Chapter 8
Paranthropus: Where Do Things Stand?

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Abstract In 1960 John Robinson suggested that the newly defined species *Zinjanthropus boisei* should be transferred to the genus *ParanthropusParanthropus* (Broom 1938) as *Paranthropus boisei* (Leakey 1959). Since then fossil evidence of two hyper-megadont early hominin taxa has come to light. One of these taxa, *Paraustralopithecus aethiopicus* (Arambourg and Coppens 1968), has been added to the *Paranthropus* genus, whereas the second taxon, *Australopithecus garhi* (Asfaw et al. 1999), has been included in a different taxon, *Australopithecus*. This contribution will tease out why different alpha-taxonomic decisions were made about the generic affinities of *Paraustralopithecus aethiopicus* and *Australopithecus garhi*. It will also review the types of data that are now available for generating and testing hypotheses about the relationships of megadont and hyper-megadont hominins. On the basis of this review, in this paper we will suggest a hypothesis, or hypotheses, that are most consistent with the current fossil and contextual data from East and southern Africa.

Keywords Analogy • Biogeography • Convergence • Homoplasy • Eastern Africa • Megadontia • Southern Africa

Introduction

In the 1970s *Paranthropus* had been all but abandoned as a hominin taxon. Many researchers familiar with the early hominin fossil record, including the dedicatee of this volume (e.g., Rak et al. 2007), do not recognize a separate genus for hypodigms they refer to as *Australopithecus robustus* and *Australopithecus boisei sensu lato* [i.e., the combined hypodigms of *Australopithecus boisei* (Leakey 1959) *sensu stricto* and *Australopithecus aethiopicus* (Arambourg and Coppens 1968)]. But some researchers, including the authors, maintain that the morphologies of these early hominins cannot be comfortably accommodated within the genus *Australopithecus*. This contribution reviews the fossil evidence for early hominins with wide faces and especially large postcanine tooth crowns [hereafter referred to as 'megadont' (i.e., *Paranthropus robustus*) and 'hyper-megadont' (i.e., *Paranthropus boisei* and *P. aethiopicus*)] hominins, examines why and how the genus *Paranthropus* was established and why some researchers have revived it, and, finally, the strengths and weaknesses of the case for continued use of the genus *Paranthropus*. We have not provided citations for the section covering the fossil evidence; the relevant references can be found in Wood and Constantino (2007) and Wood and Schroer (2013).

Fossil Evidence

Southern Africa

The first evidence of hominins with wide, flat faces, large and robust mandibular corpora and especially large (i.e., megadont) postcanine tooth crowns was the TM 1517 cranium recovered in 1938 from the cave site of Kromdraai in the Blaauwbank Valley, South Africa. The first discoveries of similar-looking hominins from Swartkrans, another breccia-filled cave complex close by in the same valley,

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were made in 1948 and since then, more than 400 hominin fossil specimens representing ca. 150 individuals have been recovered in breccia dumps, or *in situ*, at Swartkrans. A third cave, Drimolen, is close by and is the second largest source of megadont hominins in southern Africa after Swartkrans. The Drimolen hominin sample includes a well-preserved skull, DNH 7, a mandible with an almost complete dentition, DNH 8, and an unusual number of immature individuals. The non-metrical morphology of the Drimolen dental remains has been interpreted as being intermediate between that of Swartkrans and Kromdraai. Two other sites in the Blaauwbank Valley, Cooper's Cave and Gondolin, have also yielded evidence of megadont early hominins. It has been suggested that the same hominin taxon, or its precursor, has been sampled at Sterkfontein, also in the Blaauwbank Valley, but other researchers who have carried out a careful analysis of the collection disagree (Table 8.1).

The best estimates of the first and last appearance dates of the megadont hominins from southern Africa comes from Swartkrans. Direct uranium-lead dating of the flowstone layers above and below the Hanging Remnant and Lower Bank deposits at Swartkrans gives an age of ca. 2 Ma for Member 1 at Swartkrans and contemporaneous deposits across the sites, thus providing a first appearance date for megadont hominins. The most recent evidence of megadont hominins in southern Africa comes from Member 3 at Swartkrans, and faunal and other evidence suggests a last appearance datum of ca. 1 Ma.

East Africa and Malawi

In East Africa, there is evidence of early hominins with even larger postcanine tooth crowns than *P. robustus*, so large that we refer to them as hyper-megadont. These unusually large tooth crowns are combined with small incisors, a small canine, and especially large and robust mandibular bodies. The first evidence of these hyper-megadont hominins consisted of a large deciduous molar, OH 3, recovered in 1955 from locality BK in Lower Bed II at Olduvai Gorge in Tanzania. It puzzled researchers, but its significance became clearer in 1959 when a well-preserved sub-adult cranium, OH 5, with massive postcanine tooth crowns and diminutive anterior teeth was recovered from locality FLK in Bed I at Olduvai Gorge. Four years later, a well-preserved adult mandible whose dentition, based on absolute and relative size, matched the dentition of OH 5 was recovered from Peninj just north of Olduvai Gorge, also in Tanzania.

