

“Lucy” Redux: A Review of Research on *Australopithecus afarensis*

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ABSTRACT In the 1970s, mid-Pliocene hominin fossils were found at the sites of Hadar in Ethiopia and Laetoli in Tanzania. These samples constituted the first substantial evidence for hominins older than 3.0 Ma and were notable for some remarkable discoveries, such as the “Lucy” partial skeleton and the abundant remains from the A.L. 333 locality at Hadar and the hominin footprint trail at Laetoli. The Hadar and Laetoli fossils were ultimately assigned to the novel hominin species *Australopithecus afarensis*, which at the time was the most plesiomorphic and geologically ancient hominin taxon. The discovery and naming of *A. afarensis* coincided with important developments in theory and

methodology in paleoanthropology; in addition, important fossil and genetic discoveries were changing expectations about hominin divergence dates from extant African apes. This coincidence of events ensured that *A. afarensis* figured prominently in the last 30 years of paleoanthropological research. Here, the 30+ year history of discovery, analysis, and interpretation of *A. afarensis* and its contexts are summarized and synthesized. Research on *A. afarensis* continues and subject areas in which further investigation is needed to resolve ongoing debates regarding the paleobiology of this species are highlighted. *Yrbk Phys Anthropol* 52:2–48, 2009. © 2009 Wiley-Liss, Inc.

Just over three decades ago, the east African early hominin species *Australopithecus afarensis* was recognized as the oldest, most apelike human ancestor. Although specimens now attributed to the species had resided in fossil collections since the 1930s, the bulk of the sample was amassed during field work in the 1970s at two sites, Hadar, Ethiopia, and Laetoli, Tanzania. Today, the species' hypodigm numbers more than 400 specimens collected from a half-dozen sites, most of which are still actively being worked (Table 1). Refinements in radioisotopic dating have established the species' first and last known appearances at 3.7 and 3.0 Ma, respectively. At the time of their discovery, these specimens constituted the first informative sample of hominin fossils older than 3.0 Ma.

Studies on subjects ranging from the rise of striding bipedal locomotion to the origin of the uniquely human pattern of growth and development to the evolution of hominin dietary adaptations have drawn heavily on data from the remains of *A. afarensis*. Taxonomic and phylogenetic research, which experienced a major renaissance in paleoanthropology beginning around the time when *A. afarensis* was discovered, has benefited from the extensive baseline data on fossil hominin skeletal and dental variation residing in the Hadar site-sample. Some of the research topics that focus on *A. afarensis*—the extent to which terrestrial bipedality was the committed form of locomotion, the degree of sexual dimorphism in body size and implications for social behavior, and the “shape” of the phylogenetic tree prior to the emergence of the *Homo* and robust australopithecine lineages, to name just three prominent examples—are still actively debated today, which merely drives home the message that finding solutions to scientific problems in paleoanthropology is not just a function of augmenting fossil sample size (or even of the completeness of remains: witness the central role of the “Lucy” skeleton in the locomotion debate).

In this article, we review 30+ years of research on *A. afarensis*. We begin by placing the discovery and recognition of the species in historical context. It is all too easy to forget that paleoanthropology was very different in 1973, when the first Hadar fossils were recovered, than it is in 2009, and what may appear today to be a “status quo” stance on *A. afarensis* developed out of a period of significant changes in both data and theoretical outlook that propelled paleoanthropology rapidly forward as a science. We think this is particularly important for students to appreciate, especially as their near-total dependence on the digital domain for access to scholarly information has kept them out of the libraries, where much of the “older” literature—and the scientific world it conveys—remains in print form. We then review the current state of knowledge of the species' main attributes as read from the bones and teeth. We have tried at least to touch on all of the main points to

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This article is dedicated to the memory of two close friends and colleagues, Charlie Lockwood (1970–2008) and Elizabeth Harmon (1965–2009), who contributed indelibly to the recent history of field and analytical research on *Australopithecus afarensis* reviewed here.

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TABLE 1. The *A. afarensis* hypodigm

Site	Age (Ma)	Skeleton	Skulls	Crania	Mandibles	Upper limb	Hand	Axial*	Lower limb	Foot	Isol. Teeth
Hadar, Ethiopia (A.L.)	3.4–3.0	288-1	333-43/86	58-22	128-23	137-48a, b	333w-4	333w-8	128-1	333w-25	161-40
		438-1	417-1	125-11	145-35	137-50	333w-5	333w-14	129-1a-c	333w-34	176-35
			444-2	162-28	188-1	223-1	333w-7	333-51	129-52	333w-51	198-17a, b
			487-1	166-9	198-1	322-1	333w-6	333-73	152-2	333-8	200-1b
			822-1	199-1	198-22	333w-22	333w-11	333-81	211-1	333-13	207-17
				200-1a	207-13	333w-31	333w-20	333-83	228-1	333-21	241-14
				224-9	225-8	333w-33	333w-23	333-101	330-6	333-22	249-26
				333-1	228-2	333w-36	333w-26	333-106	333w-37	333-26	249-27
				333-2	237-3	333-11	333w-29	333-134	333w-40	333-28	293-3
				333-23	266-1	333-12	333w-35	333-152	333w-43	333-36	309-8
				333-24	277-1	333-29	333w-38	333-155	333w-56	333-37	333w-2
				333-45	311-1	333-38	333w-39	333-156	333-3	333-47	333w-9a, b
				333-84	315-22	333-87	333w-53	333-161	333-4	333-54	333w-10
				333-105	330-5	333-94	333w-54	333-164	333-5	333-55	333w-28
				333-112	330-7	333-98	333-14	333x-12	333-6	333-60	333w-42
				333-114	333w-1	333-107	333-15	444-7	333-7	333-71	333w-48
				333-116	333w-12	333-109	333-16	444-8	333-9	333-72	333-30
				333-125	333w-27	333-119	333-17	444-9	333-39	333-75	333-35
				413-1	333w-46	333-124	333-18	444-10	333-41	333-78	333-44
				423-1	333w-52	333-127	333-19	444-11	333-42	333-79	333-52
				427-1	333w-57	333-128	333-20	444-12	333-61	333-102	333-66
				439-1	333w-58	333-129	333-25		333-85	333-115a-m	333-67
				442-1	333w-59	333-130	333-27		333-95	333-145	333-68
				444-1	333w-60/32	333-141	333-31		333-96	333-147	333-76
				457-2	333-59	333-144	333-33		333-110	333-167	333-77
				486-1	333-74	333-149	333-40		333-111	333-168	333-82
				651-1	333-97	333-150	333-46		333-120	333x-21a, b	333-90
				701-1	333-100	333-153	333-48		333-123		333-99
				770-1	333-108	333n-2	333-49		333-126		333-103
				922-1	333n-1	333x-5	333-50		333-131		333-104
					400-1a	333x-6/9	333-56		333-132		333-165
					411-1	333x-14	333-57		333-135		333-166
					418-1	333x-16	333-58		333-140		333x-1
					432-1	444-13	333-62		333-142		333x-2
					433-1	444-14	333-63		333-145		333x-3
					436-1	444-15	333-64		333-147		333x-4
					437-1		333-65		333-154		333x-17
					437-2		333-69		333-157		333x-20
					440-1		333-80		333-158		333x-25
					443-1		333-88		333-160		366-1
					582-1		333-89		333-162		388-1
					604-1		333-91		333-163		400-1b
					620-1		333-93		333x-26		438-2
					729-1		333-122		545-3		438-3
					766-1		333-141		827-1		441-1
					996-1		333-144				444-6
					1030-1		333-148				444-16
					1045-1		333-149				444-29
					1180-1		333-150				444-30
							333x-13a, b				452-18
							333x-18				462-7
							438-4				465-5
							444-3				466-1
							444-4				557-1
							444-5				655-1
							1044-1				660-1
											697-1
									699-1		
									762-1		
									763-1		
									772-1		
									777-1		
									1017-1		
									1117-1		
									1256-1		

(Continued)

TABLE 1. (Continued)

Site	Age (Ma)	Skeleton	Skulls	Crania	Mandibles	Upper limb	Hand	Axial*	Lower limb	Foot	Isol. Teeth
Dikika, Ethiopia (DIK)	>3.4–3.3	1-1			2-1						
Maka, Ethiopia (MAK-VP)	3.4				1/2 1/6 1/12 1/83	1/3 1/111			1/1		1/4 1/13
Koobi Fora, Kenya (KNM-ER)	3.4–3.3			2602							
Laetoli, Tanzania (LH)	3.7–3.5	21		Garusi 1 5	2 4 10 13					Footprints	M. 42323 Garusi 3 1 3a-t 6a-e 3/6a-c 8 11 12 14a-k 15 16 17 19 23 24 25 26 30 31
Tentative: Omo (Usno), Ethiopia	3.0										W7-23 W8-751 W8-978 W8-988 B7-39a, b B8-23a B8-4q L1-667
Bahr-el-Ghazal, Chad (KT)	(3.0–3.5)				KT12/H1 KT 40						
Belohdelie, Ethiopia (BEL-VP)	3.8			1/1							

*Axial inventory for Hadar does not include isolated ribs and rib fragments from A.L. 333/333w.

emerge from the three decades of research on *A. afarensis*, but cannot claim to have been exhaustive. Moreover, our own perspective on the species and its role in the debates over one subject or another has meant emphasizing some points of view at the expense of others; we hope we have been fair in characterizing these different points of view. Finally, we attempt a concluding synthesis—a mini-biography of *A. afarensis*, for we know enough now about this species to begin to phrase fairly refined questions about the paleobiology of this species. In this final section, we point to areas where fresh research is needed to address still unanswered questions.

