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Paranthropus paleobiology

Paul J. Constantino

Biological Sciences, paulconstantino@gmail.com

Bernard A. Wood

George Washington University

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Abstract

The last major review of the group of early hominins called the 'robust' australopiths was in 1988. Since then new fossils, and reassessments of existing fossils, have substantially expanded the range of evidence that can be used to investigate the paleobiology of the group of early hominin taxa we will refer to as belonging to the genus Paranthropus. We review the new morphological evidence and use it to test hypotheses about the paleobiology of Paranthropus taxa. First, does the new morphological evidence affect views about how many species should be recognized within Paranthropus? Second, does the new evidence allow us to draw any conclusions about evolutionary trends within Paranthropus? Third, does the new evidence, or the results of reassessing the existing fossil evidence, increase our understanding of the phylogenetic relationships among Paranthropus taxa? In particular, do any lines of evidence help test the hypothesis that Paranthropus species constitute a monophyletic group? We examined variation within Paranthropus with respect to simple linear mesiodistal (MD), labiolingual (LL) and buccolingual (BL) measurements of tooth crowns. First, new data from Swartkrans, Drimolen and Coopers support the hypothesis that the fossil record from southern Africa samples a single Paranthropus taxon. New data from East African sites suggest that the Paranthropus hypodigm from East Africa samples two closely related taxa, P. boisei and P. aethiopicus. The new data also fail to falsify the hypothesis that at least a specific distinction should be maintained between the southern and East African hypodigms of Paranthropus. Three studies have investigated Paranthropus taxa for evidence of anagenetic evolution. Two concentrated on craniodental remains; one looked at the P. boisei hypodigm, the other at a single site sample of P. robustus from Swartkrans. The third looked for any evidence of a trend in cranial capacity through time in P. boisei sensu lato and P. boisei sensu stricto. This study found that cranial capacity did show a steady increase in P. boisei sensu stricto between 2.4 and 1.4 Myr, whereas the two former studies found little evidence of temporal trends in dentognathic variables. Finally, most research published in 1988 and thereafter is consistent with Paranthropus monophyly, but some authors contend that conventional craniodental hominin data, be they metrical or non-metrical, may not be reliable indicators of phylogeny.

Key words: Paranthropus, Variation, Taxonomy, Cladistics, East Africa, Southern Africa.

Paranthropus paleobiology

Paul Constantino & Bernard Wood*

Introduction

We are pleased to have the opportunity to contribute to a volume that recognizes Emiliano Aguirre's many important contributions to paleoanthropology. Our topic may seem out of place in a celebration of a career crowned by Emiliano's role in launching and sustaining important research at Atapuerca and elsewhere in Iberia. However, in his "pre-Atapuerca" life Emiliano paid particular attention to the hominins and fauna recovered from sites in East Africa and from the southern African cave sites. He also addressed the problem of how many hominin species were sampled at one of the cave sites, Makapansgat. Specifically, one of his papers argued that in addition to *Australopithecus africanus* the Makapansgat hominin fauna might also include evidence of a second hominin species, *A. robustus* (Aguirre, 1970).

Our contribution to this volume picks up on Emiliano's Aguirre's interest in hominin alpha taxonomy and biogeography, for it concerns a group of hominins represented in both East and southern Africa. First recognized at one of the southern African cave sites, Kromdraai, it is the group of hominin taxa many researchers refer to informally as the 'robust' australopiths, but we will, at least provisionally, refer to them as *Paranthropus* taxa.

Most, if not all, researchers now accept that no *Paranthropus* taxa are likely to have been directly ancestral to modern humans. One of the reasons is that most of the fossil evidence for *Paranthropus* is coeval with taxa that many consider have

stronger claims to be ancestral to early and later extinct *Homo* taxa, and thence to *H. sapiens*. Perhaps this is the reason why as a group *Paranthropus* taxa were relatively neglected until it became the focus of an international workshop organized by Fred Grine at The State University of New York at Stony Brook (now The University of Stony Brook) in 1987. One of the many tangible outcomes of the workshop was the edited volume *Evolutionary History of the "Robust" Australopithecines* (Grine, 1988). This volume was instrumental in establishing *Paranthropus* as a group whose paleobiology deserved the attention of paleoanthropologists by demonstrating that it was a "crucial source of information" for "reconstructing hominid evolutionary relationships" (Ward, 1991: 482). Coincidentally, the previous year Wood and Chamberlain (1987) had published a paper-length synopsis of *Paranthropus* taxa, and 1986 was marked by the announcement of the discovery of the cranium KNM-WT 17000 from West Turkana (Walker *et alii*, 1986). Although the implications of the KNM-WT 17000 cranium (and the other West Turkana hominins announced at the same time) were considered in papers in Grine (1988) it was perhaps too early to be able to assess their impact.

However, since 1988, with a few exceptions, the attention of paleoanthropologists has mostly been focused on either the earliest hominins, or on the evolution of modern humans. But since 1988 new *Paranthropus* specimens have been discovered, the affinities of some hominin fossils known prior to 1988 have been assessed, or reassessed, imaging techniques have made morphology accessible that was once inaccessible, and morphological details originally ignored have now been

* CASHP and Department of Anthropology, The George Washington University, 2110 G St. NW, Washington DC 20052 USA.

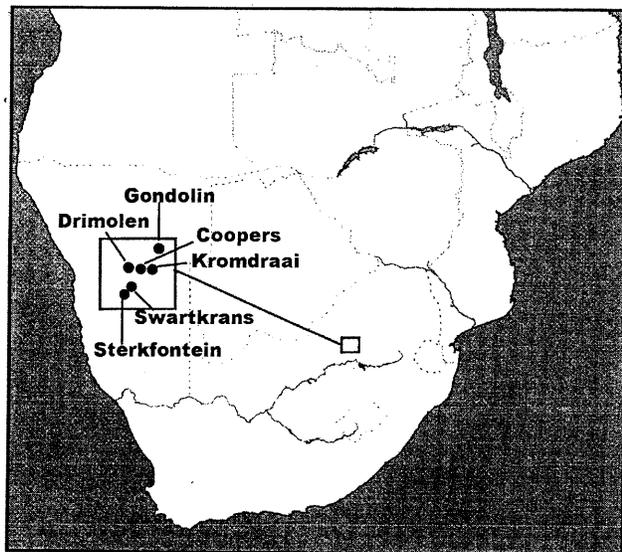


Fig. 1. Southern Africa Site Map (adapted from Delson *et alii*, 2000)

exploited. Other studies have diligently attempted to improve our understanding of the paleobiology of *Paranthropus* by examining one, or more, of its constituent taxa with respect to morphological variability, functional morphology, ontogeny, paleoecology, and even their capacity for stone tool manufacture. Thus, apart from an initial brief review of *Paranthropus* taxonomy that will take us back to 1938, the rest of our paper will concentrate on reviewing some of the advances in our understanding of the paleobiology of *Paranthropus* that have accrued from 1988 onwards.

We begin by reviewing the new morphological evidence, and then consider if it has made any significant change to the parameters of the dental metrics of the two regional *Paranthropus* hypodigms. We then refer to other post-1988 research if it contributes to answering any of the following three questions. First, has morphological evidence, or any other category of evidence accumulated from 1988 onwards, affected views about how many species should be recognized within *Paranthropus*? Second, does the new evidence allow us to draw any conclusions about evolutionary trends within *Paranthropus*? Third, does any new or existing fossil evidence, or any newly introduced (i.e., post-1988) analytical techniques, increase our understanding of the phylogenetic relationships among *Paranthropus* taxa? In particular, do any lines of evidence help test the hypothesis that *Paranthropus* species constitute a monophyletic group?

