PV. 1963. Cranial capacity of *Zinjanthropus* and other australopithecines. Nature 197:743–746.

78 Demes B, Creel N. 1988. Bite force, diet, and cranial morphology of fossil hominids. J Hum Evol 17:657–670.

79 Walker AC. 1981. Diet and teeth: dietary hypotheses and human evolution. Philos Trans R Soc Lond B 292:57–64.

80 Hylander WL. 1988. Implications of *in vivo* experiments for interpreting the functional significance of "robust" australopithecine jaws. In: Grine FE, editor. Evolutionary history of the "robust" Australopithecines. New York: Aldine de Gruyter. p 55–83.

81 Wood BA, Aiello LC. 1998. Taxonomic and functional implications of mandibular scaling in early hominins. Am J Phys Anthropol 105: 523–538.

82 Walker A, personal communication. 2006.

83 Grine FE. 1981. Trophic differences between gracile and robust *Australopithecus:* a scanning electron microscope analysis of occlusal events. S Afr J Sci 77:203–230.

84 Scott RS, Ungar PS, Bergstrom TS, Brown CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436:693–695.

85 Boaz NT, Hampel J. 1978. Strontium content of fossil tooth enamel and diet of early hominids. J Paleontol 52:928–933.

86 Sillen A, Hall G, Armstrong R. 1995. Strontium calcium ratios (Sr/Ca) and strontium isotopic ratios (87Sr/86Sr) of *Australopithecus robustus* and *Homo sp.* in Swartkrans. J Hum Evol 28:277–285.

87 Plavcan JM. 2000. Inferring social behavior from animal dimorphism in the fossil record. J Hum Evol 39:327–344.

88 Plavcan JM. 2003. Scaling relationships between craniofacial sexual dimorphism and body mass dimorphism in primates: implications for the fossil record. Am J Phys Anthropol 120:38–60.

89 Smith BH. 1991. Age of weaning approximate age of emergence of the first permanent molar in non-human primates. Am J Phys Anthropol (suppl):163–164.

90 Dean MC. 2000. Progress in understanding hominoid dental development. J Anat 197:77–101.

91 Aiello LC, Montgomery C, Dean C. 1991. The natural history of deciduous tooth attrition in hominoids. J Hum Evol 21:397–412.

92 Harvey PH, Clutton-Brock TH. 1985. Life history variation in primates. Evolution 39:559–581.

93 Aiello L, Wood B. 1994. Cranial variables as predictors of hominine body mass. Am J Phys Anthropol 95:409–426.

94 Kappelman J. 1996. The evolution of body mass and relative brain size in fossil hominids. J Hum Evol 30:243–276.

95 de Sousa A, Wood B. 2007. The hominin fossil record and the emergence of the modern human central nervous system. In: Kaas JH, editor. The evolution of primate nervous systems. Oxford: Elsevier. p 291–336.

96 Beynon A, Wood B. 1987. Patterns and rates of enamel growth in the molar teeth of early hominids. Nature 326:493–496.

97 Weidenreich F. 1935. The *Sinanthropus* population of Choukoutien (locality) with a preliminary report on new discoveries. Bull Geo Soc China 14:427–466.

98 Smith RJ. 2005. Species recognition in paleoanthropology: implications of small sample sizes. In: Lieberman DE, Smith RJ, Kelley J, editors. Interpreting the past: essays on human, primate, and mammal evolution in honor of David Pilbeam. Boston: Brill Academic Publishers. p 207–219.

99 Delson E, Tattersall I, Van Couvering JA, Brooks AS, editors. 2000. Encyclopedia of human evolution and prehistory, 2nd ed. New York: Garland Publishing.

100 Tobias PV. 1991. Olduvai Gorge, vol. 4. The skulls, endocasts and teeth of *Homo habilis*. Cambridge: Cambridge University Press.