HISTORICAL CONTEXT

The 1970s witnessed dramatic additions to the early fossil record of African hominins and breakthrough

advances in determining the chronological, geological, and paleoecological contexts of the most important fossil-bearing African sites. In the several years prior to the recognition of *Australopithecus afarensis*, in 1978, the sites of Koobi Fora and Ileret in Kenya, and Sterkfontein and Swartkrans in South Africa, produced important, often quite complete, craniodental and postcranial specimens of early hominins (Tobias, 1973, 1976). Radioisotopic dating of tephra in the Lake Rudolf (now Turkana) basin sequence pushed the east African paleontological record back beyond 2.0 Ma in the Koobi Fora and Shungura Formations and reinvigorated biochronological studies that established a temporal sequence for the south African hominin-bearing “cave” sites, with Makapansgat and Sterkfontein anchoring the early end, at ca. 3.0–2.8 Ma (e.g., Vrba, 1975; Howell, 1978).

Most paleontologists, by and large rejecting or ignoring young (ca. 5.0 Ma) molecular-clock-derived ages for the divergence of African great ape and human lineages (e.g., Sarich, 1974), promoted the fragmentary craniodental remains of middle Miocene *Ramapithecus* as representing an open-country-adapted stem hominin (e.g., Simons, 1976), based principally on perceptions of a nonsectorial C/P₃, thick postcanine tooth enamel, and dentognathic traces of masticatory ruggedness as foreshadowing configurations in Plio-Pleistocene *Australopithecus* (sensu lato).¹ By virtue of its relatively unspecialized—encoded in the term “gracile”—masticatory apparatus and mid-Pliocene chronological placement, *Australopithecus africanus*, as represented at Sterkfontein and Makapansgat, was commonly interpreted as the direct descendant of *Ramapithecus* and the ancestor of *Homo* and the “robust” species of *Australopithecus*, *A. robustus* and *A. boisei* (e.g., Pilbeam, 1972; Tobias, 1973, 1976; but see Robinson, 1972, for a nonconformist’s view). But between *Ramapithecus* and *Australopithecus* stretched a mostly empty fossil record as hominin specimens older than 3.0 Ma were exceedingly rare. Isolated tooth crowns from the Usno Formation and Member B of the Shungura Formation, a maxillary fragment from Laetoli (Garusi I), an isolated mandibular molar from Lukeino, Kenya (KNM-LU 335), and a temporal bone fragment from Chemeron in the Baringo Basin, Kenya (KNM-BC 1), were thought to represent east African populations of *A. africanus* (or of a species very similar to it) between 3.0 and 3.5 Ma (Pilbeam, 1972; Howell and Coppens, 1976; Howell, 1978; Tobias, 1978).² A fragment of a slender mandibular corpus with a small but heavily worn M₁ from Lothagam in Kenya (KNM-LT 329) was deemed sufficient to extend the record of *A. africanus* back to the latest Miocene (e.g., Pilbeam, 1972; Tobias, 1978). The assignment of this poorly preserved east African material to *A. africanus*, though usually tentatively expressed, was based less on detailed trait-by-trait comparisons with relevant South African fossils than on the absence of specialized craniodental morphology associated with the “robust” australopiths [as characterized by John Robinson’s (e.g., 1954, 1963) influential “dietary hypothesis” of adaptive and phylogenetic differentiation of australopith lineages]; it was more or less the default taxonomic assignment for “gracile” Pliocene hominins.

The discovery in 1972 of the large-brained, flat-faced *Homo* cranium KNM-ER 1470 in deposits at Koobi Fora, Kenya, thought initially to be as old as 2.9 Ma based on ⁴⁰Ar/³⁹Ar dates for the overlying KBS tuff (Leakey, 1973), reinforced evidence, from Swartkrans (1950s) and Olduvai Gorge (1960s), for the ancient coexistence of *Homo* and *Australopithecus* lineages and appeared to project this temporal overlap well back into the Pliocene. Although paleontologists soon noted the biochronological anomaly presented by the mammalian fauna coming from the sub-KBS tuff levels that yielded the hominin skull—an age of younger than 2.0 Ma was in much closer agreement with faunal data from the

nearby Shungura Formation of the Turkana basin, which was subsequently confirmed by further rounds of radioisotopic dating [Lewin (1987) presents a lively popular account of this debate and its resolution]—the 1470 cranium profoundly impacted thinking about hominin taxonomy and phylogeny by highlighting the morphological divergence of specimens attributed to the genus *Homo* from those of contemporary *Australopithecus* (Tobias, 1976, 1978; Wood, 1976; Delson et al., 1977; Howell, 1978). Subsequent discoveries at Koobi Fora underscored the probability of contemporaneous taxonomic diversity among the later Pliocene hominins of eastern Africa (Leakey, 1974; Leakey and Walker, 1976).

It was in this framework that the hominin fossils from Hadar, Ethiopia, and Laetoli, Tanzania, were discovered, analyzed, and interpreted.

FIRST DISCOVERIES AND EARLY IMPRESSIONS

Hadar

The central Afar basin was first surveyed in detail by geologist Maurice Taieb in the 1960s. In 1972, Taieb, Donald Johanson, and Jon Kalb surveyed several fossiliferous areas in the western portion of this area and in 1973 the International Afar Research Expedition (IARE) was formed by Taieb, Johanson and Yves Coppens to begin intensive exploration of richly fossiliferous Pliocene fluviolacustrine deposits exposed along the Awash River near its junction with the seasonally dry Kada Hadar tributary, which lends its name to the Hadar site (see Fig. 1). Hominin fossils were recovered in the first field season; these are portions of what were thought to be a single individual’s lower limb remains (A.L. [Afar Locality] 128-1: proximal femur; A.L. 129-1 a, b, c: distal femur, proximal tibia, proximal femur) and a fragment of temporal bone (A.L. 166-9). In 1974 the first hominin jaws and teeth were recovered, including a maxilla with complete adult dentition (A.L. 200-1) and several mandibles with teeth (A.L. 198-1, A.L. 266-1, A.L. 277-1), but these were nearly eclipsed by the partial skeleton with associated mandible and fragmentary cranium that came to be known as “Lucy” (A.L. 288-1). Although all of these specimens were surface finds, their excellent state of preservation and unprecedented degree of association of skeletal parts testified to highly favorable depositional and taphonomic contexts [including, as determined subsequently, an unusually high depositional rate relative to the fluviolacustrine settings at other east African hominin sites (Campisano and Feibel, 2007)], which was reinforced by the abundant, well preserved vertebrate fauna that was collected during this early phase of the Hadar field work. In November, 1975, Michael Bush discovered A.L. 333, two adjoining hillsides and associated drainage gullies whose surfaces were littered with hominin fossils. Between 1975 and 1977, most of the IARE’s paleontological effort was devoted to extracting the hominin remains from A.L. 333, which, by the close of field work in January, 1977, numbered ~200 separately catalogued specimens representing many skeletal and skull parts of at least 13 adult and subadult individuals, and to determining their source horizon through excavation—a successful operation that yielded 13 in situ hominin specimens in 1976.

¹In this article, we use a traditional taxonomic approach to the grouping of species within a broadly encompassing (indeed, paraphyletic) genus *Australopithecus*, while recognizing the likelihood that a subset of these species likely form a monophyletic group (i.e., *Paranthropus*).

²The Chemeron specimen was already suspected of being younger, as was confirmed subsequently (see Hill et al., 1992).

