Hominid Cranium From Omo: Description and Taxonomy of Omo-323-1976-896

Zeresenay Alemseged,[1]* Yves Coppens,[2] and Denis Geraads[3]

[1]*Institute of Human Origins, Arizona State University, Tempe, Arizona 85287-4101*
[2]*Chaire de Paléoanthropologie et Préhistoire, Collège de France, 75005 Paris, France*
[3]*CNRS, UPR 2147, F-75014 Paris, France*

ABSTRACT Omo-323-1976-896, a partial hominid cranium dated to ca. 2.1 from the Member G, Unit G-8 of the Shungura Formation, lower Omo Basin of Ethiopia, is described. It is suggested that the specimen is an adult male based on the well-developed and completely fused sagittal crest; heavily worn teeth; relatively large canine; and size of the articular eminence. Omo-323 consists of fragments of the frontal, both temporals, occipital, parietals, and the right maxilla, and is attributed to *Australopithecus boisei*, making it the oldest known cranium of this species. The specimen shares features with *Australopithecus aethiopicus* (KNM-WT 17000), thus supporting the existence of an evolving East African robust lineage between ca. 2.6–1.2 Ma. The morphology of Omo-323 increases our knowledge of the intraspecific variability of *A.boisei*. Am J Phys Anthropol 117: 103–112, 2002. © 2002 Wiley-Liss, Inc.

Hominid remains were part of the mammalian fauna recovered from the Shungura Formation, in the lower Omo basin, Ethiopia, since the beginning of systematic exploration and research in 1967 (Arambourg and Coppens, 1967, 1968; Howell, 1968). About 220 hominid specimens, most falling in the time range 3–2 Myr, were collected by two international research teams. Despite this effort, this period of hominid history is still poorly known compared with the 4–3 Myr interval, which is represented by hominid remains from Hadar and Middle Awash (Ethiopia), Laetoli (Tanzania), Allia Bay and Kanapoi (Kenya), and Bahr el Ghazal (Chad) (Taieb et al., 1975; Johanson and Taieb, 1976; White, 1977, 1980, 1985; Johanson et al., 1978, 1982; Kimbel et al., 1994; White et al., 1981, 1984, White et al., 1994; Asfaw, 1987; Leakey et al., 1995; Brunet et al., 1995, 1996). Sites dated to 3–2 Myr are also outnumbered by those younger than 2 Myr, such as those at Koobi Fora and other East and southern African sites (Brown and Feibel, 1985; Feibel et al., 1989; Grine, 1988; Brain et al., 1988). The Shungura Formation is therefore still the only well-dated and relatively continuous sequence that allows researchers to trace the evolution of hominid lineages in the 3–2 Myr interval.

Several aspects of the evolution of the robust australopiths remain unclear. First, there is no consensus on whether these taxa form a monophyletic group, or not, (White et al., 1981; Rak, 1983; Kimbel, 1984; Kimbel et al., 1988; Suwa, 1988; Wood and Chamberlain, 1987; Wood, 1988; Skelton and McHenry, 1992; Suwa et al., 1996; Strait et al., 1997). Secondly, concerning the East African robust

australopithecines, there is a clear divergence between those workers who recognize A. aethiopicus (White et al., 1981; Rak, 1983; Kimbel, 1984; Kimbel et al., 1988; Suwa, 1988; Grine, 1988; Wood and Chamberlain, 1987; Wood, 1988; Skelton and McHenry, 1992; Suwa et al., 1996; Strait et al., 1997) and those who consider that its hypodigm falls within an acceptable range of variation for a paleontological species, and who therefore include it within A. boisei (Walker and Leakey, 1988; Brown et al., 1993). Some have suggested that A. boisei is not closely related to A. aethiopicus (Skelton and McHenry, 1992; Ramirez-Rozzi, 1993). For those who accept the existence of an East African robust australopith lineage, the modalities of morphological changes within the lineage are not completely understood, notwithstanding the contributions of Suwa (1988), Suwa et al. (1996), and Wood et al. (1994).

Cranial hominid remains are especially rare between 3–2 Myr. For example, before the discovery of KNM-WT 17000 (Walker et al., 1986), the East African robust australopith lineage in this period was represented only by teeth and mandibles. As a result, all cranial elements encountered in this time interval are of great value. More fossil evidence is

essential to improve our understanding of intra- and interspecific variability and the relationships among the different hominid taxa. However, thorough description and analysis of existing fossil specimens within the 3–2 Myr time period can also contribute substantially to our understanding. The objective of this paper is to describe and assess the systematic significance of the fragmentary cranium, Omo-323-1976-896 (hereafter referred to as Omo-323) from the Shungura Formation of Ethiopia.

CONTEXT AND PRESERVATION

Omo-323 was recovered in 1976 from stratigraphic unit G-8 of Member G, dated to around 2.1 Myr (Coppens and Sakka, 1980; Guillemot, personal communication; Feibel et al., 1989). Fragments were labeled with letters in the sequence of discovery, but many have been joined subsequently. To our knowledge, the lettered fragments have never been published. Thus, in this paper fragments that can be joined will be differentiated by letter.[1]

The Omo-323 cranium comprises the following fragments and composite fragments:

1. Omo-323-1976-896a. Frontal fragment, including the glabella, the medial thirds of both supraorbital margins, the anterior part of the frontal squama, and the superior portion of the nasal bones.
2. Omo-323-1976-896b. Left temporal fragment, including the mastoid process, mandibular fossa, petrous pyramid, and tympanic elements.
3. Omo-323-1976-896c. Posterior calvarial fragment, including parts of the occipital squama, right parietal, and temporal, the latter including the mandibular fossa.
4. Omo-323-1976-896d. Fragment of right petrous pyramid.
5. Omo-323-1976-896e. Fragment of left zygomatic process.
6. Omo-323-1976-896f. Fragment of right and left parietals, including part of the sagittal crest.
7. Omo-323-1976-896g. Right maxillary fragment, with the worn crowns and roots of P^3–M^1.
8. Omo-323-1976-896h. Isolated upper left canine with heavily worn and labially damaged crown, but complete root.
9. Omo-323-1976-896i. Left P^4, with heavily damaged crown but almost complete roots.

Hereafter, each fragment will be referred to as Omo323-896 a, b, or c, etc.