Table 8.1 Timeline of important events in the discovery and analysis of the fossil evidence of *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Paranthropus robustus*. After Wood and Schroer (2013)

1938	Recovery of TM 1517 from Kromdraai and its publication by Robert Broom as the holotype of *Paranthropus robustus*
1939	A single tooth was found at Cooper's Cave. Fossils found since have been assigned to *P. robustus*
1949	Recovery of SK 6 from Swartkrans and its publication by Robert Broom as the holotype of *Paranthropus crassidens*
1952	Publication of the *Swartkrans Ape-Man* monograph by Robert Broom and John Robinson
1955	Recovery of OH 3 from Olduvai Gorge, with hindsight the first *Paranthropus* specimen to be discovered in East Africa
1958	Publication of John Robinson's monograph the *Dentition of the Australopithecinae* that spelt out the dental differences between *P. robustus* and *Australopithecus africanus*
1959	Mary Leakey discovers the remains of OH 5 at FLK in Olduvai Gorge and its publication by Louis Leakey as the holotype of *Zinjanthropus boisei*
1960	John Robinson first uses the name combination *Paranthropus boisei*
1964	Kamoya Kimeu recovers a remarkably well preserved mandible from Peninj that matches the OH 5 cranium
1967	Publication of Phillip Tobias' seminal analysis of the OH 5 cranium
1967	Revecory of the first hyper-megadont postcanine teeth from the Omo-Shungura Formation, in the following year Arambourg and Coppens assign to the new taxon *Paraustralopithecus aethiopicus*aethiopicus
1969	Recovery of the KNM-ER 406 cranium from the site that was then known as East Rudolf
1971	A partial face from Chesowanja (KNM-CH 1)is categorized as a possible female specimen of *P. boisei*
1973	A partial cranium from Koobi Fora (KNM-ER 732) is recognized as confirmatory evidence of substantial size and shape sexual dimorphism in *P. boisei*
1985	Recovery of the first and only well-preserved crania of *P. aethiopicus* (KNM-WT 17000) from West Turkana in Kenya
1993	Publication of Bob Brain's monograph on the site and hominin fossil evidence from Swartkrans. Recovery of the first well-preserved skull of *P. boisei* (KGA 10-525) from Konso in Ethiopia, published in 1997
1994	Recovery of the first well-preserved skull of *P. robustus* (DNH 7) from Drimolen in South Africa
1999	Publication of the first hominid teeth recovered from Gondolin
1999	A maxillary fragment from the site of Malema, Malawi is provisionally assigned to *P. boisei*, greatly expanding the known range of this taxon

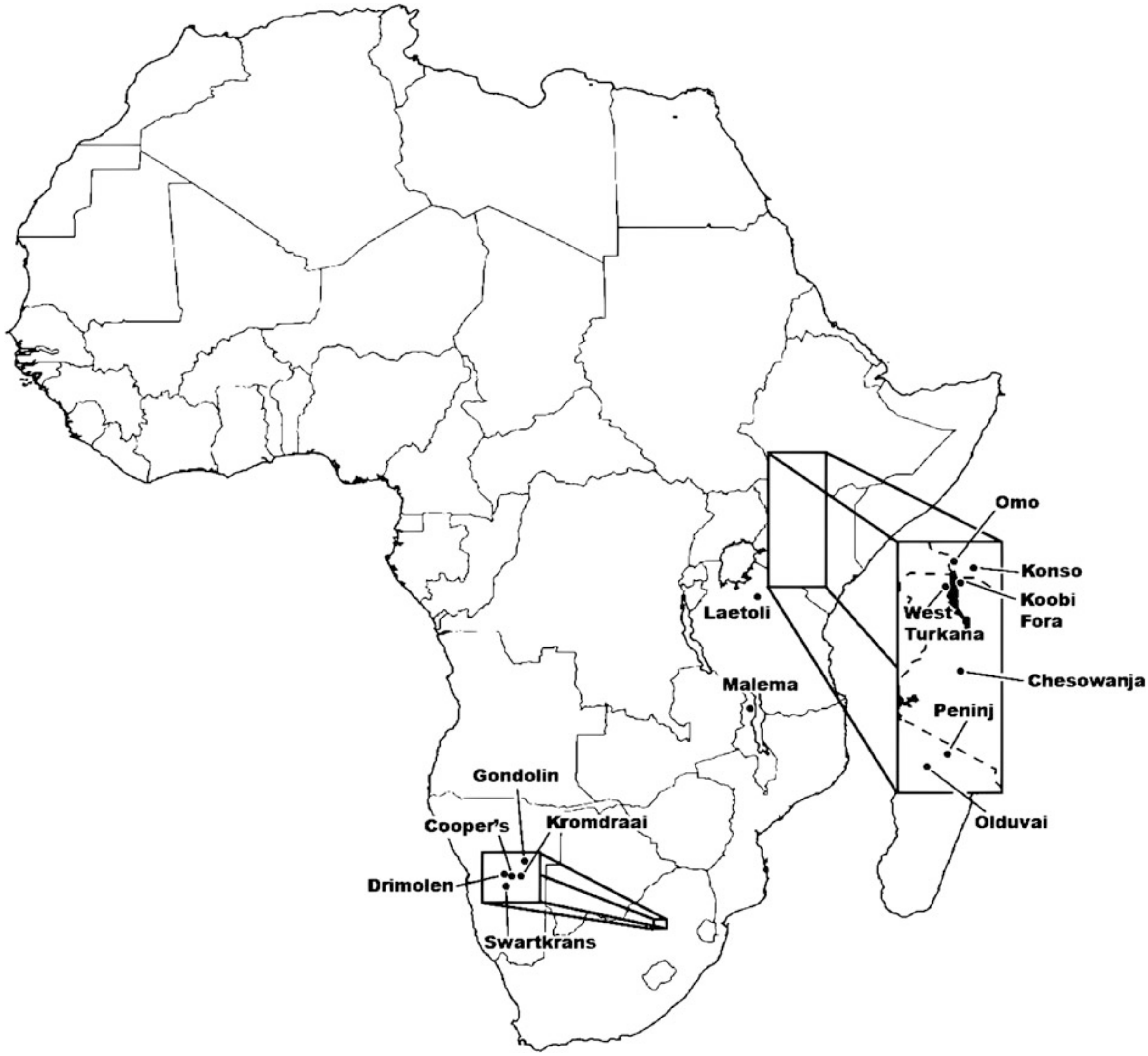

Fig. 8.1 Map of the sites that contribute to the hypodigms of *Paranthropus aethiopicus*, *Paranthropus boisei* and *Paranthropus robustus*. Redrawn after Wood and Schroer (2013)