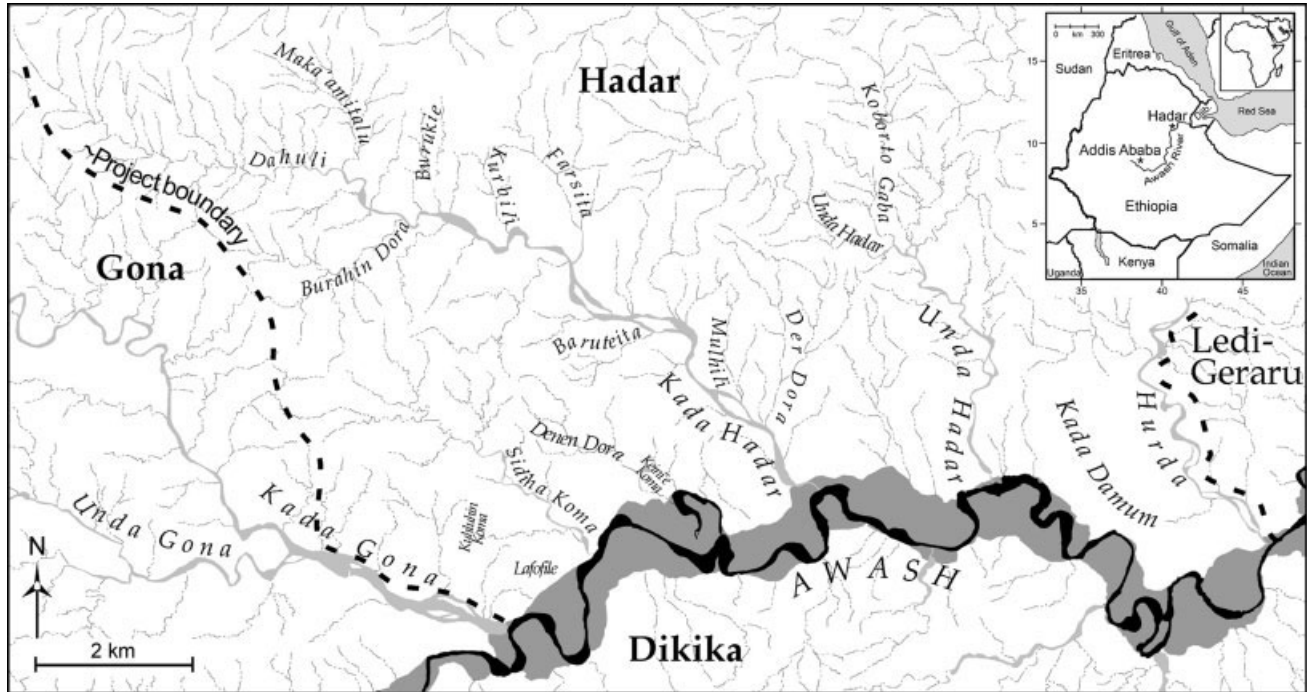


Fig. 1. Map showing location of Hadar.

The Hadar Formation (see Fig. 2) was first recognized for the fossiliferous rocks at Hadar by Taieb et al. (1972: 820), and later divided into four members (from bottom to top: Basal, Sidi Hakoma, Denen Dora, Kadar Hadar), delimited by volcanic marker beds (Taieb et al., 1975: 1297–1298). Hominin fossils found during the 1970s field work derived from the three upper members, with the “Lucy” skeleton being the youngest specimen (from the lower Kada Hadar Member-KH-1 submember). Initial biochronological comparisons (affinities of the mammalian fauna to collections from the Usno Formation and Members A-C of the Shungura Formation of the lower Omo River basin were noted) suggested a temporal range of ~4.0 to 3.0 Ma for the Hadar fossils (Taieb et al., 1974, 1975, 1976). The first rounds of K/Ar dating, conducted by J.L. Aronson at Case Western Reserve University, produced ages broadly consistent with inferences from the fauna (Taieb et al., 1975, 1976; Aronson et al., 1977; Walter and Aronson, 1982). Thus, the Hadar specimens constituted the first substantial collection of fossil hominin remains securely dated to older than 3 Ma.

Subsequent K/Ar dating and evaluation of the mammalian fauna suggested that the base of the section exposed at Hadar was as old as 3.6 Ma (Walter and Aronson, 1982; White et al., 1984), but the geochemical fingerprint of the Sidi Hakoma Tuff (SHT), marking the base of the oldest richly fossiliferous unit at Hadar, was found to be the same as those of the Tulu Bor Tuff (Koobi Fora Formation), and tuffs B-β and U-10 (Shungura and Usno Formations, respectively), which were shown to be no older than about 3.3 Ma (Brown, 1982; Brown and Cerling, 1982; Sarna-Wojcicki et al., 1985). Subsequently, single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating confirmed a ca. 3.42 Ma age for the SHT and determined ages for other tuffs in the Hadar Formation: TT-4, 3.24 Ma; Kada Damum Basalt, 3.30 Ma; Kada Hadar Tuff (KHT), 3.20 Ma; BKT-2, 2.96 Ma (see Fig. 2) (Renne et al., 1993; Walter and Aronson, 1993; Walter, 1994).³

Preliminary systematic interpretations of the Hadar hominins (Taieb et al., 1975; Johanson and Taieb, 1976) aligned fairly closely with the prevailing views of taxonomic diversity summarized above. Lower limb material from A.L. 128 and A.L. 129 as well as the A.L. 288-1 partial skeleton—all noted to share very small size—were affiliated with the Sts. 14 partial skeleton of *A. africanus* from Sterkfontein. The heavily pneumatized temporal bone (A.L. 166-9) and a large partial proximal femur with a flattened neck (A.L. 211-1) were said to show affinities with “robust” australopiths (as represented at Olduvai Gorge [OH 20] and Swartkrans [SK 82, 97]). The bulk of the dental and gnathic material was thought to resemble fossils attributed to *Homo* from Kenya (i.e., KNM-ER 1590, KNM-ER 1802) and Indonesia (i.e., Sangiran 4). However, Johanson and Taieb (1976: 296–297) pointed out that the fit of the 1973–1974 Hadar hominin collection to these previously recognized taxa was not perfect: the temporal bone’s flat mandibular fossa and weak articular eminence; the Lucy mandible’s narrow “V-shaped” dental arcade; and the “guttered nasal margin and alveolar prognathism” of the A.L. 200-1 maxilla pointed to more “primitive” conditions than encountered among the samples of then-known *Australopithecus* species. In a report to the Eighth Pan African Congress in September 1977 (published in 1980), Johanson (1980) dropped mention of a “robust” australopith taxon in the Hadar collection and emphasized the primitive morphology (e.g., unicuspid P_3 , V-shaped mandible, high humerofemoral index) represented by the Sterkfontein-like A.L. 288-1 skeleton and other specimens at the small end of the size range. Although the larger Hadar jaws continued to be referred to *Homo*, the large skeletal size range observed in the extensive, new sample from the single locality A.L. 333 evoked

³Ages adjusted for revised age of analytical standards (C. Campisano, pers. comm., Renne et al., 1998).

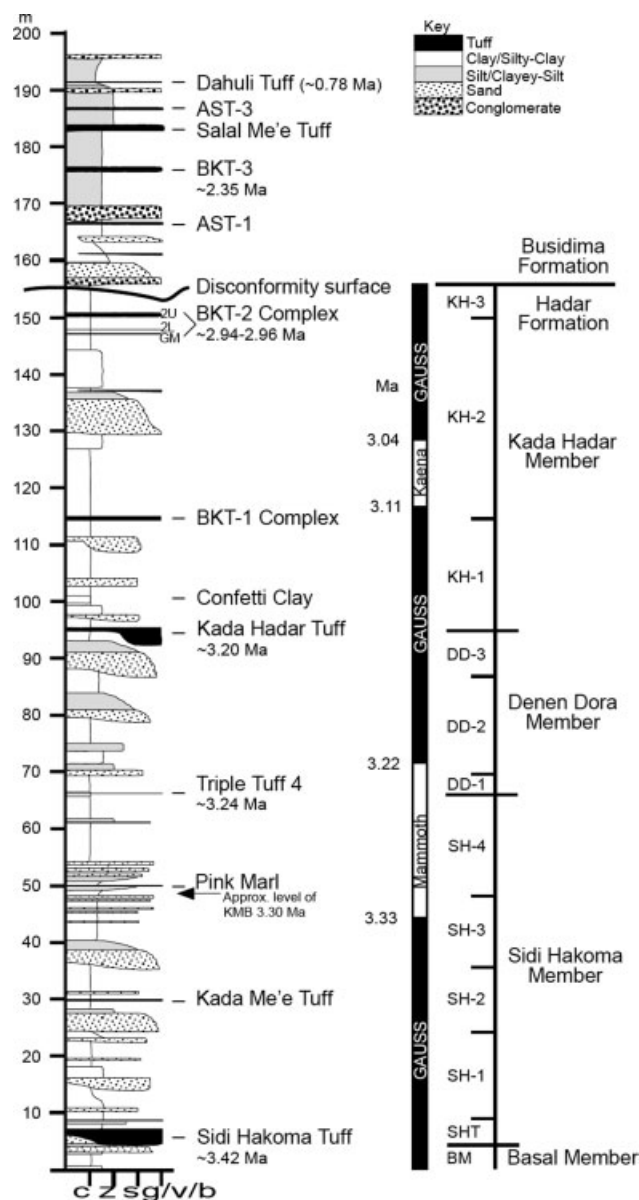


Fig. 2. Stratigraphic section of Hadar Formation (courtesy C. Campisano).

an alternative taxonomic hypothesis: “that the entire sample represents a single, highly variable taxon . . .”

