

‘A tale of two taxa’

Bernard Wood

CASHP, Department of Anthropology, 2110 G St NW, Washington, DC 20052, USA
e-mail: bwood@gwu.edu

Phillip Tobias was intimately involved in the systematic analysis of two early hominin taxa, *Zinjanthropus* (now *Paranthropus*) *boisei* and *Homo habilis*. This paper compares and contrasts the way the fossil evidence for these taxa that has accumulated over the past half century has altered our perceptions of them. There is more consensus about the interpretation of *P. boisei* than there is about *H. habilis*. This may be because the former almost certainly belongs to a derived extinct hominin subclade.

INTRODUCTION

Phillip Tobias' reputation as a scientist rests on his achievements in many sub-fields of biological anthropology, but his contributions to paleoanthropology are pre-eminent. Phillip Tobias has been actively involved in the recovery of the fossil evidence for hominin evolution from southern African cave sites, especially at Sterkfontein, but he has also made substantial contributions to the analysis of the hominin fossil record. This short review focuses on his involvement with the analysis of the fossil record of two early hominin taxa, *Zinjanthropus boisei* and *Homo habilis*.

It is exactly 50 and 46 years, respectively, since the first fossil evidence of *Z. boisei* and *H. habilis* was recovered from Olduvai Gorge, Tanzania. This contribution introduces the two taxa, and shows how our perceptions of them have changed, or not changed, through time. It also examines to what extent any shifts in interpretation have been influenced by the accumulation of new fossil evidence, or by changes in analytical philosophy.

ZINJANTHROPUS BOISEI

Fossil evidence

With hindsight, the first evidence of an *Paranthropus robustus*-like hominin from East Africa was OH 3, a specimen comprising two early hominin teeth (a deciduous mandibular canine and a large molar) found in 1955 at locality BK in Lower Bed II, Olduvai Gorge in Tanzania (Leakey, 1958). However, the taxonomy of OH 3 was uncertain until the discovery in 1959 of OH 5, a well-preserved adolescent cranium from FLK at the base of Olduvai Gorge's Bed I (Leakey, 1959). Louis Leakey took the view that the new cranium differed "from both *Australopithecus* and *Paranthropus* much more than these two genera differ from each other" (Leakey, 1959: 491) and consequently he created a new genus and species — *Zinjanthropus boisei* Leakey, 1959 — for the OH 5 cranium. Thereafter, other specimens from Olduvai Gorge have been referred to the same taxon, including a fragmented cranium OH 30 and several isolated teeth (OH 26, 32, 38 and 46).

By the time Louis and Mary Leakey made their announcement in April 1964 of the discovery of a robust, megadont, *Z. boisei*-compatible mandible from the Peninj site close to the western shore of Lake Natron (Leakey & Leakey, 1964), Louis Leakey had relegated *Zinjanthropus* to the status of a subgenus of *Australopithecus* (Leakey *et al.*, 1964). Three years later Tobias (Tobias, 1967) went further still and abandoned even the subgeneric distinction and transferred the hypodigm of *Zinjanthropus boisei* Leakey, 1959 to the genus *Australopithecus* as *Australopithecus boisei* (Leakey, 1959) Tobias, 1967. Subse-

quently, when evidence began to accumulate supporting the hypothesis that *P. robustus* and *A. boisei* might be sister taxa, some researchers decided to use the genus *Paranthropus* for the taxa within that clade. Thus, *A. robustus* would revert to *P. robustus*, and *A. boisei* would become *Paranthropus boisei* (Leakey, 1959) Robinson, 1960.

In the meantime, fossil evidence assigned to *P. boisei* has been recovered from the Omo region (specifically from the Shungura Formation) and Konso Gardula (now called Konso) in Ethiopia, from what was initially called East Rudolf (and which is now referred to as East Turkana or Koobi Fora), West Turkana and Chesowanja in Kenya, and from Malema in Malawi.

Changing interpretations

Cranial morphology

Although the OH 5 cranium resembled crania attributed to *P. robustus*, it was soon apparent that it was significantly different and distinctive, and its distinctiveness is still apparent half a century, and many additional specimens, later.

There are two reasons for the distinctiveness of *P. boisei*. The first is that it displays a substantial amount of apparently autapomorphic morphology. This is morphology only found in this hominin taxon. Autapomorphies of *P. boisei* include the extensive bony overlap at the joint between the squamous part of the temporal bone and the lateral border of the parietal (Tobias, 1967), the morphology of the midface and malar regions (Tobias, 1967; Rak, 1983), and the degree of molarization of the premolars (Tobias, 1967; Suwa, 1988).