History and taxonomy of *Paranthropus*

Southern African evidence

The genus *Paranthropus* was established in 1938 by Robert Broom to accommodate fossil hominin remains found in June of that year at the Kromdraai Cave in the Blauwbank Valley, just

upstream from Sterkfontein (Broom, 1938) (Fig. 1). An adult, presumably male, cranium, TM 1517, was made the type specimen of *Paranthropus robustus* Broom, 1938. Subsequent discoveries made at Kromdraai in 1941 (TM 1536), and in the middle 1950s (TM 1600-1 and 1604-5) were added to the hypodigm of *P. robustus*. By 1988 close to 20 specimens had been recovered, sampling a minimum of six individuals and all assumed to belong to *P. robustus* (Vrba, 1981).

The second species to be included in the genus *Paranthropus* was established to accommodate hominin fossils recovered by Broom and Robinson from Swartkrans Cave, on the opposite side of the Blauwbank Valley and less than a mile downstream from Sterkfontein, in 1948. A subadult partial mandible, SK 6, was designated the type specimen of *Paranthropus crassidens* (Broom, 1949). In Broom's judgment the new fossils were sufficiently distinct from the Kromdraai hominins to justify their inclusion in a separate species, but he suggested that "this new type of ape-man... is allied to *Paranthropus*" and accordingly he included them in that genus. Fieldwork at Swartkrans prior to 1988 resulted in the accumulation of a sizeable collection of hominins, most of which (but not all—for example see Broom and Robinson, 1949) have been assigned to *P. crassidens*.

Two years after Broom's 1949 announcement Washburn and Patterson (1951) suggested that the differences between the hypodigms of *Australopithecus* and *Paranthropus* did not justify the recognition of a second genus (i.e., *Paranthropus*). The same conclusion was reached by Le Gros Clark (1955, 1964) and Campbell (1963), but see Leakey (1959) and Robinson (1965) as examples of assessments that accepted *Paranthropus* as a valid taxon. In 1967, after a lengthy consideration of the case for a generic distinction between *Australopithecus* and *Paranthropus*, Tobias (1967) concluded that "the dental differences between the two taxa... are far less marked than had been assumed" claiming that his study showed that "there is no adequate basis for maintaining that the two taxa are generically distinct" (*ibid.*: 231). Thus, Tobias added his weight to the suggestion that *Paranthropus* should be subsumed into, and thus be a junior synonym of, the genus *Australopithecus*. Other commentators reserved their judgment about *Paranthropus*. For example Mayr (1963: 342) suggested that "it may well depend on future finds whether or not we want to recognize *Paranthropus*".

Similarly, long before 1988 most researchers had dispensed with the specific distinction between the Kromdraai and Swartkrans hypodigms of *Paranthropus*. For example, Campbell (1963: 67) recognized the Swartkrans hypodigm as one of two subspecies of *A. robustus*, and in his review of *Australopithecus* taxonomy Tobias (1967: 223-5) only provides definitions of two species, *A. africanus* and *A. robustus*. Elsewhere in his text Tobias makes it plain he regards the Swartkrans hypodigm as either a "population" of *Paranthropus* (i.e., *A. robustus*) (Tobias, 1967: 214), or at most a subspecies of *A. robustus*. Indeed in later work (e.g., Tobias, 1995) Tobias refers to the subspecies *A. robustus crassidens* and *A. robustus robustus*. There is an

intriguing entry for *A. boisei crassidens* in the index of Tobias (1967), but the page referred to (*ibid*: 24) is not enlightening. However, not all researchers have been willing to dismiss the claims for a second southern African species of *Paranthropus*. For example, Riesenfeld (1955), Howell (1978), and Grine (1981, 1982) all followed Broom's lead and maintained a species-level distinction between the Kromdraai and Swartkrans hypodigms of *Paranthropus*.

East African evidence

The first evidence of a *Paranthropus*-like East African hominin consisted of the specimen OH 3, comprising two teeth, a deciduous mandibular canine and a large molar, found in 1955 at locality BK in Lower Bed II, Olduvai Gorge, Tanzania (Leakey, 1958) (Fig. 2). The taxonomy of OH 3 was uncertain until the discovery in 1959 of OH 5, a well-preserved adolescent cranium from FLK, in Bed I, also at Olduvai Gorge (Leakey, 1959). Louis Leakey took the view that the new cranium "differs from both *Australopithecus* and *Paranthropus* much more than these two genera differ from each other" (Leakey, 1959: 491) and consequently he created both a new genus and a new species, *Zinjanthropus boisei*, for the cranium. Thereafter, prior to 1988 other specimens from Olduvai had 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 the announcement in April 1964 of a mandible likely to be from the same taxon as OH5 at the Peninj site close to the western shore of Lake Natron (Leakey and Leakey, 1964), Louis Leakey had been persuaded to relegate *Zinjanthropus* to the status of one of three sub-genera of *Australopithecus* (Leakey *et alii*, 1964). Three years later Tobias (1967) went further still and abandoned even the sub-generic distinction and treated what eight years before had been *Zinjanthropus boisei* (Leakey, 1959) as *A. boisei*, one of what then were four species of *Australopithecus*. Subsequently, prior to 1988 the hypodigm of what we refer to as *Paranthropus boisei* had been augmented by discoveries from the Omo region (specifically from the Shungura Formation), from what was then called East Rudolf and which is now referred to as Koobi Fora (Leakey and Leakey, 1978), and from Chesowanja in the Baringo basin.

The last *Paranthropus* taxon to be recognized was initially included in a separate genus, *Paraaustralopithecus*, as *Paraaustralopithecus aethiopicus* (Arambourg and Coppens, 1968). The type specimen is Omo 18.18 (or 18.1967.18), an edentulous adult mandible recovered from Member C of the Shungura Formation, Omo Region, Ethiopia, in 1967. Subsequently, *Paraaustralopithecus* was subsumed into *Paranthropus* as its junior synonym (Chamberlain and Wood, 1985), with the result that *Paraaustralopithecus aethiopicus* Arambourg and Coppens, 1968 became *Paranthropus aethiopicus* (Arambourg and Coppens, 1968) Chamberlain and Wood, 1985. Suwa (1988) made a careful study of the

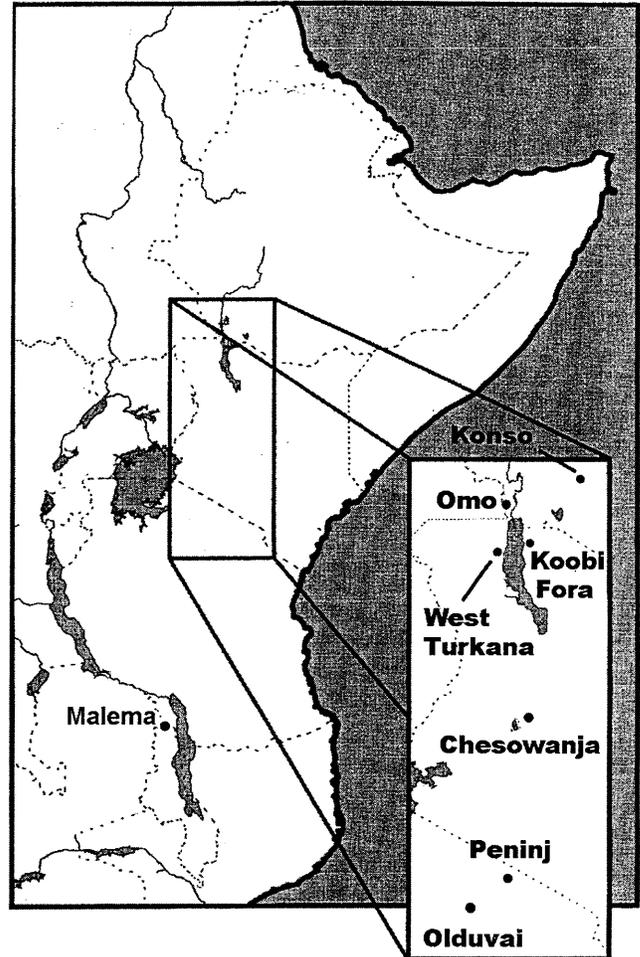


Fig.2. East African Site Map (adapted from Delson *et alii*, 2000)

cuspid morphology of the mandibular premolar tooth crowns and concluded that large pre-2.3 Myr tooth crowns from the Shungura Formation should be assigned to *P. aethiopicus*. Many researchers consider that this hypodigm was augmented by the discovery of the cranium KNM-WT 17000 and the mandible KNM-WT 16005, but the discovery team was more cautious and attributed these two specimens to *Australopithecus boisei sensu lato* (Walker *et alii*, 1986). For a list of known *Paranthropus* sites and associated information, see Table 1.