Laetoli

Situated about 50 km south of the “Side Gorge” at Olduvai Gorge, in northern Tanzania (see Fig. 3), the site of Laetoli has been known to science since the 1930s. Louis and Mary Leakey collected fossils from the area on their first visit in 1935 and Ludwig Kohl-Larsen made further collections in 1938–1939 (Leakey et al., 1976). Both expeditions resulted in hominin discoveries that remained for many years in paleoanthropology’s dimly lit corners. The Leakey visit yielded a mandibular canine (M 18773) that was deposited in the collections of the Natural History Museum (London) as a fossil monkey until it was identified as hominin by White (1981).⁴ Kohl-Larsen recovered a fragment of

hominin maxilla with both premolars (“Garusi I”; a heavily worn M³ of another individual was found several km away), which Weinert later (1950) named *Meganthropus africanus*. Remane (1951, 1954) described the Garusi I premolar morphology as apelike—particularly the mesiocervical enamel extension on the buccal face of P³ and this tooth’s two buccal roots—but Robinson (1953: 9) was skeptical: “There seem to be no important features about the specimen differentiating it from *Plesianthropus* [i.e., *A. africanus*], but this does not mean that additional material would not bring such differences to light.” Senyürek (1955) re-emphasized the specimen’s distinctive premolar morphology, additionally noting the large occlusal area of the P³ relative to the P⁴, leading him to assign it to *Praeanthropus africanus* [resuscitating Hennig’s (1948) generic name for the fossil, which, in the absence of an accompanying species name, was a *nomen nudum* and thus had been unavailable]. The specimen was only occasionally mentioned subsequently.

Field work directed by Mary Leakey in the 1970s clarified the stratigraphic relationships of the sediments at Laetoli (identifying at least two age-distinctive sets of deposits: the older Laetolil Beds and the younger Ndolanya Beds), pin-pointed the age of the hominin fossil-bearing Laetolil Beds via radioisotopic dating (ca. 3.46–3.76 Ma) (Fig. 4; Drake and Curtis, 1987), and recovered some two dozen additional hominin specimens, chiefly jaws and teeth but including a partial skeleton of a juvenile (LH-21) (Leakey et al., 1976; White, 1977b, 1980b; Kyauka and Ndessockia, 1990). Hominin footprint trails were discovered in the Laetolil Beds in 1978 (see below).⁵

In their initial interpretive statements about the Laetoli hominin sample, Leakey et al. (1976: 466) recognized “only one phylogenetic entity or lineage,” which resembled that of *A. africanus* of southern Africa and early *Homo* of eastern Africa. As had first impressions of the Hadar material, the early statements on the Laetoli hominins identified primitive characteristics “possibly consistent with their radiometric age,” including the unequally developed cusps and skewed occlusal outline of P₃; and the presence of a C/P₃ diastema, inclined symphyseal axis, bulbous anterior corpus, and low placement of the mental foramen on the adult mandible (LH-4). These attributes of the 1970s Laetoli sample corroborated the observation of primitive dental morphology in the Garusi I maxilla. Leakey et al. (1976: 466) nevertheless suggested “placement of the Laetolil [sic] specimens among the earliest firmly dated members of [the genus *Homo*].”⁶

⁴The Natural History Museum (London) accession number for this specimen has been changed to M. 42323 (R. Kruszynski, pers. comm.).

⁵Recent field work at Laetoli directed by T. Harrison has led to the recovery from the Laetolil Beds of additional fossils of *A. afarensis*, which await description. The Ndolanya Beds (2.5–2.7 Ma) have yielded a maxillary fragment attributed to *Paranthropus aethiopicus* (Harrison, 2002).

⁶The place name was later changed to *Laetoli*, which is the correct transliteration of the Masai word, but the formal name of the sedimentary deposits, published in 1976, must remain the Laetolil Beds (Leakey and Hay, 1979). *Laetoli* or *Olaitole* is a river valley to the south of the main collecting localities; the main complex of fossil localities, with most of the hominin discoveries, occurs in the *Garusi* River Valley (T. Harrison, pers. comm.), which is the location name attached to the Kohl-Larsen discoveries of the 1930s.



Fig. 3. Map showing location of Laetoli.

The logic underpinning the first taxonomic attributions of the Hadar and Laetoli hominins was rooted in the likelihood of multiple hominin lineages extending back into the Pliocene. How far back was anyone's guess, given the patchy fossil record older than 2.0 Ma in eastern Africa, but the contrast in craniodental anatomy between the new material and the later "robust" australopiths, together with the scanty and ambiguous evidence for *A. africanus* outside of southern Africa (see above), made the decision to assign the bulk of the Hadar and all of the Laetoli materials to *Homo* seem logical. [Tobias (1980a; written in 1977) was a notable exception. He argued that the Hadar and Laetoli hominins represented early east African populations of *A. africanus*, a position he (1980b) defended after the recognition of *A. afarensis* in 1978; see below.] Again, however, the analytical focus was less on characters shared uniquely by the relevant samples and later representatives of the *Homo* lineage than on "specialized" ("robust") features they *lacked* in common. In the articles published between 1973 and 1976, there is little concern that genus-level taxonomic

classification is a phylogenetic, not only a phenetic, exercise; cladistic philosophy and methods had only just begun to make a strong impact on paleoanthropology (e.g., Eldredge and Tattersall, 1975; Delson et al., 1977; Tattersall and Eldredge, 1977).

The recognition of *Australopithecus afarensis*

Tim White and Don Johanson's comparative study of the Hadar and Laetoli samples, culminating in lengthy sessions conducted at the Cleveland Museum of Natural History in December, 1977 (see Fig. 5), was a turning point in the taxonomic and phylogenetic interpretation of the Plio-Pleistocene hominin fossil record. (W.H.K. was at the time a graduate student under C. Owen Lovejoy at Kent State University and Johanson's research assistant at the Museum, where the Hadar fossils were on loan for study from the Ethiopian government.) Three main conclusions emerged from this comparative exercise: 1) closely similar dental and mandibular corpus anatomy between the Hadar and Laetoli samples; 2) rel-

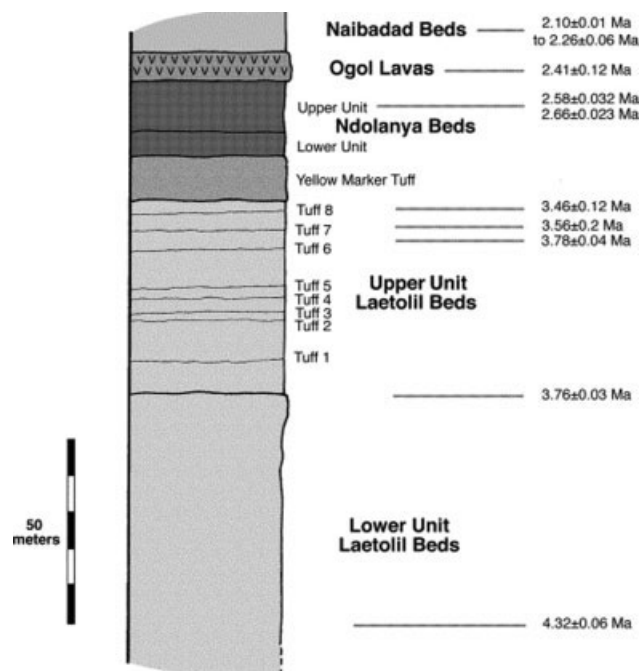


Fig. 4. Stratigraphic section of the Laetoli Beds (after Su and Harrison, 2007).

actively uniform (in the extant hominoid context) morphology across a considerable range of variation in Hadar dental and mandibular size; 3) strongly apelike anterior dentition, face, and cranial vault in the A.L. 333 assemblage, the latter two areas which were for the first time emerging from under matrix cover in the Cleveland preparation lab.