In 1967, a mandible, Omo 18-1967-18, with alveoli that suggested the postcanine teeth were large was recovered from Member C in the Shungura Formation in southern Ethiopia, and since then a fragmentary hyper-megadont cranium and several hyper-megadont mandibles and numerous isolated teeth have been recovered from the Shungura Formation. However, the largest collection of hyper-megadont crania and mandibles in East Africa comes from sites nearby on the eastern and western shores of Lake Turkana in northern Kenya. Two hemi-mandibles with robust bodies, KNM-ER 403 and 404, plus an abraded and edentulous palate, KNM-ER 405, were collected in 1968, and since then a succession of crania and calvariae (e.g., KNM-ER 406, 407, 732, 733, 13750, 23000) and mandibles (e.g., KNM-ER 729, 3230) have been recovered from what was then known as East Rudolf and what is now called Koobi Fora, or East Lake Turkana. Morphologically similar cranial remains have also been found in sediments across that lake in a region known as West Turkana (e.g., KNM-WT 16005, 17000, 17400) (Fig. 8.1).

The next East African site to yield evidence of a hyper-megadont hominin was Chesowanja in Kenya, where in 1970 a right hemiface and anterior cranial base, KNM-CH 1, was recovered from the Chemoigut Formation. The morphology of the face and the absolute size and proportions of the dentition were judged to be similar to those of OH 5 and the Koobi Fora fossils. Further evidence from the Horn of Africa came in the early 1990s when a well-preserved skull, KGA 10-525, was recovered at Konso (initially called Konso Gardula) in Ethiopia, and subsequently a maxilla was

Paranthropus aethiopicus
KNM-WT 17000

Paranthropus boisei
KNM 406

Paranthropus robustus
SK 48

Fig. 8.2 Left lateral views of the well-preserved holotype cranium of *Paranthropus aethiopicus*, and representative crania of *Paranthropus boisei* and *Paranthropus robustus*. Not to scale. Redrawn after Wood and Schroer (2013)

discovered at Malema in Malawi. The latter discovery was significant from a biogeographical standpoint because it extended the southern extent of the range of hyper-megadont hominins by more than five hundred miles.

The oldest well-preserved evidence of hyper-megadont hominins from East Africa comes from ca. 2.7−2.6 Ma strata in Member C at Omo-Shungura, and if a maxilla from the Ndolanya Beds at Laetoli is included in the hypodigm, then this would also point to an estimated first appearance date between 2.7 and 2.5 Ma. The lack of hyper-megadont hominins with small incisors and canines in the older sediments at Omo-Shungura and in the lower Lomekwi Member at West Turkana suggests that the ca. 2.7 Ma first appearance date of these hominins is likely to be close to the time of origin, or immigration, of the East African hyper-megadont hominins. The youngest known remains are most likely two isolated teeth recovered from Olduvai Gorge (OH 3 and 38) dating to ca. 1.3 Ma, or the remains from Konso in Ethiopia dated to ca. 1.4 Ma. However, because there are no major East African hominin sites in the period between ca. 1.3 and 1.0 Ma, we have no reliable information about how long these hominins might have persisted in East Africa beyond these last appearance dates.

From time to time, researchers have suggested that megadont hominins with large, robust mandibles have been found outside of Africa (e.g., Robinson 1954), but none of the candidates have turned out to match the distinctive morphology seen in early hominins found at sites in southern and eastern Africa (Fig. 8.2).

Taxonomy

When Broom (1938) announced and described the TM 1517 cranium from Kromdraai, he claimed that its shorter, flatter face, its small canines and incisors, and the differences in the size and shape of its molars and premolars compared to those of *Australopithecus africanus* from Taung and *Australopithecus transvaalensis* from Sterkfontein, were worthy of recognition at the generic level, so Broom designated TM 1517 as the holotype of a new genus and species, *Paranthropus Paranthropus robustus*. When the first megadont hominins were recovered in November 1948 from what was then called the “pink breccia” at Swartkrans, Broom (1949) designated the SK 6 mandible as the holotype of *Paranthropus crassidens*, but he gave no morphological reasons for making a specific distinction between the hominins from Swartkrans and Kromdraai. The initial species-level distinction between *P. crassidens* and *P. robustus* was soon amended to the subspecific level (Robinson 1954, 1956, 1968; Campbell 1963), and although Howell (1978) restored the specific distinction between the Kromdraai and Swartkrans samples and Grine (1985) described differences between the deciduous dentitions of the two samples, most researchers view the differences between the megadont hominins recovered from the two sites as consistent with variation *within* a single species rather than the type of variation found *between* species.

As for the taxonomy of the initial fossil evidence from East Africa, although OH 5 was initially placed in a novel genus and species, *Zinjanthropus boisei* Leakey 1959, five years later Louis Leakey and colleagues, without explanation, demoted *Zinjanthropus* to the level of a subgenus as *Australopithecus* (*Zinjanthropus*) (see Leakey and Leaky 1964), and not long afterwards one of those authors abandoned any generic distinction between *Zinjanthropus* and *Australopithecus* (Tobias 1967). Researchers now refer to the taxon as *Australopithecus boisei* or *Paranthropus boisei* (Table 8.2).