DESCRIPTION AND COMPARISON
Sex and age

In Omo-323, the sagittal crest is strong and completely fused; canine, premolars, and molars are heavily worn; the preserved canine is bigger than those in OH 5; and the articular eminence (and the glenoid region in general) is close in size to male specimens of robust australopiths. We think therefore that Omo-323 is an adult male specimen.

Frontal bone (Fig. 1D,E)

The frontal fragment (Omo323-896a) consists of the glabella, the anterior part of the frontal squama, and medial parts of both supraorbital margins. Posteriorly the bone is preserved up to a distance of 36 mm from the glabella. Laterally, the supraorbital tori are broken medial to the zygomaticofrontal suture. Endocranially, the impressions of the frontal lobes are preserved up to a distance of 23.5 mm posteriorly from their tips. The region anterior to the tips of the insertions of the lobes is abraded, exposing badly damaged frontal sinuses. A good portion of the ethmoid notch is visible in this region.

The supraorbital notch is well-defined on the right. The superior aspect of the supraorbital tori is characterized by foramina, and the glabellar region is vermiculate. The supraorbital tori are narrower anteroposteriorly than those of A. robustus (e.g., SK-48) and KNM-ER 406, and still narrower than those of OH 5. The form of the supraorbital tori is variable in robust australopiths (Brown et al., 1993), but the general form of the tori and the orientation of the orbital rims in Omo-323 are similar to what is observed in KNM-WT 17000. The tori are weak and anteroposteriorly narrow. The anteroposterior distances measured at the lateral parts of the tori, as preserved, are 10.7 mm on the left and 9.4 on the right. However, instead of being flat on their superior surface as they are in KNM-WT 17000, they are sagittally convex.

The glabella is not as prominent in Omo-323 as it is in most A. boisei and A. robustus specimens, in which it is located on a rounded projection. In Omo-323, as in A. aethiopicus and some A. boisei specimens (KNM-ER 13750 and KNM-ER 23000), the region between the medial ends of the supraorbital margins is recessed. Moreover, the glabella in Omo-323 is bounded by two depressions, one above and the other below.

The frontal trigon in Omo-323 is shallow as in KNM-WT 17000, but the temporal lines bounding it posteriorly are not as well-defined. Posteriorly the frontal is preserved up to a distance of 24.3 mm from the chord connecting the highest points on the superior parts of the supraorbital tori. At this level, the thickness of the frontal squama is 6.2 mm on the right and 5.8 mm on the left. Based on the cresting pattern and narrowness of the frontal, it can be inferred that the postorbital constriction was strong in Omo-323.

Endocranially, the deep anterior fossae are slightly asymmetrical. The right is situated more anteriorly than the left. The 9 mm of preserved frontal crest is 2.5 mm wide and widens posteriorly. On the left side of the base of the crest is a groove which resembles that seen

---

[1]In some papers and on some casts, the specimen is referred to as Omo-323-1976-898. This should be corrected, as the latter represents the hominid talus found in the same locality.
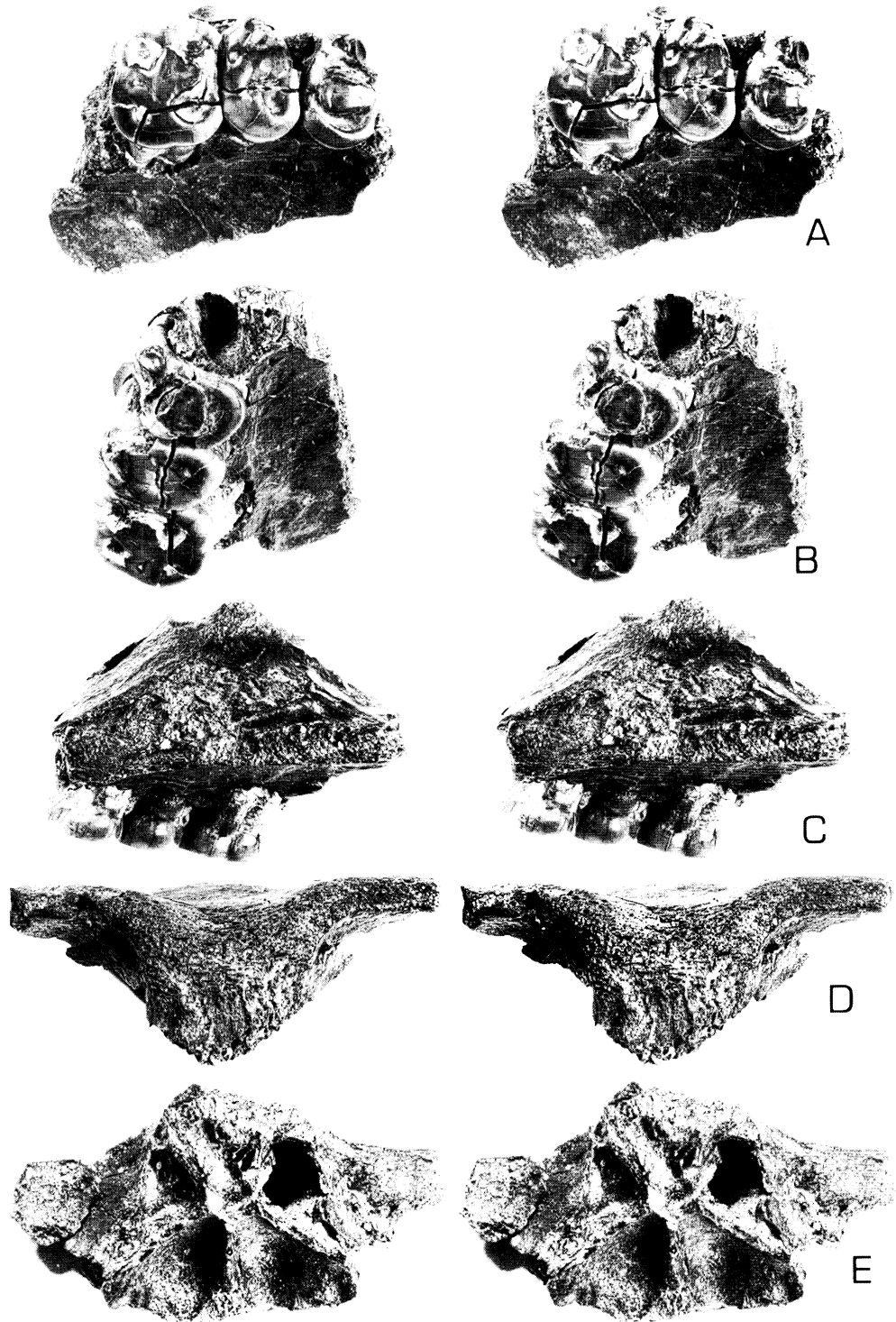
Fig. 1. Omo-323. Stereo views. **A, B:** Right maxilla occlusal view (Omo-323-896g). **C:** Right maxilla medial view (Omo-323-896g). **D:** Frontal anterior view (Omo-323-896a). **E:** Frontal endocranial view (Omo-323-896a). Scale, ×1 for all.