As vividly recalled in Johanson and Maitland Edey’s *Lucy: The Beginnings of Humankind* (1981), while White argued forcefully for including both Hadar and Laetoli samples in a single, variable, strongly dimorphic species, Johanson cited Lucy’s small size, anteriorly narrow (“V-shaped”) mandibular tooth row, and single-cusped P₃ in support of the already published multiple-species interpretation of the Hadar hominins. White’s argument focused on the difficulty of separating the Hadar sample into morphologically distinct craniodental subsets either within or across time planes. Although it was possible to see Lucy as falling at one extreme of the Hadar range of size and morphological variation, and outside of the range of variation for the much smaller Laetoli assemblage, each character (including small size) making up part of her unique anatomy could be found in a slightly different morphological setting elsewhere in the combined sample. Lucy’s anteriorly narrow lower dental arcade could be ascribed to small size and probable female status based on comparison with great apes, in which variation in arcade shape was associated with dimorphism in canine crown/root size and implantation.

With paleoanthropology’s emphasis on Robinsonian masticatory distinctions in the *Australopithecus* skull and dentition providing a powerful interpretive backdrop, the apparent functional and adaptive unity of the Hadar and Laetoli craniodental remains overshadowed plausible divisions of the Hadar sample based on individual elements of the morphological pattern. Thus, a con-

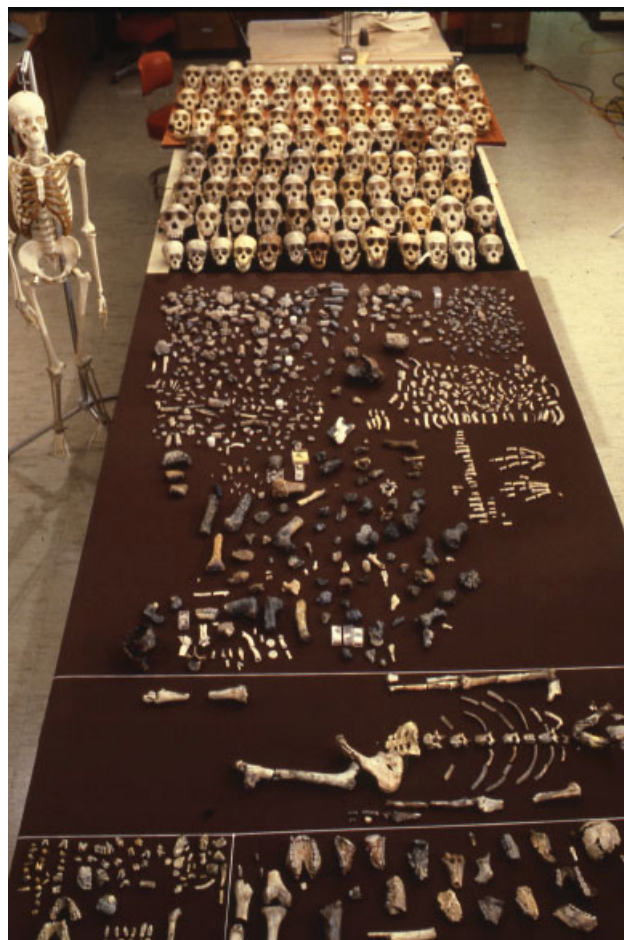


Fig. 5. Hadar hominin fossils assembled for comparative study at Cleveland Museum of Natural History, circa 1979. The A.L. 333 sample occupies the largest area at the center between “Lucy” and Hamann-Todd collection chimpanzee skulls; casts of the Laetoli hominins are at lower left. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

sensus emerged in the “Berkeley-Cleveland” research group that the newly discovered Pliocene hominins represented a single, though impressively variable, species.

Once the decision was made to treat the entire combined sample as a single species, the links between the Hadar and Laetoli hominins and the *Homo* lineage, though tenuous from the outset, were further weakened, as a primitive craniodental profile emerged as the pooled sample’s dominant morphological signature. In addition to the mandibular corpus and P₃, which were mentioned though not emphasized in the two 1976 *Nature* reports (see above), two fossils in the A.L. 333 collection strongly influenced the perception of primitive (apelike) anatomy in the Hadar sample: A.L. 333-1, an adult face with teeth, featured expansive but posteriorly positioned zygomatics, a prognathic snout with a strongly convex subnasal surface and moderately large, procumbent incisors, and a huge (though broken) canine crown and root, while A.L. 333-45, a partial adult calvaria, presented a small endocranial cavity, posteriorly convergent temporal lines forming compound crests with the nuchal lines,

shallow mandibular fossae, and heavily pneumatized lateral cranial base structures. Juxtaposing these specimens conveyed a cranial *gestalt* more similar to that of a large male chimpanzee or of a female gorilla than to that of other then-known australopiths. In short, the morphology of the Hadar and Laetoli teeth, jaws, and crania appeared strongly apelike and adaptively uniform, a combination of attributes that tempered concerns about high morphological variability in a single species, and, along with ancient geological age, marked the path toward recognizing a new taxon for these hominins.

Johanson, White and Yves Coppens introduced the species *Australopithecus afarensis* in an article for the Cleveland Museum of Natural History's house journal *Kirtlandia*, which was scheduled for publication in the fall of 1978.⁷ Mary Leakey originally had been the third author of the article, but she was unhappy with the attribution of the new species to *Australopithecus* and withdrew her authorship just as issue #28 was rolling off the presses, necessitating a reprinting of the entire run and a delay of publication until mid-winter (see Lewin, 1987, for a recounting of this episode).

Because *Kirtlandia* is not available online and may be hard to locate for many readers, we here reproduce the original diagnosis of *A. afarensis* in its entirety (Johanson et al., 1978, p 6–7):

A species of *Australopithecus* distinguished by the following characters:

Dentition. Upper central incisors relatively and absolutely large; upper central and diminutive lateral incisors with strong lingual basal tubercles, upper incisors with flexed roots; strong variation in canine size, canines asymmetric, lowers with strong lingual ridge, uppers usually with exposed dentine strip along distal edge when worn; P₃ occlusal outline elongate oval in shape with main axis mesiobuccal to distolingual at 45° to 60° to tooth row, dominant mesiodistally elongate buccal cusp, small lingual cusp often expressed only as an inflated lingual ridge; diastemata often present between I²/C and C/P₃; C/P₃ complex not functionally analogous to pongid condition.

Mandible. Ascending ramus broad, not high; corpus of larger specimens relatively deep anteriorly and hollowed in region of low mental foramen that usually opens anterosuperiorly; moderate superior transverse torus; low, rounded inferior transverse torus; anterior corpus rounded and bulbous; strong posterior angulation of symphyseal axis; postcanine teeth aligned in straight rows; arcade tends to be subrectangular, smaller mandibles with relatively narrow incisor region.

Cranium. Strong alveolar prognathism with convex clivus; palate shallow, especially anteriorly; dental arcade long, narrow, straight sided; facial skeleton exhibiting large, pillar-like canine juga separated from zygomatic processes by deep hollows, large zygomatic processes located above P⁴/M¹ and oriented a right angles to tooth row with inferior margins flared anteriorly and laterally; occipital region characterized by compound temporal/nuchal crests (in larger specimens), concave nuchal plane short anteroposteriorly; large, flattened mastoids; shallow mandibular

fossae with weak articular eminences placed only partly under braincase; occipital condyles with strong ventral angulation.

The type specimen was Laetoli mandible LH-4, which at the time of the new species' publication had already been described (White, 1977b); it would take some time before the extensive Hadar collection could be readied for full publication (in a special issue of *American Journal of Physical Anthropology*, 57 (4), 1982).

In relation to other australopith species, almost all of the diagnostic features of the *A. afarensis* skull and teeth were primitive, an inference based on conditions common in the extant great apes and middle-late Miocene hominoids. The conclusion that the Hadar and Laetoli hominins represented a single, ancient, primitive, adaptively unified, yet morphologically highly variable species of *Australopithecus* ran counter to prevailing schemes of Plio-Pleistocene hominin evolution in eastern Africa, which, as we have seen, emphasized the likelihood of multiple lineages and at least two adaptive grades (corresponding to genera *Australopithecus* and *Homo*) extending as far back in time as the early Pliocene. It also narrowed the morphological gap between middle-late Miocene great apes (including *Ramapithecus*, which, due to new Eurasian discoveries, had begun to lose its humanlike distinctions from other Miocene hominoids) and earliest hominins, lending support to a growing feeling among some paleoanthropologists that a young divergence date (late Miocene) between African great ape and human lineages, as suggested by the molecular evidence, was not far off the mark (e.g., Greenfield, 1979; Pilbeam, 1979).