Hominin fossil evidence attributed to *Paranthropus* from 1988 onwards

We present a summary of the morphological evidence for *Paranthropus* that has been discovered, described in detail, or newly designated since 1988. Sites from southern Africa are discussed prior to sites from East Africa. Within each region, sites with the earliest published hominin discoveries are

TABLE 1. Summary of the nature and context of *Paranthropus* fossil evidence

Region	Site	Formation	Age of Hominins (Myr)	Dating Method	Nature of the evidence	Taxa
East Africa	West Turkana, Kenya	Nachukui	2.5-2.35	radiometric; marker beds	KNM-WT 17000 (cranium), KNM-WT 16005 (mandible)	<i>P. aethiopicus</i>
			2.3-1.6		Various specimens	<i>P. boisei</i>
	Koobi Fora, Kenya	Koobi Fora	2.2-1.88	radiometric; tephrostratigraphy; fission-track, marker beds	KNM-ER 1500 (partial skeleton) and others	<i>P. boisei</i>
			1.88-1.65		KNM-ER 406, 407, 732 (all crania) and others	<i>P. boisei</i>
			1.65-1.39		KNM-ER 729, 3230 (both mandibles) and others	<i>P. boisei</i>
	Omo, Ethiopia	Shungura	2.6-2.3	radiometric; marker beds	Omo 18-18 (edentulous mandible; holotype of <i>P. aethiopicus</i>), and others, mostly isolated teeth	<i>P. aethiopicus</i>
			2.3-1.2		Various specimens, mostly teeth	<i>P. boisei</i>
	Chesowanja, Kenya	Chemoigut	2.0-1.5	biostratigraphy; radiometric of capping layer	KNM-CH1 (partial cranium), other fragments	<i>P. boisei</i>
	Konso, Ethiopia	Konso	14	radiometric; tephrostratigraphy; marker beds	KGA 10-525 (skull), and others	<i>P. boisei</i>
	Malema, Malawi	Chiwondo	15	biostratigraphy	RC 911 (maxilla)	<i>P. boisei</i>
Peninj, Tanzania	Humbu	1.7-1.3	radiometric; magnetostratigraphy	Peninj mandible	<i>P. boisei</i>	
Olduvai Gorge, Tanzania	Olduvai	1.9-1.7	radiometric; biostratigraphy	OH 5 (cranium; holotype of <i>P. boisei</i>)	<i>P. boisei</i>	
		1.7-1.2		Various specimens	<i>P. boisei</i>	
		1.8-1.5		>300 <i>Paranthropus</i> specimens total, mostly isolated dental	<i>P. robustus</i> (<i>P.</i>	
Southern Africa <i>crassidens</i>)	Swarthkrans, South Africa	Monte Christo	1.5-1.0	biostratigraphy	remains, including SK6 (holotype of <i>P. crassidens</i>)	<i>P. robustus</i> (<i>P.</i>
			1.5-1.0			<i>P. robustus</i> (<i>P.</i>
			1.5-1.0			<i>P. robustus</i> (<i>P.</i>
Kromdraai, South Africa	Monte Christo	2.0-1.5	biostratigraphy; reversed polarity	Close to 30 <i>Paranthropus</i> specimens, including TM1517 (skull; holotype of <i>P. robustus</i>)	<i>P. robustus</i>	
Drimolen, South Africa	Monte Christo	2.0-1.5	Overall faunal assemblage composition; no absolute dates	>80 hominins, including DNH 7 (nearly complete female skull) and DNH 8 (male mandible)	<i>P. robustus</i>	

considered first followed by sites with the next earliest discoveries, and so on. All newly discovered fossil evidence attributed to *Paranthropus* is listed in Table 2.

Southern Africa

Swarthkrans

In a chapter of his 1988 book, Grine provided a preliminary analysis of the craniodental fossils from the Member 1 "Lower Bank" deposit and from Members 2 and 3 at Swarthkrans, and a year later he presented a more detailed description of these same fossils (Grine, 1989). Out of 62 total specimens attributed to *Paranthropus*, 18 were from Member 1 "Lower Bank", 31 were from Member 2, and 11 were from Member 3. The two remaining fossils, both individual teeth, came from the

ill-defined interface between Members 1 and 2. Most of the specimens are isolated teeth but other specimens include SKX 21204, a right mandibular corpus of a juvenile with erupting I_2 and exposure of the developing P_4 crown, SKW 12, a left adult maxilla with P^3-M^3 , SKX 162, a right juvenile maxilla with $C-P^4$, SKX 265, an edentulous left adult maxilla, and SKX 4446, a right subadult mandibular corpus with P_4-M_2 . The 62 specimens are believed to represent approximately 50 individuals. Grine concluded that minimal directional evolution is occurring in *Paranthropus* throughout the time of the Swarthkrans deposition, with no evidence that the early Swarthkrans fossils are more like the Kromdraai hypodigm of *P. robustus* than the later Swarthkrans fossils. Thus, Grine (in Brain, 1993) continued to use *P. crassidens* Broom, 1949 as the specific designation

TABLE 2. Fossil evidence of *Paranthropus* recovered, assigned, or described since 1988

Does not include specimens already described in Grine (1988). Abbreviations are as follows: COB=Coopers, DNH=Drimolen, GDA=Gondolin, KGA=Konso, KNM-ER=Koobi Fora, KNM-WT=West Turkana, Rc=Malena, SK/SKW/SKX=Swartkrans, Stw=Sterkfontein.

Region and Sites		Skulls /crania / cranial frags.	Mandibles	Maxillae	Isolated teeth	Postcrania
East African Rift Valley System	Existing Sites	KNM-WT 17400 KNM-ER 13750 KNM-ER 23000 Omo 323-896	KNM-ER 15930 KNM-ER 16841 KNM-ER 25520	KNM-ER 1804	KNM-WT 17396 KNM-ER 15940 KNM-ER 15950 KNM-ER 17760 KNM-WT 17396 KNM-WT 18600	
	New Sites	KGA 10-525 KGA 10-1455	KGA 10-570	RC 911 KGA 10-506	KGA 10-565 KGA 10-900 KGA 10-1720 KGA 10-2705 KGA 10-2741	
Southern Africa	Existing Sites	SKW 11 SKW 29 SKW 2581	SKW 5	SKW 8	SK 14132 SK 14133 SKW 6 SKW 10 SKW 14 SKW 15 Stw 566 Stw 569	SK 2598 SK 3121 SK 25600 SK 24601 SKW 19 SKX 10641 SKX 15468 SKX 19495 SKX 38653
	New Sites	DNH 7 DNH 20 DNH 60 COB 101	DNH 8 DNH 5 DNH 6 DNH 10 DNH 12 DNH 19 DNH 21 DNH 44 DNH 46 DNH 51 DNH 68	DNH 3 DNH 22 DNH 41 DNH 47	GDA-2 DNH 1 DNH 2 DNH 4 DNH 14 DNH 15 DNH 16 DNH 17 DNH 18 DNH 23 DNH 25 DNH 26 DNH 27 DNH 29 DNH 36 DNH 38 DNH 40 DNH 42 DNH 54 DNH 56 DNH 58 DNH 59 DNH 67 DNH 72 DNH 73 DNH 74 DNH 75 DNH 77 DNH 78 DNH 80 DNH 82	DNH 44

for the Swartkrans remains, and *P. robustus* Broom, 1938 for the Kromdraai fossils.