In his “preliminary diagnosis” of OH 5, Leakey (1959) drew attention to twenty distinctive features (e.g., malar morphology, the anterior accentuation of the sagittal crest, and the imbalance between the diminutive canines and the

Table 8.2 List of the sites and a summary of what fossil evidence they contribute to the hypodigms of *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Paranthropus robustus*. After Wood and Schroer (2013)

Region	Site	Formation	Age of remains (Ma)	Dating method	Nature of the evidence	Taxa
Eastern Africa	Laetoli, Tanzania	Ndolanya	2.7−2.5	Radiometric	EP 1500/01 (maxilla)	*P. aethiopicus*
	Omo, Ethiopia	Shungura	2.6−2.3 2.3−1.2	Radiometric, magnetostratigraphy, tephrostratigraphy	Omo 18-18 (edentulous mandible; holotype of *P. aethiopicus*) and others, mostly isolated teeth Various specimens, mostly teeth	*P. aethiopicus* *P. boisei*
	West Turkana, Kenya	Nachukui	2.5−2.35	Radiometric, magnetostratigraphy, tephrostratigraphy	KNM-WT 17000 (cranium) KNM-WT16005 (mandible) Various specimens	*P. aethiopicus* *P. boisei*
	Malema, Malawi	Chiwondo	2.5−2.3	Biostratigraphy	HCRP-RC-911 (maxilla)	*P. boisei*
	Koobi Fora, Kenya	Koobi Fora	2.2−1.88 1.88−1.65 1.65−1.39	Radiometric, tephrostratigraphy	KNM-ER 1500 (partial skeleton) and others KNM-ER 406, 407, 732 (all crania) and others KNM-ER 729, 3230 (both mandibles) and others	*P. boisei*
	Chesowanja, Kenya	Chemoigut	2.0−1.5	Biostratigraphy, radiometric dating of capping layer	KNM-CH1 (partial cranium), other fragments	*P. boisei*
	Olduvai, Tanzania	Olduvai	1.9−1.7 1.7−1.2	Biostratigraphy, radiometric	OH 5 (cranium; holotype of *P. boisei*) Various specimens	*P. boisei*
	Peninj, Tanzania	Humbu	1.7−1.3	Radiometric; magnetostratigraphy	Mandible	*P. boisei*
	Konso, Ethiopia	Konso	1.45−1.3	Radiometric, tephrostratigraphy	KGA 10−525 (skull) and others	*P. boisei*
Southern Africa	Kromdraai, South Africa	Monte Cristo	2.0−1.5	Biostratigraphy, magnetostratigraphy	Close to 30 *Paranthropus* specimens, including TM 1517 (holotype of *P. robustus*)	*P. robustus*
	Drimolen, South Africa	Monte Cristo	2.0−1.6	Overall faunal assemblage composition; no absolute dates	>80 hominins, including DNH 7 (nearly complete female skull) and DNH 8 (male mandible)	*P. robustus*
	Gondolin, South Africa	Eccles	1.9−1.5	Biostratigraphy, magnetostratigraphy	GA 1 and GA 2 (isolated teeth)	*P. robustus*
	Cooper's Cave, South Africa	Monte Cristo	1.9−1.4	Biostratigraphy, uranium-lead dating	Various specimens, mostly isolated dental specimens	*P. robustus*
	Swartkrans, South Africa	Monte Cristo	1.8−1.0	Biostratigraphy	>300 *Paranthropus* specimens total, many isolated dental remains, including SK 6	*P. robustus*

massive postcanine dentition) that he felt justified naming a novel genus and species for the cranium. When Tobias (1967) presented his detailed analysis of OH 5, he concluded that it showed affinities with *Australopithecus africanus* and more closely with *P. robustus* (he referred to the latter as *Australopithecus robustus*), but he also detailed a suite of characters in which OH 5 differed from the *P. robustus* hypodigm. Tobias' interpretation of these differences is best put in context by the following quotation, "the Olduvai australopithecine differs from *Australopithecus robustus* in a manner similar to that in which the latter differs from *Australopithecus africanus*" (Tobias 1967:233). Tobias went on to conclude that "the australopithecines had differentiated into a series of taxa, characterized by differing degrees of enlargement of the cheek teeth and naturally, of the supporting structures, muscular prominences, masticatory stress columns, and so on…." (Tobias 1967:228). Yet, as painstaking and detailed as Tobias' analysis was it was based on a single specimen and the results must be affected by the limitations that attend any study of one fossil

(Smith 2005), no matter how careful the study and how well-preserved the fossil.

Despite that caveat, for most researchers discoveries of ca. 2.3−ca. 1.3 Ma fossils at East African sites around Lake Turkana have been consistent with recognizing a single hyper-megadont species. The exceptions are Delson's (1997) suggestion that the evidence from Konso (Suwa et al. 1997) might justify a reassessment of *Paranthropus* taxonomy, and the possibility that discoveries at Gondolin (Menter et al. 1999) and Drimolen (Keyser 2000; Keyser et al. 2000) may help close the morphological gap between *P. robustus* and *P. boisei*. However, Wood and Lieberman (2001) concluded "the Konso specimens 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 eastern and southern Africa had increased rather than decreased. The balance of the evidence suggests a single hyper-megadont taxon inhabited East Africa between ca. 2.3 and ca. 1.3 Ma; the only evidence we presently have for *Australopithecus garhi* (see below), which also has large premolars and molars, is ca. 200 kyr earlier.

The pre-2.3 Ma evidence of hyper-megadont hominins from East Africa presents a more complex story. Arambourg and Coppens (1968) had made the ca. 2.6 Ma Omo 18-1967-18 mandible the holotype of a new species and genus, *Paraustralopithecus aethiopicus*. Few researchers now recognize *Paraustralopithecus* as a separate genus, but many consider that the pre-2.3 Ma hyper-megadont hominins from Omo-Shungura and West Turkana (e.g., KNM-WT 17000) belong to a species distinct from *A.* or *P. boisei*, and they refer to the taxon as either *Australopithecus aethiopicus* or *Paranthropus aethiopicus*. The hypodigm of this species would include a well-preserved adult cranium from West Turkana (KNM-WT 17000) together with mandibles (e.g., KNM-WT 16005) and isolated teeth from the Shungura Formation (Suwa et al. 1994, 1996). Some would also include the L. 338y-6 juvenile cranium in Member E of the Shungura Formation, and a maxilla from the ca. 2.3 Ma Ndolanya Beds at Laetoli, in the taxon.