The naming of *A. afarensis* in and of itself occasioned relatively little reaction [though Tobias (1980b), as noted above, maintained that the Laetoli and Hadar samples represented two subspecies of *A. africanus*]. There was some initial skepticism concerning the pooling of all of the Hadar fossils in a single species, perhaps because it threatened the idea that multiple east African hominin lineages had separate early Pliocene roots (Leakey and Walker, 1980). Subsequently, a spate of papers argued for multiple species in the Hadar hominin assemblage, either on craniodental (Olson, 1981, 1985; Falk et al., 1995) or postcranial (Senut, 1983; Tardieu, 1983) evidence. Olson argued that derived characters aligned one Hadar morph with *Homo* (palatal depth) and a second morph with "robust" *Australopithecus* (mastoid region inflation, nasal bone shape, premolar molarization). Counterarguments pointed to the failure of the morphs to maintain discreteness when examined in the context of variation both within the Hadar sample and in other hominin species and to problems with polarity definition for cranial base features (Kimbel et al., 1985; see below). Senut identified primitive (small; apelike) and derived (larger; humanlike) distal humeral patterns in the Hadar sample, while Tardieu did the same for the knee; the implication was that an apelike australopith morph was partly arboreal and the derived one—*Homo*—fully bipedal. Some workers (e.g., Stern and Susman, 1983; Susman et al., 1984; but see McHenry, 1986) were prepared to accept functionally divergent morphs based on sex but not on species differences. But the existence of discrete Hadar postcranial morphs was not addressed in depth until recently and has been found wanting on morphometric grounds (Lague and Jungers, 1996; Lague, 2002; Harmon, 2006).

⁷As reviewed by Groves (1999), *Australopithecus afarensis* is actually a replacement name for *Meganthropus africanus* Weinert (holotype: Garusi I) because within the genus *Australopithecus* the species name *africanus* is occupied by Dart's name for the Taung specimen. In 1999 the International Commission on Zoological Nomenclature conserved the species name *afarensis*, which now supersedes *africanus* even outside of the genus *Australopithecus* (Opinion 1941, ICZN).

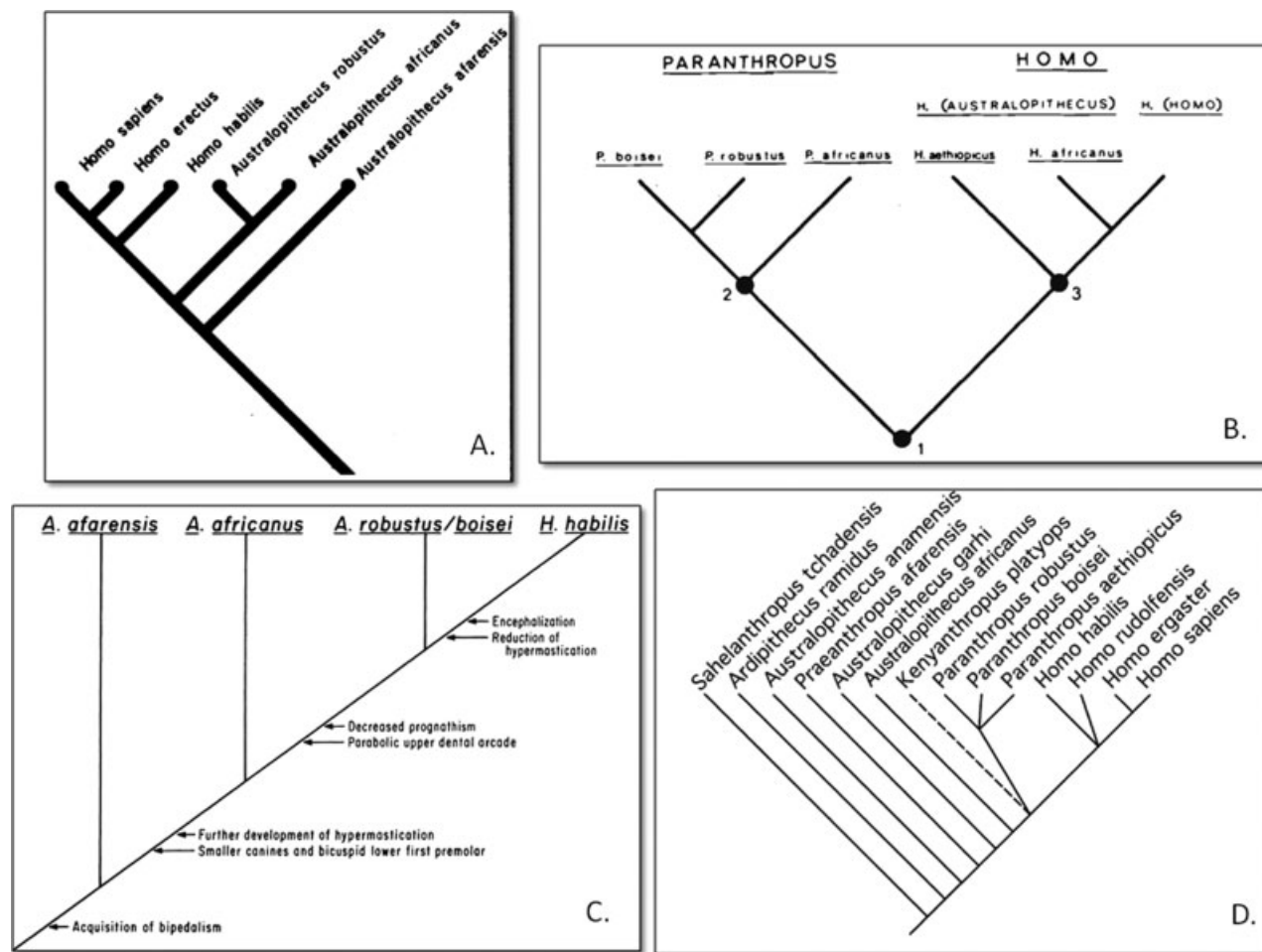


Fig. 6. Cladograms of fossil hominin relationship after the recognition of *Australopithecus afarensis*. **A.** The cladogram of Johanson and White (1979). *A. afarensis* was the sister species to all later hominins, and *A. africanus* was the sister to the “robust” australopiths (the authors were not yet convinced that the eastern and southern African populations were taxonomically distinct). **B.** The cladogram of Olson (1981, 1985). Olson thought that the Hadar sample was divisible taxonomically into two species, each a basal taxon on one of two major clades (*Homo*, *Paranthropus*). The Laetoli sample was included in the Hadar *Paranthropus* species hypodigm. **C.** The cladogram of Skelton et al. (1986). *A. afarensis* was basal to all subsequent hominins, but *A. africanus* was the sister to both the robust australopith and *Homo* clades. **D.** The cladogram of Strait and Grine (2004). This cladogram is similar to that of Skelton et al. (1986) in positing a sister-group relationship between *Homo* and “robust” australopith clades, with *A. africanus* and *A. afarensis* (here *Praeanthropus afarensis*; see footnote 7 in text) basal to both. A feature of virtually all cladistic analyses that treat the Hadar and Laetoli samples as representing a single species is the basal position of *A. afarensis* with respect to subsequent hominin taxa.

Phylogenetic implications

What proved most controversial was the phylogenetic hypothesis promoting *A. afarensis* as the basal taxon from which two lineages emerged after 3.0 Ma, one leading to *Homo habilis* (sensu lato) and the other to the late robust australopiths (*A. robustus* and *A. boisei*), with *A. africanus* as the temporally intermediate basal taxon of the latter lineage (Johanson and White, 1979; White et al., 1981; Kimbel et al., 1984; see Fig. 6). [This interpretation was presaged in White’s (1977a) Ph.D. dissertation, in which ramus and corpus morphology of hominin mandibles from Sterkfontein and Makapansgat were argued to share with robust australopiths adaptations, albeit in less developed form, to exerting and withstanding high magnitude occlusal loads that were absent in east African fossils attributed to *Homo*.] For Johanson, White and Kimbel, the strongly plesiomorphic denti-

tion, face, and cranial vault of *A. afarensis* threw into relief features of *A. africanus* that pointed toward masticatory specialization. The permanent premolars and especially the molars from Sterkfontein (Member 4) and Makapansgat tended to be intermediate in size between those of *A. afarensis* and the “robust” australopiths. The deciduous molars (Taung, Sterkfontein) were more molarized than in *A. afarensis*. Crown-flattening occlusal wear extended forward along the dental row to the canines (whereas in *A. afarensis*, at comparable wear stages, the canines stood above the surfaces of heavily worn cheek teeth). *Australopithecus africanus* mandibular corpora were thicker in relation to height, with fuller contours under the premolars, and the few intact rami were taller. Zygomatic bones were inflated, with roots positioned further anterior in relation to the tooth row. The cranial cresting pattern implied a stronger emphasis on the vertical (anterior) fibers of the temporalis muscle

than in *A. afarensis*. Derived aspects of *A. africanus* facial form were highlighted in Y. Rak's 1980 Ph.D. dissertation (published in book form in 1983): hollowing of the central face; flattening of the subnasal surface; development of solid "anterior pillars" along side the nasal aperture; obliteration of the canine fossa, and other features seemed to cement the position of *A. africanus* in a monophyletic robust clade in which adaptations for heavy mastication had evolved through an incipient stage represented by the hominin fossils from Taung, Sterkfontein and Makapansgat (with particularly strong morphological ties to *A. robustus* of southern Africa). These observations propelled the argument that to maintain *A. africanus* in the role of common ancestor to *Homo* and the "robust" australopiths would entail high levels of evolutionary "reversal" in the masticatory system, as, according to this hypothesis, the teeth, mandible and facial skeleton of early *Homo* were essentially symplesiomorphic.