In the same year Susman (1989) published an analysis of the postcranial specimens from Swartkrans. Sixteen fossils came from Member 1, ten from Member 2, and eleven from Member 3. None of the specimens are associated with craniodental remains, so their taxonomy has to be determined in some other way. However, Susman (1988b, 1989) notes that in Member 1, 95% of the craniodental remains are attributed to *Paranthropus* with only <5% believed to represent early *Homo*. He therefore concluded that it would be highly likely that some, if not most, of the sixteen postcranial specimens from Member 1 also belong to *Paranthropus*. Susman (1988b) also notes that the pollical metacarpal SK 84 is similar to the thumb metacarpal of KNM-WT 15000 from East Africa (the Nariokotome *Homo ergaster* skeleton), whereas the SKX 5020 pollical metacarpal is not. Thus, he suggested that SKX 5020 probably belongs to *Paranthropus*.

In 1993, Grine and Daegling described a mandible from the Swartkrans Member 1 "Hanging Remnant" breccia. Originally discovered in 1970-1971 in two separate pieces, skilled preparatory work showed it to be a nearly complete lower jaw of *P. robustus* preserving both corpora, much of the left ramus, and all of the postcanine teeth. However, the crowns of LP₃ and LM₁ are damaged and the M₃s are just erupting. The alveoli of the anterior dentition are preserved. The corpus of SKW 5 is comparatively broad and shallow, but is otherwise similar to other mandibles of *P. robustus*.

In 1994, Grine and Strait published 22 previously undescribed fossils from the Member 1 "Hanging Remnant" (21 attributed to *P. robustus*; 1 to *Homo*). They identified an ossified styloid process on the temporal bone of SKW 2581, a feature previously unreported for *P. robustus*, but otherwise the morphology of the new fossils was within the range of variation known from Member 1.

Fifteen additional Swartkrans hominin postcranial bones were described by Susman *et alii* (2001). Of these, nine were attributed to *Paranthropus* and included two femoral heads, three distal humeri, a proximal radius, two proximal phalanges and a middle phalanx. Six of the newly assigned *Paranthropus* fossils came from Member 1, one from Member 2, and two from Member 3. Susman *et alii* (2001) used these new specimens to estimate body mass. Their conclusions suggest that females of both *Paranthropus* and *Homo* weighed approximately 30 kg, with male *Paranthropus* weighing ca. 42 kg and male *Homo* (aff. *H. erectus*) ca. 55 kg.

Sterkfontein

Clarke (1988) proposed that the hominins in Member 4 at Sterkfontein sampled two taxa, namely *A. africanus* and a taxon represented by Stw 505, which Clarke considered a possible ancestor of *Paranthropus*. However, when the Stw 505 cranium was described in more detail by Lockwood and Tobias (1999) they concluded that it was morphologically distinct from

Paranthropus, and they chose to include it in *A. africanus*. Nevertheless, three years later Lockwood and Tobias (2002) once again raised the possibility of a second taxon in Member 4 when their analysis of the Member 4 cranial remains suggested that Stw 183 and Stw 255 were distinct from *A. africanus*, with each exhibiting "some derived characters of *A. aethiopicus*, *A. robustus*, and/or *A. boisei*" (Lockwood and Tobias, 2002: 446). However, an analysis by Wood (1991b) that focused on dental metrics found no evidence that "the Sterkfontein Member 4 hypodigm... is excessively variable" (Wood, 1991b: 75) when compared with either a fossil hominin reference sample (*P. boisei*) or extant reference sample (*Gorilla*). A more recent analysis of variation in dental crown shape by Moggi-Cecchi (2003) supported Wood's (1991b) results and found no conclusive evidence of a second species in Sterkfontein Member 4. Given the significant number of studies that have suggested the possibility of more than one species in this Member (Clarke, 1988, 1994a, 1994b, 1996; Kimbel and White, 1988; Kimbel and Rak, 1993; Lockwood, 1997; Lockwood and Moggi-Cecchi, 1998; Lockwood and Tobias, 2002) a comprehensive analysis combining cranial, mandibular, and dental evidence is needed to provide a more complete picture of morphological variation within this Member.

Kuman and Clarke (2000) analyzed the artifacts and associated hominin remains from Sterkfontein Member 5, which they concluded might have had a more complex geological history than first thought. One section, called the 'Oldowan infill' and faunally dated to ca. 2.0-1.7 Myr, contains numerous excavated artifacts (3245) and four hominin specimens of which two, Stw 566 and Stw 569, are assigned to *P. robustus*.

Gondolin

Two hominin teeth, a partial crown of a left M₁ or M₂, and a left M₂, were found in this cave, which is ca. 15 miles northwest of Swartkrans (Menter *et alii*, 1999). The first tooth is too fragmentary to attribute to a taxon although the authors point out that it is "probably not a 'robust' australopithecine" (Menter *et alii*, 1999: 303). The second tooth, GDA-2, is larger than any existing *P. robustus* molar, but is within the upper range of variation of *P. boisei*. Its discoverers assigned it to *Paranthropus* sp. indet.

Drimolen

This site is ca. 4 miles northwest of Swartkrans, and faunal correlation suggests the cave was filled ca. 1.5-2.0 Myr ago (Keyser, 2000). In the first eight years of excavation over 80 *P. robustus* specimens have been recovered (Keyser *et alii*, 2000), including DNH 7, an almost complete skull (Keyser, 2000). Keyser *et alii* (2000) claim it bridges the gap between the Swartkrans and Kromdraai hypodigms of *P. robustus*. The DNH 7 skull is believed to be female, and if so the pattern of sexual dimorphism in *P. robustus* is similar to that

seen in *P. boisei* (Wood *et alii*, 1994). A few of the hominin fossils from Drimolen have been attributed to *Homo* (sp. indet.).

Cooper's

In 2000, preliminary results of a new source of evidence of *P. robustus* were presented at the annual meeting of the American Association of Physical Anthropologists (Steininger and Berger, 2000). The specimen (COB 101) was a crushed partial right face including the maxilla with a right P³ and a disarticulated supraorbital torus. Since then, more evidence of *P. robustus* has been found at Cooper's Cave, including three isolated teeth (two deciduous molars and an unworn left M²), an edentulous juvenile mandible fragment, and numerous cranial fragments. Faunal correlations indicate that the specimens from this site are between 1.6-1.9 Myr (Berger *et alii*, 2003). Interestingly, this may be yet another site containing multiple hominin species as other specimens from this site have been attributed to *A. africanus* and *Homo* sp. indet. (Steininger and Berger, 2000).