The second reason that *P. boisei* is distinctive is that it displays novel combinations of features. These include the degree of disparity between the size of the crowns of the canines and those of the postcanine teeth (Tobias, 1967), and the combination of a coronally-orientated petrous temporal bone and a small neurocranium (Tobias, 1967; Dean & Wood, 1982). Modern humans and archaic *Homo* all have a coronally-orientated petrous temporal bone, and australopithecids have small neurocrania, but only in *P. boisei* are they found in combination.

Intraspecific variation

A well-preserved specimen like OH 5 provides detailed information about morphology, but it cannot provide information about the extent and nature of variation within the taxon to which it belongs. Subsequent discoveries at sites other than Olduvai Gorge have expanded our knowledge of intraspecific cranial variation within *P. boisei* in two main ways. First, the recovery of several crania that have the same general overall morphology as OH 5 (e.g. KNM-ER 406, 733, 13750 and 23000; KGA 10-525) have provided researchers with an understanding

of which morphology of *P. boisei* really is taxonomically distinctive and relatively invariant [e.g. postcranial tooth crown and root morphology (Wood & Abbott, 1983; Wood *et al.*, 1988)], and which morphology previously regarded as 'distinctive' (e.g. the location of the highest point of the sagittal crests) turns out to vary among individuals within *P. boisei* (Wood, 1991; Brown *et al.*, 1993). Second, as additions were made to the hypodigm of *P. boisei*, especially from Koobi Fora, it became apparent from the mandibular and dental evidence that *P. boisei* subsumed substantial variation in overall size. But even though the OH 5-like crania listed above differ in morphological detail they all display ectocranial crests and by analogy with extant higher primates they all seem to be examples of large-bodied males. If one of the factors contributing to the substantial intraspecific size variation seen in the mandibles and teeth was sexual dimorphism, where were the crania belonging to the smaller-bodied female individuals, and what did they look like? It is probable that crania such as KNM-ER 407 and 732, and KNM-WT 17400 sample smaller-bodied females. The size differential between these crania and the presumed male crania is consistent with the mandibular evidence, and the results of multivariate analytical comparisons suggest that the shape differences between the two sets of crania are similar to those between male and female crania of the extant African ape clade (Wood, 1991).

Postcranial evidence

There is no associated skeleton that can reliably be linked with *P. boisei*. The partial associated skeleton KNM-ER 1500 has been assigned to *P. boisei* (Grausz *et al.*, 1988; Mc Henry & Coffing, 2002), but the morphology used to do so, the rounded profile of the base of a mandibular corpus fragment, is not autapomorphic for *P. boisei*. A rounded mandibular base is also found in some mandibles belonging to *Homo habilis sensu lato*. For different, but probably equally tenuous, reasons researchers have suggested that KNM-ER 1464, a talus, and OH 36, an ulna (Aiello *et al.*, 1999), may belong to *P. boisei*.

Taxonomy

The only taxonomic controversies relating to *P. boisei* involve the boundary of its hypodigm, its integrity, and the distinction between *P. robustus* and *P. boisei*.

The first of the three controversies concerns the placement of the boundary of the hypodigm of *P. boisei*. Should the hypodigm of *P. boisei* be interpreted less inclusively so as to exclude the hypodigm of *P. aethiopicus*, in which case we should refer to the taxon as *P. boisei sensu stricto*? Or should it be interpreted more inclusively to subsume the hypodigm of *P. aethiopicus*, in which case we should refer to the single taxon as *P. boisei sensu lato*? One of the reasons for retaining a taxonomic distinction between *P. boisei* and *P. aethiopicus* is that from ca. 2.3 Myr (the boundary between *P. aethiopicus* and *P. boisei*) until the time *P. boisei sensu stricto* disappears from the fossil record, the latter taxon shows a remarkable degree of morphological stasis (Wood *et al.*, 1994). Furthermore, none of the differences between *P. aethiopicus* and *P. boisei sensu stricto* continue as trends within the latter taxon.

The second controversy relates to the integrity of the taxon. Dean (1988) and Groves (1989) have both suggested that the size variation within *P. boisei*, and particularly variation in mandible size, exceeds that to be expected within a single species. However, when account is taken of taphonomic factors, variation in mandibular size was not found to be excessive (Silverman *et al.*, 2001).