in the crest of OH 5. The tips of the frontal lobes are narrow. The morphology of this region was recently found to distinguish robust australopith morphology from A. africanus (Falk et al., 2000). We compared this region in Omo-323 and OH 5, using plasticine to make negatives of the endocast. We also compared it with the endocast of Sts 5 and drawings of other specimens (Falk et al., 2000). We noted that in Omo-323 the impressions of the lobes are narrow anteriorly as in

OH 5, but unlike the latter they quickly become wider superoposteriorly. In contrast, they clearly differ from the frontal lobes of A. africanus, in which the anterior parts are wide.

Temporal bone (fig. 2c,d)

The left temporal bone (Omo-323-896b) preserves the mastoid process, petrous pyramid, and mandibular fossa. The right temporal is in two pieces (part
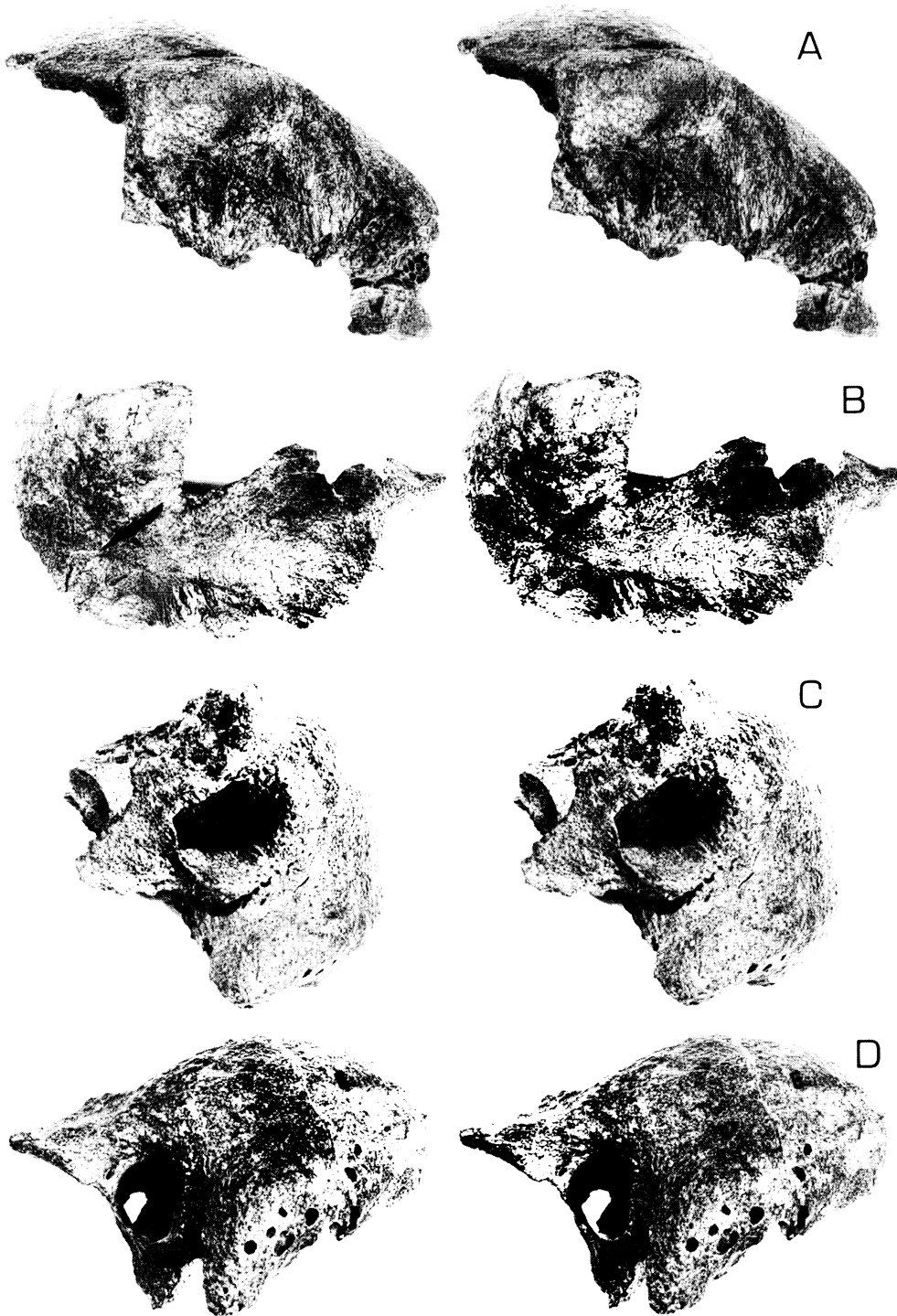
Fig. 2. Omo-323. Stereo views. **A:** Occipital inferior view (Omo-323-896c); scale, ×2/3. **B:** Occipital posterolateral view (Omo-323-896c); scale, ×3/5. **C:** Temporal inferolateral view (Omo-323-896b). **D:** Temporal lateral view (Omo-323-896b); scale, ×1 for C and D.

of Omo-323-896c and Omo-323-896d). The first is in contact with the occipital (Omo-323-896c) and stretches from asterion to the anterior limit of the articular eminence. However, this area is only partially preserved, as the temporal squama, part of the mastoid process, and much of the petrous pyramid are lacking. The second (Omo-323-896d) is a fragment of the posterosuperior part of the right petrous pyramid, with the internal auditory meatus and superior rim of the petrous pyramid.