East Africa

Koobi Fora

Hominin evidence found since 1988 and assigned to *Paranthropus* includes more of KNM-ER 1804, a fragmentary maxilla with a permanent M² crown, KNM-ER 13750, a partial adult cranium and endocast, and KNM-ER 15930, a left mandibular corpus with three permanent molar crowns and roots or partial roots of the canine and premolars. The three hominins were initially announced by Walker *et alii* in 1986 but were later described in more detail by Leakey and Walker (1988). Additional evidence of *Paranthropus* from Koobi Fora includes KNM-ER 23000, a ca. 1.9 Ma calvaria (Brown *et alii*, 1993). Brown *et alii* (1993) drew attention to the ways that the new calvaria illustrated the polymorphic nature of the *P. boisei* hypodigm citing KNM-ER 23000 as being most similar to OH 5 with respect to the pattern of the middle meningeal vessels, and the supraorbital tori, to KNM-ER 406 with respect to the triangular shape of the occipital and the high lambda, and to the recently described KNM-ER 13750 with respect to the morphology of the parietal bones. A right mandibular corpus, KNM-ER 25520, with M₂, M₃ and the roots of M₁, was discovered in 1992, but has only recently been described (Brown *et alii*, 2001). It is within the range of variation of the existing *P. boisei* hypodigm.

West Turkana

Four fossil specimens from the west side of Lake Turkana, KNM-WT 16005, a fragmentary adult mandible, KNM-WT 17000, an adult cranium, KNM-WT 17396, an isolated left molar, and KNM-WT 17400, an anterior cranium including much of the face, were described in detail by Leakey and Walker (1988). They assigned these specimens to *A. boisei*, but they repeated their previous suggestion (Walker *et alii*, 1986) that if the specific distinction between specimens such as KNM-WT

17000 and KNM-ER 406 is maintained with a larger sample "then the name *A. aethiopicus* would be available and valid" (Leakey and Walker, 1988: 23). Among the morphological differences they cited between the earlier and later material are an increase in cranial capacity, a more flexed cranial base, and decreased facial prognathism (Leakey and Walker, 1988).

Suwa (1989) examined the single premolar tooth attributed to KNM-WT 17000 and confirmed that it is a left P⁴. He also discovered the left P⁴ root and was then able to complete the attachment of the tooth crown to the cranium. This revealed a shallow palate for KNM-WT 17000, apparently similar to that of *P. robustus* from Swartkrans. The comparison of anterior tooth row length (I¹-C) to posterior tooth row length (P³-M³) places the specimen as "broadly intermediate between the Swartkrans and Sterkfontein samples, though closer to the former" (Suwa, 1989: 799). Suwa claimed that the P⁴ evidence supports recognizing KNM-WT 17000 as belonging to a species distinct from *P. boisei*, and he suggested that it samples a population in existence before any cladogenetic event that resulted in the East and southern African *Paranthropus* taxa we see in the post-2.3 Myr hominin fossil record.

Two more teeth from West Turkana, KNM-WT 17396, a left M₃, and KNM-WT 18600, a left P³, were described in Brown *et alii* (2001). Both specimens were said to be within the range of variation of the *P. boisei* hypodigm.

Omo

The cranium Omo-323-1976-896, which had been recovered in nine fragments in the Shungura Formation in 1976, was recently described in detail for the first time (Alemseged *et alii*, 2002). At 2.1 Myr it is the oldest known cranium of *P. boisei*. Alemseged *et alii* (2002) list several features the cranium shares with either *P. boisei* or *P. aethiopicus*, and the authors suggest Omo-323-1976-896 emphasizes "the anagenetic link between *A. aethiopicus* and *A. boisei*" (Alemseged *et alii*, 2002: 111). They also add "the nature of the projection of the mastoid process" as an additional example of a polymorphic character within *P. boisei* (*ibid*: 111).

White and Falk (1999) challenged Holloway's (1981) attribution of Omo L338y-6 to *A. africanus* rather than to *Paranthropus*. Their metrical analysis was unable to place the Omo L338y-6 fossil with either taxon, but White and Falk suggest that the presence of an enlarged left occipital sinus, believed absent by Holloway, indicates taxonomic affinity with *Paranthropus*.

Konso

Fossil evidence for *P. boisei* from Konso, located in Ethiopia, northeast of Kenya's Turkana region, is notable for several reasons (Suwa *et alii*, 1997). Its location adds to the geographic range of *Paranthropus* and as such may increase our understanding of the effects of geography on morphological variation. At 1.4 Myr-old they are some of the

TABLE 3. Size-adjusted dental CVs for *Paranthropus*

Population / Site Sample	Overall Mean	Incisor Mean	Canine Mean	Premolar Mean	Molar Mean
Drimolen	7.9	11.5	9.0	5.3	8.4
Swartkrans + Kromdraai	6.5	7.6	7.5	5.7	5.9
<i>P. robustus s.l.</i> , pre-1988	5.9	7.3	6.6	5.4	5.4
<i>P. robustus s.l.</i> , as of 2003	6.9	7.8	7.4	6.1	6.7
<i>P. boisei s.l.</i> , pre-1988	8.3	11.8	8.7	6.5	8.6
<i>P. boisei s.l.</i> , as of 2003	8.0	11.8	8.7	6.5	8.1

youngest *Paranthropus* fossils in East Africa, and KGA 10-525 is the first associated cranium and mandible of *P. boisei*. The Konso fossils were found in the same stratigraphic horizon as several early Acheulean artifacts, thus indicating possible sympatry of *Paranthropus* and *Homo*, if Acheulean artefacts can be reliably linked with *Homo* and not *Paranthropus*.

The cranial capacity of the Konso skull (KGA 10-525), at 545 cm³, is slightly higher than previously recorded for *P. boisei*. Other features which reportedly exceed the known range of variation in *P. boisei* include laterally facing zygomatics, the breadth of the palate and nasal aperture, the high position of the infraorbital foramen, and the posteriorly positioned sagittal crest. Some traits such as the laterally facing zygomatics resemble the pattern found in *P. robustus* while others such as the posteriorly positioned sagittal crest had only previously been found in *P. aethiopicus*.

Malema

A discovery in Malawi extended the known range of *P. boisei sensu lato* over 700 miles to the south (Kullmer *et alii*, 1999). The specimen, RC 911, is a maxilla fragment with left M¹ and partial M². A mandible, UR 501, attributed to *Homo rudolfensis* and found in the same level as RC 911, but at a different locality, suggests once again possible sympatry of *P. boisei* with at least one other hominin taxon.

Olduvai

Aiello *et alii* (1999) attributed the OH 36 ulna to *P. boisei* largely on the grounds that it was distinct from other ulnae believed to belong to the genus *Homo*. Comparison with KNM-ER 1500, postcranial material attributed by some (Grausz *et alii*, 1988), but not all (e.g., Wood, 1991a), researchers to *P. boisei*, was not possible due to the poor preservation of the KNM-ER 1500 ulna. Aiello *et alii* admit their proposal is speculative and suggested that the problems associated with allocating limb bones to *P. boisei* "remind us of how little we know about the evolution of the hominin postcranium" (Aiello *et alii*, 1999:109).

The effect of the new dental specimens on the taxonomy of *Paranthropus*

This section of the paper examines variation within *Paranthropus* with respect to simple linear mesiodistal (MD),

labiolingual (LL) and buccolingual (BL) measurements of the tooth crowns. Specifically we addressed the following questions. First, how do the new data from Drimolen affect any differences between the material from Kromdraai and that from Swartkrans (i.e., between *P. robustus* and *P. crassidens*)? Second, how do the new data from the southern African cave sites, including the Swartkrans material described since 1988 but excluding Cooper's site due to the lack of published data, affect our assessment of how many taxa are represented within the southern African hypodigm of *Paranthropus*? Third, how do the new data from East Africa affect our assessment of how many taxa are represented within the East African hypodigm of *Paranthropus*? Lastly, have the new data from both southern and East Africa blurred or maintained the distinction between the southern and East African hypodigms of *Paranthropus* (i.e., between *P. boisei sensu lato* and *P. robustus sensu lato*)?