The third debate is whether the differences between

P. robustus and *P. boisei* justify them being treated as separate species. For example, finds such as KGA 10-525 and KNM-ER 23000 have caused some researchers (e.g. Delson, 1997) to call for a re-examination of the distinction between *P. boisei* and *P. robustus*. Suwa *et al.* (1997) suggested that the Konso skull includes traits, such as a zygomaticomaxillary fossa and a median maxillary torus, that are found in *P. robustus*, but not in the *Paranthropus* fossil record from East Africa. However, Wood & Lieberman (2001) found no evidence that the Konso skull had added significantly to the variation within the hypodigm of *P. boisei*. A second reason to reconsider the taxonomy of East and southern African *Paranthropus* is that one of the hominin teeth from the southern African site of Gondolin exceeds the size range known for *P. robustus*, but it is within the size range known for *P. boisei* (Menter *et al.*, 1999). However, the results of a recent metrical analysis suggest that the southern and East African regional hypodigms of *Paranthropus* are still significantly different, and thus there continue to be good reasons to maintain the specific distinction between *P. robustus* and *P. boisei* (Constantino & Wood, 2004).

HOMO HABILIS

Fossil evidence

A few weeks before they found the OH 5 cranium in 1959, the Leakeys had recovered OH 4, a hominin lower third molar embedded in a mandible fragment, also from Bed I, but at locality MK, in Olduvai Gorge, Tanzania. Not surprisingly, the unpromising looking fragment was laid aside while the Leakeys concentrated on reconstructing and assessing OH 5. Later in the same year they recovered OH 6, consisting of a hominin lower premolar, an unerupted upper molar tooth and some cranial fragments, from an erosion gully below the site where OH 5 was discovered, and the following year OH 7, a partial skull cap, mandible and hand bones, was recovered from locality FLKNN, also in Olduvai Gorge's Bed I.

The new material was evidently from a hominin taxon that was very different from the one to which OH 5 belonged. The neurocranium was larger than that of OH 5, and it showed no sign of OH 5's distinctive morphology, such as the marked postorbital constriction and the ectocranial crests. In 1960 the Leakey's also recovered postcranial bones including the skeleton of a hominin foot, OH 8, so John Napier, an expert in the evolution of locomotion, was invited to be the third member of the team that assessed the significance of the new Olduvai discoveries.

The three researchers decided that OH 4, 6, 7 and 8 belonged to the same taxon, and they concluded that the new taxon, and not what was then still called *Z. boisei*, was the maker of the crude stone tools that had been found in Bed I. They reasoned the hand bones of OH 7 were from a hand that was capable of the dexterity required to make the Oldowan stone tools, and they considered that the morphology of the OH 8 foot was consistent with it being the foot of a hominin capable of the type of striding bipedal gait used by modern humans. The researchers reasoned that the preserved features of the second Olduvai early hominin set it apart from the early hominin taxa known from the southern African cave sites. They also concluded that, despite its small endocranial volume, many of the preserved features of the second Olduvai early hominin were like those of later *Homo*. Thus, they decided to allocate the fossils to a new species, within the genus *Homo*, as *Homo habilis* Leakey, Tobias and Napier, 1964.

Since then hominin fossils found at Olduvai, and at Koobi Fora and Hadar in East Africa, and from Sterkfontein and

possibly Swartkrans (e.g. Grine, 2001) and Drimolen in southern Africa have, with varying degrees of conviction, been added to the hypodigm, both formally as *H. habilis* and informally as 'early *Homo*'.

Changing interpretations

Cranial morphology

As material from Koobi Fora was steadily being added to the unofficial hypodigm of *H. habilis*, researchers began to question whether a single taxon could reasonably subsume all that variation. However, there was no unanimity about the best way to sort the *H. habilis sensu lato* hypodigm into two taxa. Some advocated splitting both the Olduvai and Koobi Fora hypodigms into 'large' and 'small' subsets (e.g. Stringer, 1986), whereas others advocated keeping the Olduvai subset of the hypodigm intact, adding some of the Koobi Fora 'early *Homo*' cranial remains to it, and recognizing a second species, *Homo rudolfensis*, within the Koobi Fora 'early *Homo*' cranial remains (e.g. Wood, 1991, 1993). Other researchers continue to hold the view that *H. habilis sensu lato* is still a 'good' taxon (Tobias, 1991).

Postcranial morphology

The allocation of postcranial specimens to *H. habilis* has always been, and still is, a controversial topic. There are only two candidates for associated skeletons of *H. habilis*, OH 62 and KNM-ER 3735, and the case is a relatively sound one for both of these specimens. But while the list of the preserved parts of the postcranial skeleton of OH 62 is an impressively long one, the condition of most of the fragments is so poor that little of value can be concluded about either the detailed anatomy or the limb proportions of OH 62 (Richmond *et al.*, 2002; Reno *et al.*, in press). Relatively little of the postcranial skeleton of KNM-ER 3735 is preserved.