Laterally the mastoid process is intact. The tympanic is largely preserved on the left side (Omo-323-896b). All elements between the petrous bone, the tympanic, and the mastoid process, i.e., the styloid process, vaginal process, and rim of the carotid canal, are absent. But medial to the tympanic, part of the jugular fossa, and a small part of the superior rim of the carotid canal which is in continuity with the jugular fossa, are visible. On the medial side of the left mastoid process, the digastric groove is not

preserved due to abrasion. The description of the temporal is based on information from both sides.

The mastoid process is abraded medially, exposing a very pneumatized surface. The pneumatization extends into the squamosal region. The abrasion is more pronounced on the right side, causing the loss of a considerable part of the mastoid process. The long axis of the mastoid process is projected further antero-inferiorly, with its tip extending beyond the coronal plane of the external auditory meatus. The distance between the most antero-inferior part of the mastoid process (the tip) and asterion is 46 mm. In OH 5 and KNM-ER 406, the process is more rounded, and it is smaller in KNM-ER 23000. In KNM-WT 17000 it is only slightly more developed than that of the great apes. The anterosuperior surface of the mastoid process in Omo-323 is separated from the tympanic plate by a mediolateral groove. In lateral view, the mastoid crest is well-defined and divides the mastoid process into postero-inferior and anterosuperior regions. The supramastoid crest, which is not pronounced in Omo-323, is closer to what is observed in KNM-ER 13750 and KNM-ER 406, whereas the crest is more developed in OH 5 and KNM-ER 23000, and is still more marked in KNM-WT 17000. There is a clear distinction between the supramastoid and mastoid crests, which are separated by a sulcus. This feature resembles the condition in *A. boisei*, particularly KNM-ER 407. In contrast, there is no such sulcus in KNM-WT 17000.

The external auditory meatus is elliptical in cross section. The major axis is 13 mm, and is parallel to the tympanic plate. The antero-inferior wall of the external auditory meatus, which is mainly represented by the tympanic, is thin. On the lateral side of the mastoid process, a weak horizontal crest is visible above the porion and is the continuation of the suprameatal crest.

The glenoid region exhibits a mixture of features observed in both *A. boisei* and KNM-WT 17000. It resembles the latter in that the articular eminence becomes wider medially to produce a broad-based, inferiorly projecting, entoglenoid process. In *A. boisei*, the entoglenoid process is more confined and projects postero-inferiorly. This is considered to be autapomorphic in *A. boisei* (Wood, 1991; Kimbel, personal communication). Omo-323 has a deep mandibular fossa with a prominent articular eminence as in *A. boisei*. Although the depth of the mandibular fossa is comparable to that of OH 5, the shape of the articular eminence, and the size, position, and form of the entoglenoid processes in Omo-323 are more similar to that of KNM-WT 17000. The width of the eminence from the ectoglenoid to entoglenoid processes is ca. 26.5 mm.

In Omo-323, the postglenoid processes are small in comparison to those of OH 5, KNM-ER 406, KNM-ER 13750, KNM-WT 17000, and *A. robustus*. The position of the process in Omo-323 is intermediate between that of KNM-WT 17000, where it is situated medially, and those of OH 5, KNM-ER 406, and KNM-ER 13750, where it is more lateral. The medially situated postglenoid process in KNM-WT 17000 is distinct, and appears to be related to the lateral expansion of the posterior root of the zygomatic arch. In Omo-323, the postglenoid process is clearly separated from the tympanic, as in KNM-WT 17000, whereas in OH 5, KNM-ER 406, KNM-ER 13750, and KNM-ER 23000, it is almost fused with the tympanic. The distance between the uppermost part of the entoglenoid and the ectoglenoid processes in Omo-323 (36.2 mm) is similar to those of KNM-WT 17000 and KNM-ER 13750.

The right temporal is broken slightly anterior to the level of the rim of the foramen ovale. The major axis of the foramen spinosum is ca. 1.8 mm long, and that of the foramen ovale is at least 6 mm. The foramen spinosum in Omo-323 contacts the sphenosquamosal suture laterally, whereas in KNM-ER 406 it is separated from the suture by about 2 mm. The foramen ovale is in contact with the sphenosquamosal suture in OH 5, whereas in Omo-323 the border of this foramen is separated from the suture by a distance of 2 mm. In contrast, the same foramen is situated completely within the sphenoid of KNM-ER 406, as in modern humans. In KNM-WT 17000 the two foramina are damaged, but the foramen spinosum seems to be situated within the suture, and the foramen ovale is separated from it by a distance of 2 mm. This condition makes Omo-323 closer to KNM-WT 17000.

The left zygomatic process of Omo-323, of which only a segment from the middle part is preserved, is thinner mediolaterally than those of *A. robustus*, KNM-ER 406, and OH 5. It is 2.3 mm thick at its superior edge, and its maximum mediolateral thickness is 7.3 mm. It resembles KNM-WT 17000 and KNM-ER 13750 in having a sharp superior edge. It is curved and convex laterally. It does not have the elevated superior margin as is the case in *A. robustus*. In addition, as pointed out by Rak (1983), there is evidence that the arch twists around its own axis, so that its posterior part faces somewhat superomedially, whereas the anterior part faces medially and downwards. On the right temporal, the supraglenoid gutter is wide. Putting all these features together, it is possible to infer that the arches of Omo-323 were more like those of OH 5. It should be noted that the zygomatic arches of KNM-ER 406 and KNM-ER 13750 are more laterally flared than those of Omo-323.

The base of the zygomatic arch, preserved on the right just anterosuperior to the ectoglenoid process, is relatively short anteroposteriorly. It becomes thinner superiorly and is laterally slightly convex as in OH 5, whereas this part is concave in KNM-ER 406 and slightly concave in KNM-WT 17000. Superior to the midpoint between the porion and the base of the zygomatic process is a groove for the middle temporal artery.

The left petrous pyramid is broken at the anterior end of the internal auditory meatus. The latter has a maximum diameter of 4.6 mm (left) and 6.3 mm (right). The petrous pyramid is sturdy, wider antero-posteriorly, but shorter mediolaterally, than that of OH 5. In Omo-323 the superior edge of the petrous pyramid is sharper than in OH 5.