The cranial evidence for *P. aethiopicus* resembles that of *P. boisei*, but the face of the former taxon is more prognathic, the cranial base is less flexed, the inferred size of the incisors and canines is larger, and the postcanine teeth are not quite so large or derived. But there is only one relatively complete *P. aethiopicus* cranium, and so the warnings of Smith (2005) about making taxonomic inferences based on small samples are especially relevant. Some researchers who are prepared to accept that a species may evolve significantly over time (e.g., Walker et al. 1986) do not recognize *P. aethiopicus* as a separate taxon and instead include the hypodigm of *P. aethiopicus* within *Paranthropus Paranthropus boisei sensu lato*.

A novel hominin species, *Australopithecus garhi*, was established by Asfaw et al. (1999) to accommodate a fragmented cranium recovered from the ca. 2.5 Ma Hatayae Member of the Bouri Formation in the Middle Awash study area in Ethiopia. *Australopithecus garhi* combines a primitive cranial morphology with large-crowned postcanine teeth; the crowns of the anterior premolars are especially large. However, unlike *P. boisei,* the canines are large and the enamel apparently lacks the extreme thickness seen in the latter taxon. A partial skeleton combining a long femur with a long forearm was found nearby, but is not associated with the type cranium (Asfaw et al. 1999) and these fossils have not been formerly assigned to *A. garhi*. Yet, despite its large postcanine tooth crowns, the cranium of *A. garhi* lacks the derived features of *Paranthropus*. Asfaw et al. (1999) suggested *Au. garhi* may be ancestral to *Homo*, but the results of phylogenetic analyses of the limited fossil evidence are not consistent with this hypothesis. The morphology of the mandibles reported in the same publication as the cranium of *Au. garhi* is in some respects like that of the mandibles associated with *P. aethiopicus*, but in some ways the dental morphology is more similar to non hyper-megadont specimens from the Shungura Formation. If it is demonstrated that the type specimen of *P. aethiopicus*, Omo 18-18, belongs to the same taxon as the mandibles that appear to match the *A. garhi* cranium, then *P. aethiopicus* would have priority as the name for the *A. garhi* hypodigm.

Australopithecus or *Paranthropus*?

Prior to the discovery of *P. boisei,* Robinson (1954) reviewed the australopith remains from southern Africa and set out the morphological features that distinguish what others have referred to as the "robust" and "gracile" remains. These were incorporated into taxonomic definitions (Robinson 1954:198) that were subsequently amended and augmented (Robinson 1968:169). These features, together with a series of detailed dental characters extracted from Robinson (1956), constitute the characters that, prior to the publication of the detailed analysis of OH 5, were claimed to distinguish *Paranthropus* (i.e., *P. robustus* plus *P. crassidens*) from *Australopithecus* (i.e., *A. africanus*).

In his detailed review of the same fossil evidence considered by Robinson, Tobias (1967) did not so much deny the existence of character differences between "robust" and "gracile" australopiths, as place a different interpretation on them. He, in common with Leakey (1959), suggested that the differences between what later became known as the "robust" and "gracile" australopiths from southern Africa were equal to, if not exceeded by, the differences between the "robust" forms from southern Africa and OH 5. But Tobias rejected the notion that the two groups should be put in separate genera and in a later paper he argued that the southern African and East African "robust" forms were allopatric populations of a single "superspecies" within the genus *Australopithecus* (Tobias 1973). Subsequent authors such as Pilbeam and Gould (1974) and Corruccini and Ciochon (1979) effectively endorsed Tobias' decision to sink *Paranthropus* into *Australopithecus* by advancing the argument that australopiths were allometrically "scaled variants" of the same morphotype. Today, many researchers follow Tobias (1967), who followed Washburn and Patterson (1951), and subsume *Paranthropus* within the genus *Australopithecus*. The term "robust" australopith is widely used to informally identify the megadont and hyper-megadont taxa within *Australopithecus sensu lato*.

Studies of the mandible, cranial base, endocranium, face, adult dentition, deciduous dentition, enamel microstructure

Table 8.3 Shared, and distinguishing, features of *Paranthropus boisei* and *Paranthropus robustus*

Trait	*Paranthropus robustus*	*Paranthropus boisei*
Face	Flat, wide, and dished compared to *Australopithecus* External anterior pillar is present, but internal structure is similar to *P. boisei*	Especially flat, wide, and dished External anterior pillar is absent, but internal structure is similar to *P. robustus*
Cranial features related to mastication	Large infratemporal fossa compared to *Australopithecus* Pronounced ectocranial cresting compared to *Australopithecus* *Gorilla*-like ramus that includes a coronoid process higher than the condylar process	Especially large infratemporal fossa Especially pronounced ectocranial cresting, suggesting greater development of the temporalis Especially wide mandibular ramus that includes a coronoid process higher than the condylar process Extensive overlap of the parieto-temporal suture
Dentition	Large, molarized postcanines, extra distal cusps, thick enamel, and accelerated development compared to *Australopithecus* Higher incidence of pitting compared to *Australopithecus* suggesting a hard and tough diet	Very large, hyper-molarized postcanines including an increased number of molar roots, higher frequency of molar roots, higher frequency of extra distal cusps, hyper-thick enamel, and similar accelerated development Lower complexity, suggesting a less mechanically challenging diet
Isotopic signal	C_3	C_4