Taxonomy

Since its announcement, *H. habilis* has rarely been out of the taxonomic spotlight. Initial reactions to the announcement of the new taxon were divided. Some researchers accepted the need for a new taxon, but did not agree with its placement in *Homo*. Others thought the new taxon was a chimera, a mixture of fossils that belonged to *Homo erectus* and others that properly belonged to *Australopithecus africanus*. As the years have passed taxonomic debates about *H. habilis* have tended to focus more on either the integrity of the taxon (which have been reviewed above), or its generic allocation. Should it be allocated to *Homo*, or to *Australopithecus*, or even to a new genus?

There are no set rules for determining how different a taxon, or taxa, should be from existing taxa for it/them to qualify for being a new genus. Wood & Collard (1999) suggested that for species to be in the same genus the species should be in the same clade and the same grade. The argument made by those who question its allocation to *Homo* is that it is not reliably linked to the *Homo* clade (i.e. relatively few characters link *H. habilis* with later *Homo*), and that functionally it resembles australopiths as much, if not more, than it does later *Homo* (Wood & Collard, 1999), but many researchers still regard *H. habilis* as a valid member of the *Homo* clade (e.g. Strait & Grine, 2004) and see no reason to doubt that what little can be reconstructed about its behavioral repertoire justifies its inclusion in *Homo*.

CONCLUSION

Although Phillip Tobias had no hand in the recovery of the fossil evidence for *P. boisei* and *H. habilis* he has played a crucial and influential role in the interpretation of that evidence. His

analysis of OH 5, the well-preserved type cranium of what many now refer to as *P. boisei*, is still a model of how attention to detail can extract a substantial amount of taxonomically and functionally useful information that most likely would have been ignored by a lesser morphologist.

No hominin for which we have a reasonable fossil record (i.e. excluding taxa such as *Australopithecus garhi*) has as much autapomorphic morphology as *P. boisei*. The task of describing this distinctive morphology and capturing its essence using non-metrical descriptions and novel metrical methods was a daunting one, and it is fortunate that Louis and Mary Leakey had the foresight to assign that task to Phillip Tobias. His exemplary monograph devoted to the OH 5 cranium (Tobias, 1967) is still the most comprehensive analysis of a single hominin fossil. It is a credit to the clarity, appropriateness, precision and accuracy of his descriptions, both non-metrical and metrical, that much of the vocabulary and many of the metrical variables he devised are still in use today. He described many of the features that we now interpret as autapomorphies of *P. boisei*.

Since the recovery of OH 3 many specimens have been added to the hypodigm of what is now usually referred to as *P. boisei*, and we have a relatively good understanding of its cranio-dental morphology. With respect to *P. boisei* it seems that we really might be 'dotting the i's' and 'crossing the t's' of the Parish Register, but that is a rash prediction. And because it is such a derived taxon, the advent of phylogenetic analysis has helped to emphasize the distinctiveness of its morphology, and thus has made it relatively easy to recognize in the hominin fossil record.

From the outset, *H. habilis* was a much more controversial taxon. There are many reasons for this. First, it is a less derived taxon than *P. boisei* and that makes the alpha taxonomy more difficult. Second, because it was claimed to be the ancestor of *H. erectus*, and thus the ancestor of modern humans, it inevitably received more attention than a taxon such as *P. boisei* that is consigned to a hominin clade which most likely made no direct contribution to later hominin evolution. Third, the behavioral interpretations made with respect to *H. habilis* were much more ambitious than those made with respect to *P. boisei*. Nonetheless, in spite of the continuing controversy, which shows no sign of dying down, Phillip Tobias' interpretations of the morphological evidence still stand. In his two-volume monograph on the Olduvai remains assigned to *H. habilis*, Tobias (1991) makes the case that there are a sufficient number of morphological threads (e.g. buccolingually-narrow mandibular postcanine tooth crowns) running through the material to justify regarding it as belonging to the same hypodigm, and this has since been confirmed (e.g. Wood, 1993). Other debates, however, are still unresolved. How much of the 'early *Homo*' material from Koobi Fora belongs to *H. habilis sensu stricto*? If not all of it does, is the balance part of the hypodigm of another 'early *Homo*' taxon, or an advanced australopith? What is the geographical range of *H. habilis sensu stricto*? Is there any evidence for *H. habilis sensu stricto* in southern Africa, or outside the African continent?

There is ample work to do to deepen our understanding of the paleobiology of both *P. boisei* and *H. habilis*, but thankfully the researchers involved will be able to draw on Phillip Tobias' substantial legacy of meticulous morphological analysis.

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