There was, however, another side to this particular phylogenetic coin, on which evidence indicated that if *A. africanus* was in fact a basal robust australopith, then a large number of derived characters shared by all hominins except *A. afarensis* must have evolved in parallel in the two daughter lineages (e.g., Wolpoff, 1983; Kimbel et al., 1984). These features covered multiple regions of the cranium, mandible and dentition, and included reduced canine size and asymmetry, uniform development of fully bicuspid P₃, reduced (average) facial prognathism, deepening of the palate, increased verticality of the mandible's symphyseal axis, deepening of the mandibular fossa, transformation from a tubular to a plate-like tympanic element of the temporal bone, loss of the compound temporal/nuchal crest and attendant modifications of the posterolateral vault sector, and so forth. All of these features argued for a common ancestor of *Homo* and the robust australopiths more like *A. africanus* than *A. afarensis*, in which they were found in a symplesiomorphic state. This was in fact the conclusion of the first formal cladistic analysis published after the identification of *A. afarensis* (Skelton et al., 1986; Fig. 6)—though at about the same time another such study (Wood and Chamberlain, 1986) found support for Olson's (1981, 1985; Fig. 6) suggestion that the Laetoli and some of the Hadar fossils themselves represented an early, relatively basal "robust" taxon, with *A. africanus* positioned as a sister taxon to *Homo* (see Kimbel, 1984, and Kimbel et al., 1985, for counterarguments).

Comparative anatomical and phylogenetic analyses published in the mid-1980s thus attempted to come to terms with the high levels of homoplasy entailed by incorporating *A. afarensis* into hypotheses of early hominin evolution (Kimbel et al., 1984; Skelton et al., 1986). Parallel evolution became an even larger preoccupation of paleoanthropologists with the discovery of the 2.5-myrr-old cranium KNM-WT 17000 of *Australopithecus aethiopicus* (Walker et al., 1986; Walker and Leakey, 1988), which, on the one hand, expressed derived morphology of the masticatory apparatus shared uniquely with late "robust" australopiths but, on the other hand, retained symplesiomorphic states (e.g., strong prognathism, posteriorly exaggerated cranial crestring, flat mandibular fossa, etc.) from an *A. afarensis*-like ancestor. In a sense, *A. africanus* became a phylogenetic orphan because in the characters in which *A. aethiopicus* was derived, *A. africanus* was primitive and vice versa; this made it much less likely that *A. africanus* was phyloge-

netically intermediate between *A. afarensis* and the late "robusts," whether as a precursor exclusively to *A. robustus* and *A. boisei* or as the last common ancestor to the robusts and *Homo* (e.g., Kimbel et al., 1988).

Although there was—and continues to be—a consensus that the late robust australopiths are sister taxa, an alternative hypothesis suggested that south African *A. robustus* and east African *A. boisei* descended from different geographically matching ancestors (*A. africanus* and *A. aethiopicus*, respectively). According to this idea, the robusts are a polyphyletic taxonomic assemblage. The cost was accepting wholesale homoplasy in the masticatory apparatus, but warranting arguments relied on the Darwinian premise that adaptive phenotypic characters are prone to evolving repeatedly among genetically similar species confronted with similar selective pressures (in this case, due to increasingly xeric late Pliocene African environments) (e.g., Wood, 1988; McHenry, 1994; Lieberman, 1997; but see Collard and Wood, 2001).

The discovery during the 1980s and 1990s of additional mid-Pliocene-age hominin fossils with different combinations of craniofacial and dental features consistent with mechanical hypotheses of heavy mastication has done little to clarify australopith phylogeny (Clarke, 1988, 1994; Asfaw et al., 1999), but most phylogenetic analyses still find that *A. afarensis* represents the sister taxon to, if not the actual ancestor of, post-3.0-myrr-old australopiths and *Homo* (Kimbel et al., 2004; Strait and Grine, 2004; Fig. 6). An exception is Rak et al.'s (2007) suggestion that *A. afarensis* is itself a basal representative of a "robust" australopith clade (reviving, in part, Olson's phylogeny; see above) based on shared, ostensibly derived details of mandibular ramus anatomy (the configuration of the coronoid process and adjacent mandibular notch; see below).

Specimens attributed to (or affiliated with) *A. afarensis* since 1978

Several sites in eastern and central Africa have yielded remains either attributable to *A. afarensis* or with close resemblances to specimens in the "reference" collections from Hadar and Laetoli (see also Table 1).

1. A partial calvaria of a small adult individual (KNMER 2602) from the Tulu Bor Member of the Koobi Fora Formation, Kenya, ca. 3.3 Ma, bears occipital squama and cranial crest morphology diagnostic of *A. afarensis* (Kimbel, 1988).
2. Isolated premolar and molar crowns from the Brown Sands and White Sands deposits of the Usno Formation, Omo River basin, Ethiopia, ca. 3.0 Ma, were assigned by Suwa (1990) to *A. aff. A. afarensis*.
3. A nearly complete mandible with teeth (MAK-VP 1/12), other mandibular and dental specimens, and a proximal femur (MAK-VP 1/1) from the Maka Sands, Middle Awash Valley, Ethiopia, ca. 3.4 Ma, are very similar to Hadar *A. afarensis* counterparts (White et al., 1993, 2000; Lovejoy et al., 2002).
4. A skull and partial skeleton of a juvenile (DIK-1-1) and a fragmentary adult mandible corpus with teeth (DIK-2-1) from the middle to lower Hadar Formation at Dikika, Ethiopia, ca. >3.4–3.3 Ma, have been assigned to *A. afarensis* (Alemseged et al., 2005, 2006). These specimens come from areas south of the Awash River that yielded remains of *A. afarensis* in

- the 1970s (e.g., A.L. 277-1, A.L. 400-1, A.L. 411-1). Specimen DIK-2-1 is the first known hominin from the Basal Member of the Hadar Formation.
5. A fragment of anterior mandibular corpus with teeth (KT12/H1) from Bahr-el-Ghazal, Chad, attributed by Brunet et al. (1996) to *A. bahrelghazali*, ca. 3.0–3.5 Ma (biochronological age range). In most features the specimen falls within the considerable range of variation documented for *A. afarensis* mandibles (but see Guy et al., 2008 and below). Additional but so far undescribed specimens from the same deposits may shed further light on the taxonomic relationship of the Chadian sample to *A. afarensis*.
 6. A partial frontal bone (BEL-VP 1/1) from Belohdelie, Middle Awash Valley, Ethiopia, ca. 3.8 Ma, was assigned by Asfaw (1987) to *Australopithecus* aff. *A. afarensis*; see footnote 8, below). The specimen was discovered when the adult frontal bone of *A. afarensis* was virtually unknown, but Kimbel et al. (2004) subsequently highlighted similarities to the frontal of A.L. 444-2 (discovered in 1992). However, because the frontal of the approximately contemporaneous taxon *A. anamensis* is unknown, assignment of the Belohdelie specimen remains tentative.
 7. Two fragmentary mandibular corpora with teeth (KNM-WT 16006, KNM-WT 8556), recovered in the early-mid 1980s from the Lomekwi Member of the Nachukui Formation (ca. 3.3 Ma), West Turkana, Kenya, were assigned to *A. afarensis* by Brown et al. (2001). Although Leakey et al. (2001) discussed these specimens in the context of their description of the species *Kenyanthropus platyops*, they did not attribute them to this taxon; they did enumerate ways in which they departed from *A. afarensis* morphology, especially in the dentition—which we can affirm from examination of the original fossils.
 8. A mandibular corpus fragment with P₃ and P₄ and canine alveolus (KNM-ER 20432) plus unassociated isolated teeth from the Lonyumun Member of the Koobi Fora Formation (ca. 3.95 Ma), East Turkana, Kenya, were classified as *Australopithecus* cf. *A. afarensis* by Coffing et al. (1994), who noted in KNM-ER 20432 primitive P₃ morphology and implied large canine size relative to usual Hadar and Laetoli conditions. It is now widely considered part of the hypodigm of *A. anamensis* (Leakey et al., 1995; Ward et al., 2001; Kimbel et al., 2006).
 9. Isolated mandibular tooth crowns of two individuals (FJ-4-SB-1a-f and FJ-4-SB-2) from Fejej locality FJ-4, southern Ethiopia, ca. 4.0–4.2 Ma (Kappelman et al., 1996), were assigned by Fleagle et al. (1991) to *A. afarensis*. The six heavily worn teeth constituting FJ-4-SB-1 preserve little if any diagnostic morphology (see also footnote 13, below) although they fall in the lower part of the *A. afarensis* size range. Specimen FJ-4-SB-2 is a relatively unworn P₄ described by Fleagle et al. (1991) as bearing features diagnostic of *A. afarensis*, but we don't think it can be distinguished from *A. anamensis*. The Fejej teeth are not, in our judgment, attributable at the species level.
 10. A set of associated mandibular, dental, wrist (hamate, capitate, lunate), hand (metacarpal 3) and foot (pedal phalanx) elements (KNM-WT 22944a-k) plus a subadult mandibular fragment (KNM-WT 22936) from the Nachukui Formation, South Turkwel, northern Kenya, with an estimated age of between 3.2 and 3.58 Ma, were affiliated with, but