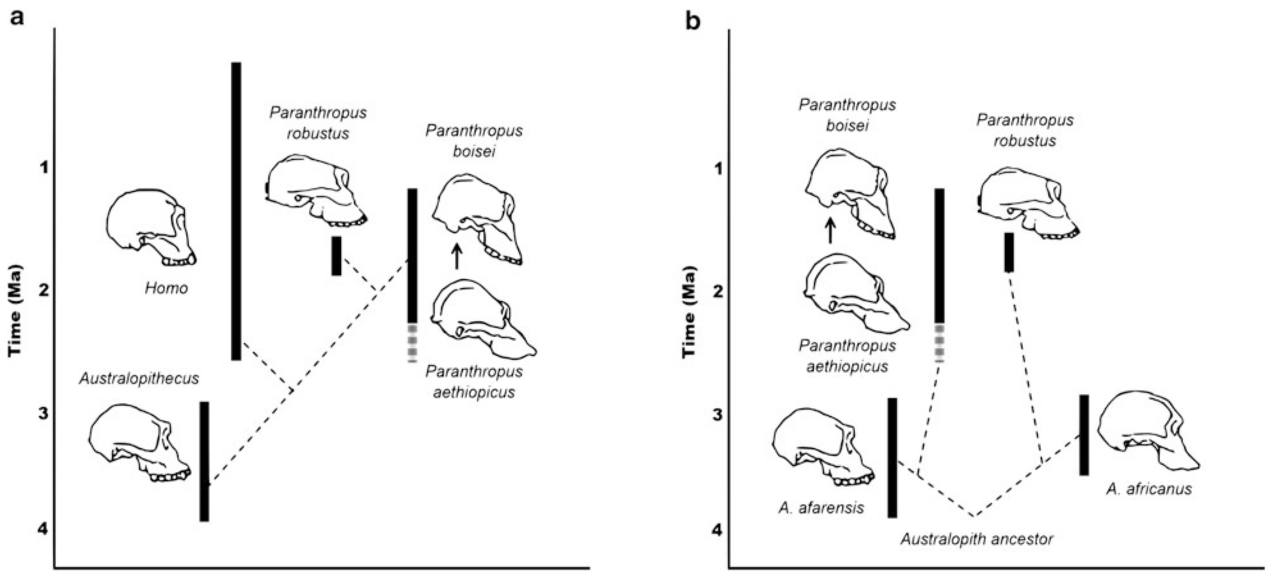

Fig. 8.3 Hypotheses about the relationships among *Paranthropus* considered in this review: **a** *Paranthropus* monophyly, **b** *Paranthropus* paraphyly. Redrawn after Strait et al. (1997)

and dental eruption pattern have all suggested ways in which the "robust" australopiths show either unique morphology or distinctive combinations of morphologies that individually are more widely distributed among early hominins. Some of these claims have been contested, but probable derived features of the skull of "robust" australopiths include a particularly thick mandibular corpus, apparently unique patterns of facial buttressing, and peculiar sutural and endocranial morphology. Dental characters special to the group include molarized mandibular premolars, preferentially enlarged mandibular molar talonids and a concomitantly high incidence of distal accessory cusps in the mandibular molars (Wood and Constantino 2007 and references therein). The case for retaining *Paranthropus* as a phenetically-distinct genus for the "robust" australopiths was cogently put by Robinson when he suggested that such a course would aptly reflect the "different adaptive patterns" (Robinson 1972:251) of the "gracile" (i.e., *Au. africanus*) and "robust" australopiths (Fig. 8.3, Table 8.3).

Phylogenetic Relationships of *Paranthropus robustus* and *Paranthropus boisei*

How are the two major taxa we have been considering, *P. robustus* and *P. boisei*, related? First, could they be so closely related that they do not deserve to be recognized as separate species? Eldredge and Tattersall (1975) suggested that the issue was "highly debatable" and some early cladistic analyses (e.g., Delson et al. 1977; Johanson and White 1979 and Skelton et al. 1986) made no distinction between the two taxa, but Johanson and White subsequently revised their position (White et al. 1981). Olson (1978) cited basicranial and dental characters that are unique to *P. boisei*, and suggested that an excessively overlapping squamosal suture may be a peculiarity of that taxon. Rak (1983) identified features of the mandible and face, respectively, that may be peculiar to *P. boisei,* and Grine (1984) listed apomorphies of the latter species' deciduous dentition. In short, these studies have supported Tobias (1967) in his assessment that OH 5 and its ilk are specifically distinct from *P. robustus*. Subsequent additions to the *P. boisei* hypodigm have underscored the current conventional wisdom that while *P. boisei* shares derived characters with *P. robustus*, even more characters set *P. boisei* apart and support its status as a taxon distinct from *P. robustus* (Wood and Constantino 2007).

But did the eastern and southern African "robust" taxa evolve from a most recent common ancestor (MRCA), exclusive to themselves, and thus form a monophyletic group, or did the megadont and hyper-megadont taxa in the two regions evolve independently – *P. robustus* from *A. africanus*, and *P. boisei* from *P. aethiopicus*? This is not a trivial question for if the two forms evolved from a most 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 known first appearance datum. Alternatively, if the two regional variants arose independently, it would be a striking example of homoplasy for at least two, and probably more, hominin lineages would have independently acquired a suite of morphology that includes postcanine megadontia and robust mandibles.

The Case for and against *Paranthropus* Monophyly

Most cladistic analyses of early hominins have found support for *Paranthropus* monophyly. Wood (1988) reviewed fifteen studies that treated the eastern and southern African "robust" taxa separately in phylogenetic analyses, all of which concluded that the two regional variants were sister taxa (though some of the studies used the same data sets, so these results are not quite as impressively consistent as they appear). Subsequently, Corruccini (1994) reviewed the results of early hominin cladistic analyses and also concluded that one of the few reliable parts of the hominin cladogram was the *Paranthropus* clade. Strait et al. (1997) subjected 60 raw and adjusted traits from five previous studies to eight parsimony analyses, and in all cases the "robust" taxa formed a single clade. Strait and Grine (2004) combined 109 non-metrical traits with 89 traits based on linear measurements and, using two differently composed in-groups, also found that the three "robust" taxa (*P. robustus*, *P. boisei* and *P. aethiopicus*) consistently formed a monophyletic group, a result also reached by the cladistic analysis by Kimbel et al. (2004). Other studies that focused on specific morphology also support the conclusions of these global phylogenetic analyses. For example, LaCruz (2007) suggested that details of the enamel cap of *A. africanus* and *P. robustus* are too dissimilar for them to be sister taxa, Villmoare and Kimbel (2011) suggested that the internal structure of the circumnasal region of the maxilla is a synapomorphy of *P. robustus* and *P. boisei*, and Gunz et al. (2012) showed that a *P. robustus* cranium, SK 48, is more likely to be a scaled variant of *P. boisei* than a scaled variant of *A. africanus*.