Occipital bone (Fig. 2A,B)

Inferiorly, only part of the right half of the occipital is preserved as part of the fragment Omo-323-896c. It is broken at the level of external occipital protuberance parallel to the sagittal plane. Anterior to this protuberance, the fragment preserves up to ca. 26 mm. There is no hint of the foramen magnum. Superiorly, the occipital preserves the right half and a small portion of the left. The lambdoidal suture is not visible externally.

The nuchal crest is sharp, but is less pronounced than those of KNM-ER 406 and OH 5, and much weaker than that of KNM-WT 17000. It forms a compound temporonuchal crest, but the crest does not continue on to the superior part of the mastoid process as in the specimens listed above, in which there is a strong noncompound crest above the mastoid. The temporal lines diverge slightly above lambda, so that Omo-323 resembles A. boisei specimens such as KNM-ER 406. The insertions of the three suboccipital muscles are well-defined. The attachment of the obliqus capitus superior runs anterolaterally from the nuchal crest to the mastoid. The rectus capitus posterior minor impression is more marked than the others, and its smooth surface runs anteromedially from the medial portion of the nuchal crest. The insertion of the rectus capitus posterior major is diamond-shaped. The overall morphology of the three muscular insertions, including their relation to the nuchal crest, resembles that of KNM-ER 13750 more closely than it does other specimens of A. boisei and KNM-WT 17000.

Compared with the juvenile hominid, L338y-6, the insertions of the suboccipital muscles are better defined in Omo-323, the nuchal crest is sharper, the occipital squama is more vertically oriented, and the rounded cerebellar fossa is deeper.

On the endocranial surface of the occipital, the right cerebellar fossa is deep and rather circular, and its medial margin is formed by a blunt, low internal occipital crest. This roundness is also observed in L338y-6, but is more triangular in SK1585 and OH 5 (Holloway, 1981). The sulci of the right transverse and sigmoid sinuses are wide but shallow. There is no evidence of an occipital/marginal sinus system on the right side. Too little is preserved to assess the pattern of venous drainage on the left side. White and Falk (1999) pointed out the presence of an occipital/marginal sinus system only on the left side in L338y-6, but this was challenged by Yuan et al. (2001). Our own observation of the same specimen shows that it is hard to tell the presence or absence of this system due to breakage. The sigmoid sinus sulcus in Omo-323 is as large as in OH 5 and is in contact with that of the transverse sinus.

Parietal bone

The parietal fragment (Omo-323-896f), which includes parts from both left and right, is the least well-preserved of the vault component of Omo-323. One fragment, measuring 47 mm anteroposteriorly and 41 mm transversely, preserves the sagittal crest all along its length. It is irregularly preserved laterally. The crest is highest at the anterior break and loses height gradually posteriorly. The sagittal crest is fused and well-developed. The second fragment (Omo-323-896c) is continuous with the occipital and temporal, preserves the right parietal up to about 26 mm superiorly from lambda, and extends on to the asterion. At this level the parietal preserves up to 22.5 and 34 mm laterally from the sagittal plane on the left and right, respectively. Though the two parietal fragments do not contact, it is possible to see that the sagittal crest does not extend postero-inferiorly on to the occipital. It extends only up to about 15 mm above lambda. The parietal bone is thin. Its thickness varies from 3–4 mm. The development of the sagittal crest and the morphology of the parieto-mastoid angle of Omo-323 are comparable to those seen in KNM-ER 406 and KNM-ER13750, and are less like the morphology of KMN-WT 17000.

Maxilla(Fig. 1A–C)

The right maxilla (Omo-323-896g) contains P^3, P^4, and M^1. The external aspect of the alveolar process is badly damaged. Superiorly the broken surface exposes the root tips of M^1 and the floor of the maxillary sinus. About 50 mm of the palate is preserved from the base of the root of the lateral incisor to the level of the posterior part of M^2. The midline is irregularly preserved. Laterally the alveolar process from the distal part of the M^1 root up to the distal part of the canine juga is preserved. Though this region is quite abraded, a small part the base of the zygomatic root is preserved. The anterior aspect of the canine juga is missing, but the nasoalveolar clivus is preserved at the level of the lateral incisor.

Palatal breadth varies between 28 mm at P^3 and 36 mm at M^1. The more vertical inclination of the nasoalveolar clivus resembles that of OH 5, and is unlike the more gentle slope of the KNM-WT 17000 clivus. The surface between the midline of the clivus and the alveolus of the right canine is flatter than in other robust specimens. There is a distinct step between the anterior root of the zygomatic process and the anterior contour of the subnasal region, as in KNM-WT 17000. This feature distinguishes Omo-323 from A. boisei specimens in which no noticeable step is found in this region. The central incisor alveolus is large, particularly in comparison to that of the lateral incisor. The root of the lateral incisor is preserved, with labiolingual and mesiodistal dimensions of 8.2 mm and 3.9 mm, respectively.

The palate is shallow compared to those of OH 5 and KNM-ER 406, but slightly deeper than that of KNM-WT 17000. The palate widens posteriorly in Omo-323, whereas the inverse is true in KNM-WT 17000. Unlike the palates of KNM-ER 406, OH 5, and KNM-WT 17000, Omo-323 does not have small transverse grooves on its surface. The canine is missing, but its alveolus measures 6.9 mm mesiodistally and 8.1 mm labiolingually.

Teeth

Isolated upper left canine (Omo-323-896h). The enamel on the buccal aspect and the root tip are damaged. The lingual side of the crown is less worn than the buccal side. This tooth was affected by interstitial wear mesially and distally. The estimated size of the Omo-323 canine crown, ca. 11 mm mesiodistally and ca. 9.6 mm labiolingually, exceeds that of OH 5. There is a shallow groove on the mesial aspect, whereas the crown is convex on its distal aspect.

Right upper third premolar. The heavily worn P^3 crown is preserved in the maxillary fragment, but enamel has been lost on the buccal aspect of the crown, exposing the dentine. Interproximal facets are preserved mesially and distally. The buccolingually expanded crown has a lingual cusp that tapers towards the tip, and the well-defined cervix resembles the form of the P^3s of OH 5.

Right upper fourth premolar. This tooth has one lingual and two buccal roots. The two buccal roots are fused up to half of their length from the cervix. They are expanded buccolingually, and their dimensions are comparable to those of OH 5. As in OH 5, the lingual side of the crown is oriented slightly mesially. The lingual side is rounded and without grooves.