The effect of the Drimolen evidence on the Swartkrans/Kromdraai distinction

There are 35 mesiodistal, labiolingual, and buccolingual dental measures that can be compared between the Swartkrans and Kromdraai hominins (including the Swartkrans specimens discovered since 1988). We calculated the ranges of these measures for each population and found that all but five are completely overlapping. Furthermore, three of the five variable ranges which are not entirely overlapping are only different by a tenth of a millimeter. In other words, the ranges overlap but one population extends beyond the other's range by 0.1mm. For two of the five variables, Kromdraai extended above the range of Swartkrans, and for the other three Kromdraai was below the Swartkrans range indicating no consistent pattern of difference. Unfortunately, due to the low number of Kromdraai specimens it is not possible to determine the statistical significance of any differences (or lack thereof) that may exist between these two groups of fossil teeth.

Drimolen falls within the combined range of the Swartkrans/Kromdraai sample for all but five of the 35 variables (86%). The five variables that did not were all below the range of the combined sample. The Drimolen specimens were below the median values of the combined Swartkrans/Kromdraai ranges for 26 (74%) of the measures. This suggests that while the Drimolen teeth are generally similar in size to the other southern African *Paranthropus* fossil evidence, they are predominantly in the lower half of the range, perhaps indicating a population-level

TABLE 4. Comparison of postcanine means. Southern vs. East African *Paranthropus*

Comparison	Tooth Type	Number of Significantly Different Variables	Average Level of Significance
Southern Africa vs. East Africa, pre-1988 specimens	premolars	9/16 (56%)	0.007
	molars	11/24 (46%)	0.006
Southern Africa vs. East Africa, specimens as of 2003	premolars	11/16 (69%)	0.014
	molars	16/24 (67%)	0.009

Dental CV*s

difference, but this may be a taphonomic artifact. The Drimolen specimens were closer to the Swartkrans averages for eleven of the variables examined and closer to the Kromdraai average for twenty-one of them. This split is consistent with an intermediate position for the Drimolen dental evidence, and with the hypothesis that the hominin fossil evidence from Drimolen, Swartkrans, and Kromdraai samples a single variable species.

We have also compared the coefficients of variation (CVs) between the site samples. Although the small size of the Kromdraai sample does not allow us to compare its variability to that of Swartkrans directly, we can combine these two samples and compare them to samples of other fossil hominin taxa, including *P. boisei sensu lato*, to see if variation within the combined sample exceeds that in other roughly contemporaneous hominin groups. Using a size-adjusted CV (hereafter denoted as CV*) (Sokal and Braumann, 1980) we calculated the variability of each dental metric in the combined Swartkrans/Kromdraai sample and compared that to the variability in several different populations including *P. boisei sensu lato* and the material from Drimolen. We also calculated and compared the average dental CV* for each sample and for each tooth type (incisors, canines, premolars and molars) (Table 3).

The CV* results show that the combined Swartkrans/Kromdraai sample does not exhibit a high level of variation compared to other site and taxon samples of *Paranthropus*. The average CV* value of the Swartkrans/Kromdraai sample at 6.5 is below the value for *P. boisei sensu lato* (8.3) and is less than the CV* for the single site *P. robustus* sample from Drimolen (7.9). However, the Drimolen sample is itself relatively variable since the CV* for all the southern African *Paranthropus* dental evidence, including that from Drimolen, is only 6.9.

The effect of post-1988 fossil evidence on the overall variability of the southern African hypodigm of *Paranthropus*

Since 1988, the southern African hypodigm of *Paranthropus* has been expanded by the discovery of Drimolen, and as a result of the efforts of Grine (1988b; 1989; Grine and Daegling, 1993; Grine and Strait, 1994) and Susman (1988; 1989; Susman *et alii*, 2001) who, with Brain, have been instrumental in publishing new and existing evidence excavated by Brain at Swartkrans. These additions to the hypodigm have resulted in an increase in the overall southern African *Paranthropus* dental CV* from 5.9 to 6.9. This increase is seen across all the tooth types (Table 3). The

range for each tooth (e.g., RI', LM's, etc.) increased by an average of 0.8 mm. However, even with this increase, the CV* for the southern African *Paranthropus* hypodigm is still less than that for *P. boisei sensu lato*, and for the single site sample from Drimolen.

The effect of post-1988 fossil evidence on variation within the East African *Paranthropus* hypodigm

Despite some important individual discoveries, in terms of the number of additional specimens the East African *Paranthropus* hypodigm has not expanded to the extent the southern African hypodigm has. Unfortunately, there are insufficient published dental measurements for *P. aethiopicus* for them to be compared with *P. boisei sensu stricto* in any meaningful statistical way.

The CV* for the overall East African *Paranthropus* dental hypodigm (*P. boisei sensu lato*) has actually decreased slightly with the addition of fossils published since 1988 (Table 2). Although the difference is small (0.3), it does indicate the level of variability has not increased significantly with the addition of the new fossil evidence. This suggests that with respect to simple dental metrics we may have an adequate East African *Paranthropus* sample. If we compare ranges of the dental metrics before and after the addition of the post-1988 evidence there is an average increase in the ranges of 0.4 mm, but this is on the basis of only six variables; the sample sizes of most East African *Paranthropus* dental metrics have not increased since 1988.

The effect of post-1988 evidence on the distinction between the southern and East African hypodigms of *Paranthropus*

An informal comparison of the means of the samples from the two regions shows that the East African *Paranthropus* dental hypodigm is larger than the southern African one for all premolar and molar teeth. While the larger size of *P. boisei sensu lato* postcanine teeth will not come as a surprise to many, the fact that this relationship holds for the width and length of every premolar and molar tooth with the addition of the new material suggests that a real population difference is being maintained between these two regions.

When examining only the premolars (8 teeth; 16 measures) nine variables (56%) were significantly different between the two regional samples prior to the addition of the post-1988 specimens. Adding the specimens published since 1988, the

number of significantly different variables increases to 11 (69%). The molars (12 teeth; 24 measures) present a similar story. Adding the new specimens increases the number of significantly different variables from 11 (46%) to 16 (67%) (Table 4). These results suggest that the distinction between the southern and East African hypodigms of *Paranthropus* is not only maintained, but has increased with the addition of new fossil specimens accumulated over the past 15 years.

We now use the results from our metric analysis of dental variables as well as the fossil evidence discussed earlier to address the questions of *Paranthropus* paleobiology set out in the introduction. In short, these questions are: (1) How many species should be recognized within *Paranthropus*? (2) Are any temporal trends evident within *Paranthropus*? (3) Can the phylogenetic relationships among *Paranthropus* taxa be determined with any reliability?

***Paranthropus* - How many species?**

Is *P. crassidens* a distinct species?

Grine is the main proponent for maintaining, or reinstating, a species level distinction among the two oldest samples of *Paranthropus* from southern Africa (e.g., Grine, 1989; Grine in Brain, 1993). As we see it, the argument is based on three observations: (1) the temporally later Swartkrans fossils are morphologically distinct from the earlier Kromdraai sample; (2) the Swartkrans fossils do not appear to change significantly despite approximately 0.8 Myr of time represented in Members 1-3; and (3) Swartkrans and Kromdraai are not far enough apart for any difference to be due to geographical variation. Little or no change over the 0.8 Myr at Swartkrans does not rule out the possibility that directional change could have occurred in the 0.2 Myr that separates Swartkrans from Kromdraai (Thackeray *et alii*, 2001). Nevertheless, arguments (2) and (3) appear to be sound. Grine's case thus rests on whether or not one accepts the evidence for the morphological distinctiveness of the remains from the two sites. The dental crown metrical data do not support more than one *Paranthropus* taxon in southern Africa, and this was also the conclusion of Wood's (1991b) study of a smaller data set. If there is a taxonomically significant difference between *P. robustus* (i.e., the Kromdraai, Drimolen, Gondolin, and Cooper's site samples) and *P. crassidens* (i.e., the Swartkrans site sample) then it does not show up in simple dental metrics. Also the single site sample from Drimolen apparently contains as much non-metrical dental variation as is seen in the combined Swartkrans and Kromdraai site samples (Keyser *et alii*, 2000).