In the face of all this analytical support for a "robust" australopith clade, why should *Paranthropus* monophyly be doubted? The reason, in a word, is homoplasy. The term was introduced by Ray Lankester who wrote that "when identical or nearly similar forces, or environments, act on two or more parts of an organism… the resulting correspondences called forth in the several parts in the two organisms will be nearly or exactly alike. I propose to call this kind of agreement *homoplasis* or *homoplasy*" (Lankester 1870, p. 39). Homoplasy, which refers to any resemblances between taxa that were not inherited from their most recent common ancestor, comes in several forms. Two types of homoplasy, analogy and convergence, are both caused by adaptation to similar environments. A third type of homoplasy, parallelism, is a by-product of development, not adaptations. Convergence usually occurs across greater phylogenetic distances than parallelism. Most cases of a fourth type of homoplasy, reversal (e.g., brain size increases and then decreases), are probably the result of natural selection, but recent work on silenced gene reactivation suggests that some reversals may also be neutral with regard to adaptation. The last type of homoplasy, homoiology, is attributed to non-genetic factors (e.g., activity-induced bone remodeling). In each case, homoplasies can be mistaken for shared derived similarities (i.e., synapomorphies), which are the principal evidence for phylogeny. As such, homoplasy complicates attempts to estimate phylogenetic relationships. Indeed, if homoplasies are sufficiently numerous, they can prevent a reliable phylogeny from being generated.

The first reason to suspect that homoplasy occurs anywhere in the hominin clade is comparative evidence from other mammalian groups evolving in Africa during the same time period, and in similar paleoenvironments, as hominins. Phylogenetic studies of bovids (Gatesy et al. 1997), hippos (Boissiere 2005), carnivores (van Valkenburgh 2007), Old World monkeys (Jablonski and Leakey 2008), elephants (Todd 2010) and equids (Bernor et al. 2010) all suggest that the evolutionary history of these groups shows evidence of substantial homoplasy during the period of time spanned by the megadont and hyper-megadont hominins. This comparative evidence does not mean that hominins *must* also have been affected by homoplasy, but it suggests it would be unwise to rule it out. Substantial homoplasy is also explicit in interpretations of the evolutionary history of non-hominin hominoids (Pilbeam 2002).

The second reason to suspect homoplasy in the hominin clade is that if consistency indices (CI) are any guide to the prevalence of homoplasy, then 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) (Wood 1988).

In the *Paranthropus* clade specifically, another reason to suspect homoplasy 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. There is empirical evidence that these characters are likely to be functionally integrated, thus potentially they are non-independent and if so, they should not be coded as individual independent characters in a cladistic analysis (Gunz et al. 2012). 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." Another reason to question the hypothesis of "robust" australopith monophyly is because there is circumstantial evidence of homoplasy in traits related to the masticatory apparatus in other parts of the hominin fossil record. For example, the faces of *Kenyanthropus platyops* and *Homo rudolfensis* are, like *P. boisei*, both orthognathic relative to earlier hominins, but whereas the former have small or moderately sized postcanine teeth the latter shows extreme postcanine megadontia. Since *K. platyops* and *H. rudolfensis* are generally not considered to be closely-related to *P. boisei*, the cited similarities among these taxa must be due to homoplasy.

Other reasons to suspect that homoplasy may impede our ability to reconstruct a reliable phylogeny for *Paranthropus* are the results of three studies that looked in detail at the dental evidence for the *Paranthropus* clade. The results of all three studies were in support of falsifying the hypothesis of *Paranthropus* monophyly. The first of the three tests involved the relative size of the areas of the cusps of the mandibular postcanine tooth crowns. Wood (1988) reasoned that if *P. robustus* and *P. boisei* were sister taxa, then it is likely they would share a common pattern of dental development and would be expected to conform to the same scaling relationships; Gunz et al. (2011) used similar logic in their investigation of overall cranial shape. According to Wood's model, differences in cusp morphology between the taxa would be predictable from a combination of size differences and the extrapolation of any scaling relationships present in the smaller-toothed taxon. But in only two of the ten analyses involving the relative size of the whole or parts of the crowns of mandibular postcanine teeth did such a scaling relationship explain the observed differences. In the other eight analyses, there was either insufficient correlation between the variables to make any allometric prediction, or the observed differences between the two taxa were not the same as those predicted by the allometric relationships observed in the smaller-crowned (*P. robustus*) taxon.

The second test considered whether *P. robustus*, the less derived of the proposed sister taxa, was closer to the primitive state of a character 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 1988; Emonet et al. 2012). In hominins, two distinct morphoclines lead from the inferred primitive condition (Wood et al. 1988). One, towards P_3 root reduction and simplification, culminates in modern humans. The second, towards greater root complexity, culminates in molar-like P_3 roots. The two *Paranthropus* taxa are *not* on the same morphocline. Instead, the roots of *P. robustus* correspond to one of the character states along the morphocline that leads towards reduced root complexity relative to the inferred primitive condition, whereas the P_3 roots of *P. boisei* correspond to the character state that shows the greatest root complexity (Wood 1988).

The third study uses the inhibitory cascade, a model that interprets the relative size of the occlusal surface of mammalian molars in terms of developmental mechanisms (Kavanagh et al. 2007), to test for similarities in the relative size of the occlusal surfaces of the postcanine teeth of the two *Paranthropus* taxa. The inhibitory cascade model has detected derived developmental conditions in the dentitions of rodents, ungulates, carnivores, and platyrrhines, and Schroer and Wood (2015) applied it to the postcanine dentition of a sample of catarrhine taxa, including fossil hominins. Extant congeners shared their fit to the inhibitory cascade of the molars; the only exception among the extant catarrhine taxa considered in this study was *Papio*, which may itself be paraphyletic (Zinner et al. 2009). When the same model was applied to *Paranthropus*, the differences in the relative size relationships observed in the molar and premolar-molar cascades in *P. robustus* and *P. boisei* were not consistent with the hypothesis that they belonged to the same genus.