Right upper first molar. This tooth preserves a very worn paracone and protocone that are connected by a transverse bridge of dentine. Wear on the metacone is less than that on the two mesial cusps; the hypocone is the least worn cusp. The parallelogram-shaped occlusal surface of this tooth resembles that of OH 5. The highest part of the occlusal surface is situated towards the central part of the trigon.

Medially and laterally, the walls of the crown between the cusps are concave, as in *A. robustus* (e.g., SK-48). This is in contrast to OH 5, in which they are rather convex. The base of the crown does not bulge medially, as do the premolars of the same individual and the molars of OH 5. Its contact with M^2 is situated at the back of the metacone. This contact surface is larger than that of OH 5 where it is situated behind the hypocone.

As can be seen from the measurements given in Table 1, the mesiodistal length of P^3 and P^4 of Omo-323 are within the range of robust australopiths and closer to that of *A. boisei*. The buccolingual widths of

TABLE 1. *Teeth dimensions of Omo-323 compared to those of* A. boisei, A. robustus, *and KNM-WT 17000*

	MD	BL	MD/BL
Omo-323			
P^3	10.5[1]	?	?
P^4	11.4[1]	16.8[1]	0.67
M^1	14.8	16.7	0.88
A. boisei			
P^3 n = 6	9.8–11.8 (10.6)	14.0–16.1 (14.9)	0.71
P^4 n = 6	11.2–12.2 (11.8)	15.5–17.3 (16.3)	0.72
M^1 n = 10	13.5–15.6 (14.4)	14.0–16.6 (15.7)	0.92
A. robustus			
P^3 n = 15	9.3–12.2 (10.1)	13.2–15.2 (14.1)	0.71
P^4 n = 19	10.2–12.1 (10.9)	13.5–16.3 (15.1)	0.72
M^1 n = 14	12.2–14.0 (13.2)	12.9–16.5 (14.6)	0.89
KNM-WT 17000[2]			
P^3	11.5	16.2	0.71

[1] Approximate dimension due to damage, BL (buccolingual) (mm), and MD (mesiodistal) (mm). Data on *A. robustus* from Grine (1988), on KNM-WT 17000 from Walker et al. (1986), and on *A. boisei* from Kimbel (unpublished).
[2] Determined by Suwa (1989) as P^4.

the two premolars of Omo-323 surpass those of *A. robustus* and are close to those of OH 5.

TAXONOMY

Coppens and Sakka (1980), in their study of the left temporal fragment of Omo-323, drew attention to 18 morphological features, including:

a. Antero-inferiorly projecting mastoid process,
b. Weak supramastoid crest,
c. Marked pneumatization of the temporal,
d. Absence of entoglenoid process and very small postglenoid process, and
e. Sharp superior edge of the petrous pyramid.

Coppens and Sakka (1980, p.193–194, our translation) concluded: ". . . this specimen shows some characters that make it close to *A. robustus* or *A. boisei*." They added, ". . . our specimen differs from *A. robustus* or *A. boisei* by its gracility."

Despite the absence of a comprehensive description and formal taxonomic attribution, the Omo-323 cranium has been included in lists of specimens and used for comparative purposes (Kimbel, 1984; Falk, 1986; Leakey and Walker, 1988; Suwa, 1988; Brown et al., 1993; Wood et al., 1994; Wolpoff, 1996).

The following features of the fragmented cranium are only found in combination in *A. aethiopicus*, *A. boisei*, and *A. robustus*:

1. A prominent sagittal crest;
2. Postorbital constriction;
3. Deep mandibular fossae;
4. Very large molars and buccolingually expanded premolars;
5. Molarized premolars;
6. Very thick enamel; and
7. Small canine compared to cheek teeth.

From the morphological descriptions and comparisons presented above, it is clear that Omo-323

shows affinities to both *A. boisei* and *A. aethiopicus* but cannot be readily assigned to either taxon. However, Omo-323 can be distinguished from *A. robustus* by its anteroposteriorly narrower supraorbital tori, less prominent glabellar region, more antero-inferiorly projecting mastoid process, laterally inflated mastoid process, smaller postglenoid process, mediolaterally thin zygomatic arch, and more buccolingually expanded premolars.

One feature that distinguishes *A. boisei* and Omo-323 is the unique antero-inferior projection of the mastoid process in the latter. Other characters that differ in Omo-323 and *A. boisei* specimens include: the less prominent glabellar region, development of the supraorbital tori, less postero-inferior projection of entoglenoid process, the sharpness of the superior edge of the petrous pyramid, and the lateral inflation of the mastoid process. The first two concern the frontal, but this region is known to be variable in *A. boisei* (Brown et al., 1993). The third feature, the postero-inferior projection of the entoglenoid process, is found in most *A. boisei* specimens, but is absent in Omo-323. Instead, the latter has a broad-based articular eminence evenly distributed anteroposteriorly, without a noticeable entoglenoid process. In these three features, Omo-323 resembles *A. aethiopicus* more closely than it does *A. boisei*.

In contrast, the remaining features that differ in Omo-323 and *A. boisei* (the sharp superior edge of the petrous pyramid and the lateral inflation of the mastoid process) are not seen in *A. aethiopicus*. However, the superior edge of the petrous pyramid is variable in *A. boisei*, being rounded in KNM-ER 23000 and sharper in OH 5. Lateral inflation of the mastoid is also observed in some *A. boisei* specimens such as KNM-ER 406 and KNM-ER 407, though it is never as pronounced as in Omo-323.

On the other hand, Omo-323 shares three features with *A. boisei*, i.e., a deep and mediolaterally expanded mandibular fossae, laterally expanded zygomatic arches that twist on their own axes, and a deep tympanic plate. There is evidence that these are derived for *A. boisei* (Rak, 1983; Wood, 1991; Strait et al., 1997). Thus, on balance we assign the Omo specimen to *A. boisei*.