Is *P. aethiopicus* a 'good' species?

Two relevant studies, Kimbel *et alii* (1988) and Suwa (1988) were included in the Grine volume. Kimbel *et alii* (1988) studied the morphology of KNM-WT 17000 and concluded that it did not belong to *P. boisei sensu stricto*, and they supported its allocation to *P. aethiopicus*. Suwa (1988) examined the

premolar morphology of the specimens from Omo and concluded that the results of his analyses "support suggestions of specific distinction between earlier and later 'robust' australopithecines of East Africa" (Suwa, 1988: 219). This study, together with the earlier papers of Walker *et alii* (1986) and Leakey and Walker (1988), initiated debate about the legitimacy of breaking up what many regard as a single anagenetic lineage, *P. boisei sensu lato*, into two time successive taxa, *P. aethiopicus* and *P. boisei*.

Several papers since Grine's 1988 book have addressed this issue. Wood's (1992) morphometric analysis of craniodental and mandibular remains concluded that the older *Paranthropus* fossil evidence from Omo and West Turkana was distinct from, but closely related to, the later remains attributed to *P. boisei sensu stricto*. Wood *et alii* (1994) assessed temporal trends in *P. boisei sensu lato* and found evidence for "a relatively abrupt change around 2.2-2.3 Myr" (Wood *et alii*, 1994: 117) in 20% of the mandibular and dental variables examined. This is consistent with the findings of Suwa (1988), and those of a later analysis by Suwa *et alii* (1996), based on evidence from the mandibular postcanine teeth. These studies have established *P. aethiopicus* as a valid taxon in the minds of many researchers. However, since then Ramirez-Rozzi concluded on the basis of enamel microstructure that "no more than one species can be recognized" (Ramirez-Rozzi, 1988: 564). Curnoe (2001) has subsequently used the coefficient of variation (CV) to test the possibility of more than one taxon being represented in the East African *Paranthropus* hypodigm. He first identified five variables in *Paranthropus* that he determined were not affected by a high level of sexual dimorphism. Then he obtained coefficients of variation for these traits by combining KNM-WT 17000 with a sample of crania attributed to *P. boisei sensu stricto* and compared these to CVs of the same measurements in bonobos. From these Curnoe concluded that the CVs for cranial capacity, superior facial breadth, interorbital midline, orbital breadth, and bizygomatic breadth in East African *Paranthropus* were not large enough to justify more than one species. Finally, Alemseged *et alii* (2002) suggested that the cranium from Omo (Omo 323-1976-896) they assign to *P. boisei* is evidence of an anagenetic link between *P. boisei* and *P. aethiopicus*.

Despite recent studies that have emphasized the polymorphic nature of *P. boisei sensu stricto* (e.g., Brown *et alii*, 1993; Suwa *et alii*, 1997) there is nothing about the nature of the polymorphism that weakens the hypothesis that *P. aethiopicus* is most likely a valid taxon that is closely related to *P. boisei sensu stricto*. The origin of *P. aethiopicus* may have been part of an episode of intensive faunal change at 2.8 Myr, and the transition to *P. boisei* occurred not long after an increase in faunal variability at 2.5 Myr (Bobé *et alii*, 2002). Based on the lack of temporal overlap between the two taxa, the possibility remains that *P. aethiopicus* and *P. boisei sensu stricto* represent a single

ancestor/descendant anagenetic lineage. The validity of *P. aethiopicus* will ultimately rest on the discovery of additional fossil evidence from between 3.0 and 2.3 My in East Africa.

Does the *P. boisei sensu stricto* hypodigm subsume more than one species?

Some researchers have suggested that the size and shape differences within the hypodigm of *P. boisei sensu stricto* are greater than one would expect from the main factors contributing to intraspecific variation (e.g., within sex variation, sexual dimorphism, geographic variation, etc.) (Dean, 1988; Groves, 1989). However, Wood *et alii* (1991) showed that the degree and pattern of the craniodental variation within *P. boisei sensu stricto* was similar to the pattern and degree of variation due to sexual dimorphism in the two extant taxa that are almost certainly most closely related to *Paranthropus*, *Homo sapiens* and *Pan*. Furthermore, when Silverman *et alii* (2001) compared variation in mandible size within *P. boisei sensu stricto* with variation in closely-related extant taxa they did not find it to be excessive, and this was without taking into account the influence of taphonomic factors such as erosion artificially reducing the size of mandibular corpora and the potential of matrix-filled cracking to artificially increase the size of the corpus. Furthermore, Wood and Lieberman (2001) found no evidence that the new Konso fossils significantly exceeded the pre-Konso range of variation of *P. boisei*. The results of our own metrical analyses are also consistent with a single variable species interpretation for the *P. boisei sensu stricto* hypodigm (Table 3).

Are the southern and East African *Paranthropus* hypodigms taxonomically distinct?

In 1967, Tobias suggested that the two regional samples of East and southern Africa should be subsumed within a single species, and the name with priority would be *P. robustus*. More recently, finds such as KGA 10-525 and KNM-ER 23000 have caused others (e.g., Delson, 1997) to call for a reexamination of the taxonomy of *Paranthropus*. Suwa *et alii* (1997) suggest that the Konso skull contains some 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. Finally, one of the hominin teeth from Gondolin exceeds the size range known for *P. robustus* but is within the size range known for *P. boisei* (Menter *et alii*, 1999). Nevertheless, the results of our own metrical analysis suggest that the enlarged regional hypodigms are still significantly different, and thus there are good reasons to maintain the specific distinction between *P. robustus* and *P. boisei* (Table 4).

Temporal trends within *Paranthropus*

Three studies have investigated *Paranthropus* taxa for evidence of anagenetic evolution. Two concentrated on craniodental remains. One of these used Loess regression methods to

search for any evidence of trends in the metrics of dental and mandibular specimens from the Omo region (Wood *et alii*, 1994), and found little evidence of consistent trends within *P. boisei sensu stricto*. The second concentrated on the sample of craniodental remains from a single site, Swartkrans, and stressed the "morphometrical similarities among the various Swartkrans lithostratigraphic samples" (Grine in Brain, 1993: p.107). The third study looked for any evidence of a trend in cranial capacity through time in *P. boisei sensu lato* and *P. boisei sensu stricto* and found that cranial capacity did show an increase in *P. boisei sensu stricto* between 2.4 and 1.4 Myr (Elton *et alii*, 2001). This is across a million year span during which there is no evidence of any increase in body mass in that taxon. Thus, the available evidence suggests that one cannot generalize about temporal trends in *Paranthropus* morphology. Each variable has to be assessed for evidence of trends.

Phylogenetic relationships among *Paranthropus* taxa

Wood and Chamberlain (1987) noted that in order for *Paranthropus* to be a valid genus, the members of that genus needed to be monophyletic (i.e., descended from a common ancestor). Therefore, the southern and East African *Paranthropus* taxa had to be more closely related to each other than to any other taxon. Although the majority of phylogenies published around that time were consistent with *Paranthropus* monophyly (e.g., Johanson and White, 1979; Tobias, 1980; Boaz [in Cronin *et alii*, 1981]; Olson, 1985; Delson, 1986; Skelton *et alii*, 1986; Wood and Chamberlain, 1986) it was more of an assumption than an empirically supported hypothesis. Thus, Wood and Chamberlain (1987) cautioned against assuming monophyly and suggested that there was preliminary evidence that indicated that at least some of the synapomorphies linking the southern and East African *Paranthropus* taxa may be homoplasies.