To be considered within the same genus, taxa do not just have to be monophyletic, but they should also be in the same grade. That is, taxa within a genus should have an adaptive regime that is more similar to the type species of that genus than it is to the type species of another genus (Wood and Collard 1999). The different relative postcanine tooth sizes of *P. robustus* and *P. boisei* suggest that their diets may not have been the same, and support for such a dietary difference has come from recent studies of stable isotopes preserved in the teeth of the two taxa. The $^{13}C/^{12}C$ signal recovered from *P. boisei* specimens from Olduvai Gorge (van der Merwe et al. 2008; Cerling et al. 2011), Chesowanja, Koobi Fora, and Peninj (Cerling et al. 2011) and from a larger sample from the Turkana Basin (Cerling et al. 2013) suggest a C_4-dominated diet for *P. boisei*. A C_4-dominated diet is fundamentally different from that of all known living and fossil hominoids, which vary from nearly pure C_3 consumers like gorillas and chimpanzees, to a diet like that of *A. africanus* and *P. robustus* (Sponheimer et al. 2006, 2013) that is dominated by, but not confined to, C_3 foods. The primate whose carbon isotope composition best matches that of *P. boisei* is the extinct baboon *Theropithecus oswaldi,* whose preferred food was most likely grass! A diet of grasses or sedges is also consistent with the dental macrowear of *P. boisei*, for the sand and grit that is inevitably included in unwashed grasses or sedges would account for the high degree of macrowear on the postcanine teeth in that taxon. The dissimilar dental microwear signals for *P. boisei* and *P. robustus* (Scott et al. 2005; Ungar et al. 2012) adds to the evidence that there are differences in the adaptive regimes of *P. robustus* and *P. boisei*.

The final reason to question *Paranthropus* monophyly concerns biogeography. Turner and Wood (1993b) assessed the probability of monophyly by examining the biogeographic patterns of African Plio-Pleistocene large mammals. They concluded that during the time range of *Paranthropus*, there was evidence in at least one mammalian group of faunal dispersal between regions, with several monophyletic groups having representatives in both regions. They suggested that while this lends credibility to the hypothesis of *Paranthropus* monophyly, it does not refute a polyphyletic origin for this group. In a second study, Turner and Wood (1993a) worked on the assumption that the well-developed masticatory system of *Paranthropus* was an adaptation to enable the consumption of tough food items in response to environmental aridity. They found that similar trends were detectable in the craniodental anatomy of other terrestrial mammals from this time period, and parallels in lineage turnover suggest that a large-scale response to environmental changes was occurring. Although this second study by Turner and Wood did not contradict the first one, it did suggest there are comparative precedents for regional mammalian lineages independently evolving similar masticatory adaptations in response to changing environmental conditions.

Differences in geological context, taphonomic history and collection methods, as well as a lack of a precise chronology in one of the regions, complicate attempts to compare the faunas of eastern and southern Africa, but access to new comprehensive datasets encouraged Patterson et al. (2014) to re-examine this critical time period in the African paleontological record. They investigated the biogeographic histories of three terrestrial African mammalian families whose fossil records span the past 3 million years to provide a comparative test of the hypothesis of *Paranthropus* monophyly. They used presence/absence data from 52 eastern African and 40 southern African fossil localities. These localities contain data for 117 species from 38 genera within the family Bovidae, and 34 species from 15 genera within the families Hyaenidae and Felidae. These assemblages were placed into 500 ka time slices and compared at both the genus and species level using the Jaccard index of faunal similarity. Results show that sampling biases have more effect on the patterns of interchange between eastern and southern African bovids than they do on the patterns of interchange seen in the Hyaenidae and Felidae. However, even when these biases are taken into account, there are persistent differences in the degree of interchange within and between these families. These findings suggest that mammalian groups (including hominins) can have very different histories of exchange between eastern and southern Africa over the past 3 million years. If these three families, especially Bovidae, are suitable proxies for the southern and eastern African megadont and hyper-megadont hominin taxa, then the results of this biogeographic comparative study are consistent with relatively independent evolutionary trajectories for the hominins in the two regions.

Conclusions

Most of the present cladistic evidence is in favor of monophyly and if one is comfortable with the conclusion that hard-tissue morphology *is* capable of recovering sound hypotheses about phylogenetic relationships established on the basis of independent genetic evidence (e.g., Strait and Grine 2004), then *Paranthropus* monophyly must be the null hypothesis. But if one is more skeptical about the ability of hard-tissue morphology to recover phylogenetic relationships (e.g., Collard and Wood 2000) or about the non-independence of traits used in cladistics analysis, then what to many researchers seems to be overwhelming evidence for *Paranthropus* monophyly seems less compelling.

According to the results of phylogenetic analyses the question of *Paranthropus* monophyly looks to be resolved, but future research must strive to determine whether the superficial and detailed similarities seen in the hard-tissue morphology of eastern and southern African *Paranthropus* taxa is due to their sharing a most recent common ancestor, or due to one or more types of homoplasy.

Much new fossil and other evidence has been accumulated since Grine's (1988) *Evolutionary History of the "Robust" Australopithecines*, but despite these developments, we are not obviously closer to resolving the conundrum of *Paranthropus.* There are rays of hope, however, in that we may be closer to reconstructing the diet of *P. boisei* and closer to understanding more about its postcranial skeleton, always assuming that it can provide reliable evidence regarding monophyly (e.g., Pilbeam 2002). What is not in doubt however, is that it is *very* unlikely that *any Paranthropus* taxon was the direct ancestor of modern humans. For many, this lessens their appeal, but to others, including the dedicatee and the authors, this makes their paleobiology more, not less, intriguing.

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