DISCUSSION

Remains of *A. boisei* have so far been found in East Africa and in Malawi (Kullmer et al., 1999). They have been recovered from the sites of Chesowanja, Peninj, Olduvai, East Turkana, West Turkana, Lower Omo Valley, and Konso. Based on the evidence now available, *A. aethiopicus* was restricted geographically to the Lower Omo Valley and west of the Lake Turkana, i.e., Upper Turkana basin. As we noted previously, the most abundant skeletal elements of East African robust australopiths are teeth and mandibles (mandibular fragments). The 18 cranial fragments (including maxillary fragments) that have been assigned to *A. boisei* date to between ca. 2.25 Myr (e.g., Omo75-14a,b) and 1.4 Myr (e.g.,

KNM-CH-1, KNM-CH 304, and KGA-10 525). On the other hand, *A. aethiopicus* is represented by the holotype mandible (Omo-18-18), the cranium KNM-WT 17000, and, according to Suwa et al. (1996), by the juvenile cranium L338y-6. We noted above that there are some differences and similarities between L338y-6 and Omo-323. We think that comparison between these two (or L338y-6 and any adult specimen) will be affected by differences in their maturity.

The oldest cranial remains of robust austraopiths date to ca. 2.6 Myr. These specimens are: L55-33 (left mandibular fragment with I_1-P_4: unit C-6), Omo18-18 (edentulous mandible: unit C-8), Omo-18-31 (third premolar: unit C-8), and Omo-84-100 (third molar). All these have been attributed to *A. aethiopicus*. The youngest cranial remains of East African robust australopiths come from Olduvai (Bed II), dated to 1.4 Myr (OH-3 and OH-38), and have been assigned to *A. boisei*.

Omo18-18 comes from unit C-8 of the Shungura Formation. The very small anterior tooth crowns (incisors and canines), the megadontia of the cheek teeth (based on alveolus dimensions), and other characters put forward by Arambourg and Coppens (1967, 1968) in their first diagnosis of *A. aethiopicus* show that the mandible belongs to a robust species.

The discovery of KNM-WT 17000 (dated to 2.5 Myr) from the Nachukui Formation at West Turkana raised the issue of the validity of the species *A. aethiopicus* (Walker et al., 1986; Brown et al., 1993). These authors assigned KNM-WT 17000 to *A. boisei* and proposed that Omo-18-18 be considered a female of this species. Subsequently, Kimbel et al. (1988) questioned the assignment to *A. boisei*, and recognized the validity of the species described by Arambourg and Coppens (1967, 1968). In particular they noted that KNM-WT 17000 retains several primitive characters shared with *A. afarensis* (Kimbel et al., 1988, p. 262). These authors concluded that KNM-WT 17000 shares only two derived characters with *A. boisei*: a heart-shaped foramen magnum, and a temporoparietal overlap at the asterion. Subsequently, Skelton and McHenry (1992) suggested that a narrow frontal and an oval-shaped surface of P^3 are shared exclusively by *A. boisei* and *A. aethiopicus*, even though they ultimately concluded that the two species were not closely related.

The validity of *A. aethiopicus* is now accepted by most researchers. Therefore, if Omo-323 belongs to *A. boisei*, it represents the oldest known cranium of that taxon. Omo-323 derives from unit G-8 of the Shungura Formation and hence has an age of 2.1 Myr. According to Feibel et al. (1989), this age may range between 2.1–2.3 Myr. Remains of *A. aethiopicus* known so far have a radiometric age of ca. 2.6 or 2.5 Myr. Fossils of *A. boisei sensu stricto* are mostly younger than 2 Myr, but Suwa (1988) and Suwa et al. (1996) showed, based on their study of dentition, that the youngest *A. aethiopicus* and oldest *A. boisei* specimens could be as old as 2.3 Myr, corresponding

to the base of Member G of the Shungura Formation. They interpreted their data as evidence of anagenetic change within an evolving East African robust lineage.

Wood et al. (1994) subsequently demonstrated differences between the mandibles and lower molars of A. boisei and A. aethiopicus, which they call Paranthropus boisei sensu stricto and Paranthropus aff. P. boisei, respectively, before and after the time interval ca. 2.3–2.2 Myr. They noted a morphological hiatus between the mandibles (and teeth) of A. aethiopicus and A. boisei. The same authors presented two possibilities for evolution in the A. aethiopicus/A. boisei lineage. These are that either the changes occurred gradually between 2.5–2 Myr, or that they are the result of a shorter-lived speciation event at ca. 2.3–2.2 Myr. They interpreted the mandibular and dental differences as evidence for the existence of an abrupt change around 2.3 and 2.2 Myr in this lineage. The evidence of Omo-323 suggests that some primitive cranial characters, e.g., the nature of the entoglenoid process as observed in A. aethiopicus, continue at least up to level G-8. Therefore, based on the fragmentary cranium, we speculate that morphological changes of the cranium happened progressively in a mosaic fashion in the lineage leading to A. boisei. In other words, while we classify Omo-323 as A. boisei, the specimen's morphology emphasizes the anagenetic link between A. aethiopicus and A. boisei. These hypotheses can only be satisfactorily tested, however, when more cranial elements are discovered from the appropriate stratigraphic levels. Finally, Omo-323 contributes one more feature (the nature of the projection of the mastoid process) to the accumulating evidence for cranial polymorphism in A. boisei.

ACKNOWLEDGMENTS

LITERATURE CITED

Arambourg C, Coppens Y. 1967. Sur la découverte dans le Pléistocène inférieur de la vallée de l'Omo (Ethiopie) d'une mandibule d'australopithecien. C R Acad Sci [III] 265:589–590.

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

Asfaw B. 1987. The Belohdelie frontal: new evidence of early hominid cranial morphology from the Afar of Ethiopia. J Hum Evol 16:611–624.

Brain CK, Churcher CS, Clark JD, Grine FE, Shipman P, Susman RL, Turner A, Watson V. 1988. New evidence of early hominids, their culture and environment from Swartkrans cave, South Africa. S Afr J Sci 84:828–235.

Brown FH, Feibel CS. 1985. Stratigraphical notes on the Okote Tuff Complex at Koobi Fora, Kenya. Nature 316:794–797.

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

Brunet M, Beauvilain A, Coppens Y, Heintz E, Moutaye AHE, Pilbeam D. 1995. The first australopithecine 2,500 kilometers west of the Rift Valley (Chad). Nature 378:273–275.