Cladistic analyses conducted since 1988 have done little to resolve the issue. As discussed earlier, Skelton and McHenry (1992) argued against *Paranthropus* being a valid clade since *P. aethiopicus* did not appear to be particularly closely related to other *Paranthropus* taxa. Strait *et alii*'s (1997) analysis, however, contradicted these results and supported *Paranthropus* monophyly. McCollum subsequently argued against the work of Strait *et alii* (1997) on the basis that many of the traits used were likely not independent and therefore some anatomical regions were unknowingly weighted in terms of the number of independent variables. Suwa *et alii* (1997) suggested that the combination of southern and East African regional traits in the Konso specimen (KGA 10-525) strengthens the case for *Paranthropus* monophyly, while Collard and Wood (2001) showed that it is unlikely that the masticatory traits that support *Paranthropus* monophyly are any more prone to homoplasy than other craniodental traits.

In summary, most research in the period since 1988 is consistent with *Paranthropus* monophyly. The cogent evidence

against monophyly was reviewed in Wood (1988), and none appears to have been published since. However, Collard and Wood (2000) have suggested that conventional craniodental data, be they metrical or non-metrical, may not be reliable indicators of phylogeny, so any support for *Paranthropus* monophyly may be weakened because of homoplasy.

Conclusions

The fossils of *Paranthropus* discovered or described since the publication of the Evolutionary History of the "Robust" Australopithecines (Grine, 1988a) have added significantly to our understanding of this important taxon. Specimens from Konso, Ethiopia have provided a better sample of the later stages of *P. boisei sensu stricto*, and the detailed description of the oldest cranium in this taxon, Omo-323-1976-896 from the Shungura Formation, has added to our knowledge of its early stages. A well-preserved skull, DNH 7, was discovered at what is proving to be a prolific hominin fossil site, Drimolen. The UR911 maxilla from Malawi has considerably expanded the geographic range of East African *Paranthropus*.

In addition to the specimens that have been discovered and described, we have also learned a good deal from new interpretations of the existing fossil evidence. Within the areas of systematics, we have come to understand that many of the traits once interpreted as being shared between *Paranthropus* and *Homo* because they were inherited from a common ancestor are either more likely the result of homoplasy, or are not shared at all. Such is the case with facial orthognathism (Leakey *et alii*, 2001) and cranial capacity relative to earlier hominins (Elton *et alii*, 2001). It has also been confirmed that *P. boisei* was hyper-robust and strongly derived in its craniofacial morphology to a degree not anticipated by comparative studies of allometry (e.g., Wood and Stack, 1980; Corruccini and Gill, 1993).

While certain fossils have increased the variability within *Paranthropus*, with the possible exception of added support for *P. aethiopicus* being a valid taxon, speciosity within this genus has not been greatly affected by the post-1988 evidence. We provisionally recognize *P. aethiopicus*, *P. boisei*, and *P. robustus* as valid taxa. Evidence for evolutionary trends within each taxon need to be further investigated on a character-by-character basis. Based on new fossil specimens (e.g., KGA 10-525, KNM-ER 23000, GDA-2) and on analyses conducted in 1988 and thereafter (e.g., Wood, 1992; Strait *et alii*, 1997) the monophyletic status of *Paranthropus* seems to be supported by most of, but by no means all (e.g., Wood, 1988) of, the evidence. However, there is a general acceptance that homoplasy is more prevalent in human evolution than was previously believed (e.g., Wood, 1992; Collard and Wood, 1999), and with the discovery of *A. garhi* (Asfaw *et alii*, 1999) it is apparent that robust mandibles with similarly megadont postcanine teeth, and with long premolar and molar tooth rows, are being associated with what are claimed to be two distinct forms of cranial morphology.

Our knowledge of *Paranthropus* behavior has also advanced significantly. There is circumstantial evidence that *Paranthropus* was a tool-user, if not a toolmaker. The bone tools from Swartkrans (Backwell and d'Errico 2001, 2003) and Drimolen (Keyser *et alii*, 2000), the results of Susman's many investigations (1988a, 1988b, 1989, 1991), and recent work at Sterkfontein Member 5 (Kuman and Clarke, 2000) are making researchers think seriously about the idea that early *Homo* was not alone in this endeavor. And why not? Studies of behavior in extant primates have shown that many of our closest relatives use, and occasionally make, tools (Boesch and Boesch, 1990; McGrew, 1992, 1998; van Schaik *et alii*, 2003) and recent work has shown that some of this behavior may be capable of being uncovered in the fossil record (Mercader and Panger, 2002). If southern African *Paranthropus* was using the tools uncovered at Swartkrans, then this could help to explain some of the results of the biochemical analyses of their diet which suggest that *P. robustus* was omnivorous (Lee-Thorp *et alii*, 1994; Lee-Thorp *et alii*, 2000; Sillen, 1992; Sillen *et alii*, 1995). A detailed investigation of the use-wear on the bone tools from Swartkrans indicates they are likely to have been used for digging into termite mounds (Backwell and D'Errico, 2001). The consumption of termites could be the reason for the proportion of C₄ relative to C₃ found in studies of *P. robustus* stable isotope composition. The results of trace mineral analyses (Sillen *et alii*, 1998) indicating that *P. robustus* occupied grasslands is consistent with this interpretation.

With respect to habitat, researchers have tended to interpret the pre-1988 evidence as suggesting that *Paranthropus* taxa favored a closed environment. However, *Paranthropus* is now believed to be a taxon that ventured into open grassland areas. In addition to the conclusions drawn from ⁸⁷Sr/⁸⁶Sr ratios derived from the southern African hypodigm (Sillen *et alii*, 1998), evidence is mounting in the form of paleoenvironmental reconstructions at Konso, Malema, and Peninj, and together with independent paleoecological analyses (Reed, 1997; Shipman and Harris, 1988) all pointing to the use of open habitats by *P. boisei*.

Studies of dental growth and development (Dean *et alii*, 1993; Dean *et alii*, 2001), inner ear morphology (Spoor, 1993), and brain shape (Falk *et alii*, 2000) all seem to be indicating that *Paranthropus* was more ape-like than previously acknowledged. It will be interesting to see how these studies can be reconciled with those that suggest evidence of later *Homo*-like behavior (e.g., Brain *et alii*, 1988; Susman, 1988a, 1988b, 1989, 1991).

Many other interesting questions await the recovery and study of additional fossil evidence. Will associated skeletons of *Paranthropus boisei sensu stricto* support, or weaken, the hypothesis that *Paranthropus* postcrania have already been correctly identified (e.g., Grausz *et alii*, 1988; Susman, 1989, 1991; Susman *et alii*, 2001)? Were *Paranthropus* and *Homo* sympatric? What was the nature of the adaptation that led to

the derived craniodental morphology of *Paranthropus*? Are *Paranthropus* taxa dietary specialists, or was their diet more eurytopic (e.g., Wood and Strait, 2004)

Hopefully *Paranthropus* will not be further relegated to the sidelines in human evolutionary studies. We are convinced that if studies of *Paranthropus* and its context are encouraged, then it will not be long before they will provide valuable insights into our understanding of the ontogeny, variation, phylogeny, functional morphology, behavior, and paleoecology of this enigmatic taxon. And in doing so we will also be providing an important comparative context for the study of hominin taxa more closely related to modern humans.

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