Brunet M, Beauvilain A, Coppens Y, Heintz E, Moutaye AHE, Pilbeam D. 1996. Australopithecus bahrelghazali, une nouvelle espèce d'hominidé ancien de la région de Koro Toro (Tchad). C R Acad Sci [III] 322:907–913.

Coppens Y, Sakka M. 1980. Un nouveau crâne d'australopithèque. In: Sakka M, editor. Morphologie évolutive: morphogenèse du crâne et origine de l'homme. Pré-congress symposium du VIII Congrès Internationational de Primatologie. Florence: CNRS. p85–194.

Falk D. 1986. Evolution of cranial blood drainage in hominids: enlarged occipital/marginal sinuses and emissary foramina. Am J Phys Anthropol 70:311–324.

Falk D, Redmond JC, Guyer J, Conroy GC, Recheis W, Weber GW, Seidler H. 2000. Early hominid brain evolution: a new look at old endocasts. J Hum Evol 38:695–717.

Feibel CS, Brown F, McDougall I. 1989. Stratigraphical context of fossil hominids from the Omo group deposits: Northern Turkana Basin, Kenya and Ethiopia. Am J Phys Anthropol 78:623–632.

Grine FE. 1988. Evolutionary history of the robust australopithecines: a summary and historical perspective. In: Grine F, editor. Evolutionary history of the robust australopithecine. New York: De Gruyter. p 509–520.

Holloway RL. 1981. The endocast of the Omo L338y-6 juvenile hominid: gracile or robust Australopithecus? Am J Phys Anthropol 54:109–118.

Howell FC. 1968. Omo research expedition. Nature 219:567–572.

Johanson DC, Taieb M. 1976. Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. Nature 260:293–297.

Johanson DC, White TD, Coppens Y. 1978. A new species of the genus Australopithecus (Primate: Hominidae) from the Pliocene of Eastern Africa. Kirtlandia 28:1–14.

Johanson DC, White TD, Coppens Y. 1982. Dental remains from the Hadar Formation, Ethiopia: 1974–1977 collections. Am J Phys Anthropol 57:545–603.

Kimbel WH. 1984. Variation in the pattern of cranial venous sinuses and hominid phylogeny. Am J Phys Anthropol 63:243–263.

Kimbel WH, White TD, Johanson DC. 1988. Implications of KNM-WT 17000 for the evolution of "robust" Australopithecus. In: Grine F, editor. Evolutionary history of the robust australopithecine. New York: De Gruyter. p 259–268.

Kimbel WH, Johanson DC, Rak Y. 1994. The first skull and other new discoveries of Australopithecus afarensis at Hadar Ethiopia. Nature 368:449–451.

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

Leakey MG, Feibel CS, McDougall I, Walker A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature 376:565–571.

Leakey RE, Walker AC. 1988. New Australopithecus boisei specimens from east and west Lake Turkana, Kenya. Am J Phys Anthropol 76:1–24.

Rak Y. 1983. The australopithecine face. New York: Academic Press.

Ramirez-Rozzi FV. 1993. Teeth development in East African Paranthropus. J Hum Evol 24:429–454.

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

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

Suwa G. 1988. Evolution of the "robust" australopithecine in the Omo succession: evidence from mandibular premolar morphology. In: Grine F, editor. Evolutionary history of the robust australopithecine. New York: De Gruyter. p 199–222.

Suwa G. 1989. The premolar of KNM-WT 17000 and relative anterior to posterior dental size. J Hum Evol 18:795–799.

Suwa G, White TD, Howell FC. 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. Am J Phys Anthropol 101:247–282.

Taieb M, Johanson DC, Coppens Y. 1975. Expédition Internationale de l'Afar, Ethiopie (3eme campagne 1974); découverte d'Hominidés plio-pléistocènes à Hadar. C R Acad Sci [D] 281: 1297–1300.

Walker AC, Leakey RFE. 1988. The evolution of *Australopithecus boisei*. In: Grine FE, editor. Evolutionary history of the "robust" Australopithecine. New York: Aldine de Gruyter. p 247–258.

Walker A, Leakey RE, Harris JM, Brown FM. 1986. 2.5-Myr *A. boisei* from west of Lake Turkana, Kenya. Nature 322:517–522.

White DD, Falk D. 1999. A quantitative and qualitative reanalysis of the endocast from the juvenile *Paranthropus* specimen L338y-6 from Omo, Ethiopia. Am J Phys Anthropol 110:399–406.

White TD. 1977. New fossil hominids from Laetoli Beds, Tanzania. Am J Phys Anthropol 46:197–230.

White TD. 1980. Additional fossil hominids from Laetoli, Tanzania: 1976–1979 specimens. Am J Phys Anthropol 53:487–504.

White TD. 1985. The hominid of Hadar and Laetoli: an element-by-element comparison of dental samples. In: Delson E, editor. Ancestors: the hard evidence. New York: Alan R. Liss. p 138–152.

White TD, Johanson DC, Kimbel WH. 1981. *Australopithecus africanus*: its phyletic position reconsidered. S Afr J Sci 77:445–470.

White TD, Moore RV, Suwa G. 1984. Hadar biostratigraphy and hominid evolution. J Vert Paleontol 4:575–583.

White TD, Suwa G, Hart WK, Walter RC, WoldeGabriel G, de-Heinzelin J, Clark JD, Asfaw B, Vrba E. 1993. New discoveries of *Australopithecus* at Maka in Ethiopia. Nature 366:261–265.

White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. Nature 371:306–312.

Wolpoff MH. 1996. Evolution of the robust australopithecines. In: Human evolution. McGraw-Hill: College Custom Series. p 331–384.

Wood BA. 1988. Are "robust" australopithecines a monophyletic group? In: Grine F, editor. Evolutionary history of the robust australopithecine. New York: De Gruyter. p 269–284.

Wood BA. 1991. Koobi Fora Research Project. Volume 4. Hominid cranial remains. Oxford: Clarendon Press.

Wood BA, Chamberlain AT. 1987. The nature and affinities of the "robust" australopithecines: a review. J Hum Evol 16:625–641.

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

Yuan MS, Holloway RL, Broadfield DC, DeGusta D, Richards G, Mowbray K, Marquez S. 2001. The missing Omo L338y-6 occipital marginal drainage pattern: There it isn't, is, isn't. Am J Phys Anthropol 32:169.