not assigned to, *A. afarensis* (Ward et al., 1999a). The dental and mandibular remains are fragmentary and poorly preserved; they do not appear to be diagnostic at the species level. The hand and wrist bones are broadly similar to specimens from Hadar (i.e., A.L. 333), but the wrist bones also exhibit several characteristics not seen in Hadar homologs (see Ward et al., 1999a). The specific taxonomic status of these fossils remains uncertain.

Chronologically controlled, morphologically diagnostic remains of *A. afarensis* range in age between ca. 3.0 and 3.7 Ma, with Hadar and Usno Formation samples at the younger end of this range, and the Laetoli specimens at the older end. If it is confirmed that the Belohdelie and Fejej sites indeed sample *A. afarensis*, then the species' temporal range would be pushed back further, to ~4.0 Ma. But better samples from these sites combined with an expanded anatomical representation of *A. anamensis* (e.g., the frontal bone) are required to further evaluate this suggestion.

The skull of *Australopithecus afarensis*

The 1970s sample of *A. afarensis* included relatively few adult cranial parts; besides the incomplete facial skeleton (A.L. 333-1) and the calvaria (A.L. 333-45) from Hadar that had proved so important in identifying the primitive cranial morphology of the species, comparative studies could count on the 1973 temporal bone (A.L. 166-9), two very fragmentary partial calottes of small individuals (A.L. 162-28, A.L. 288-1), a craniofacial fragment with part of the cranial base (A.L. 58-22), three maxillae (A.L. 199-1, A.L. 200-1, A.L. 333-2), and assorted small fragments (from A.L. 333). Adult mandibles were, as usual, more common, and, as noted, were already suspected of bearing distinctive morphology. The best preserved non-mandibular skull material was from very young individuals in the A.L. 333 sample (partial cranium A.L. 333-105; associated maxilla and mandible A.L. 333-43/86; the Laetoli partial juvenile skeleton LH-21 also included skull fragments). In the absence of more complete material, a composite reconstruction stood in for the adult *A. afarensis* skull (Kimbel et al., 1984; Kimbel and White, 1988a) until renewed Hadar field work in the 1990s–2000s resulted in the recovery of two mostly complete adult skulls (A.L. 444-2, A.L. 822-1) and craniofacial portions of a third (A.L. 417-1) (Kimbel et al., 1994, 2003, 2004). As these new fossils were being prepared and studied, field teams working elsewhere in eastern Africa discovered remains of previously unknown species, both older (*Australopithecus anamensis*; Leakey et al., 1995; Ward et al., 2001) and younger (*Australopithecus garhi*; Asfaw et al., 1999) than *A. afarensis*, which have clarified the nature and timing of the transformation of the skull and dentition in early australopithec evolution (Lockwood et al., 2000; Kimbel et al., 2006; White et al., 2006; see below).

Here, we summarize the most important aspects of the *A. afarensis* skull and their implications for adaptive evolution and phylogeny.

The cranium and associated mandible. Associated crania and mandibles are rare in the early hominin fossil record; accordingly, the three *A. afarensis* skulls give an unprecedentedly detailed view of a single australopithec species' upper and lower jaws in occlusion. The snout contour is unique among hominoids, with a prognathic, convex (apelike) nasoalveolar surface passing to a straight, relatively upright mandibular symphyseal

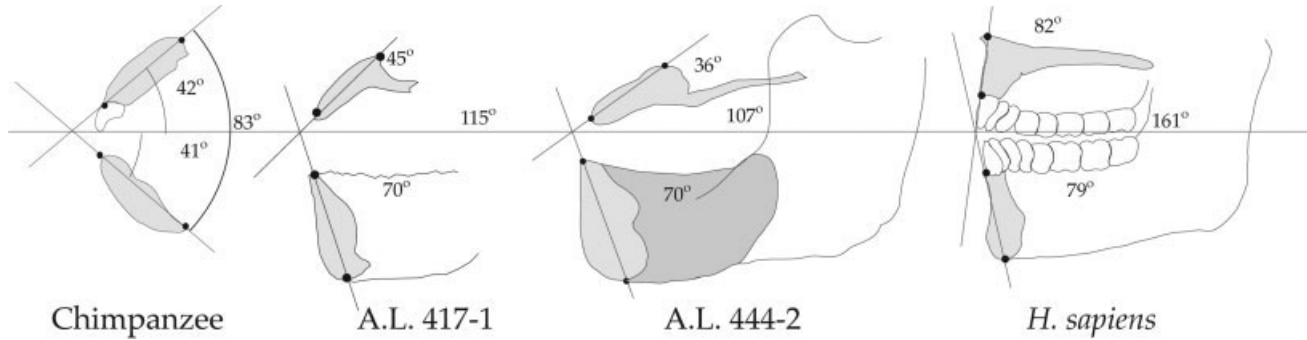


Fig. 7. Snout contours of *A. afarensis* skulls (Reproduced from Kimbel WH, Rak Y, Johanson DC. The skull of *Australopithecus afarensis* © 2004 by Oxford University Press. By permission of Oxford University Press.).

outline with an anteriorly positioned gnathion point (see Fig. 7). Although symphyseal inclination is variable in *A. afarensis* (Kimbel et al., 2004), the contrast between the primitive upper and derived lower snout contours in the associated specimens is marked, implying that evolution in this aspect of the face was mosaic in *Australopithecus*. In the temporally antecedent *A. anamensis*, a more completely apelike configuration may be inferred from the KNM-KP 29281 mandible and KNM-KP 29283 maxilla, which though from different individuals, give a composite view of a fully convex profile, with a strongly receding, convex symphyseal outline to match the apelike arched subnasal contour. The Laetoli sample of *A. afarensis*, interestingly, is intermediate in morphology here, judging from the Garusi I maxilla and the LH-4 mandible (Kimbel et al., 2006).

Another aspect of skull morphology conveyed for the first time by the new associated specimens concerns the tremendous disproportion between mandibular corpus depth under the postcanine teeth and height of the face below the orbits (in the coronal plane of the orbits) (Kimbel et al., 2004). In the African great apes, the mandibular corpus depth equals a little more than half of the orbitoalveolar height but in *A. afarensis* the average is just under 70%. Relatively great corpus height is also present in the SK 12 mandible and maxilla of *A. robustus*, but it may not characterize *A. africanus*, at least to judge by the mandible and maxilla of Sts. 52 (ca. 50%), which, it must be emphasized, is not fully adult.⁸ This relationship is unknown in *A. anamensis* and *A. garhi*, but may be discernible in the Konso, Ethiopia, *A. boisei* skull (Suwa et al., 1997) and in the recently discovered material of *A. robustus* from Drimolen, South Africa (Keyser, 2000), the details of which are not yet published.

The upper face. In contrast to the protruding subnasal segment of the face, the nasomaxillary component (between nasospinale and nasion) is much more upright in *A. afarensis*, as it has also been inferred from the KNM-KP 29283 maxilla of *A. anamensis* (Ward et al., 2001), another departure from the African great ape pattern (see Fig. 8). This difference, which gives the impres-



Fig. 8. Lateral views of maxillae of *A. afarensis* from the 1990s Hadar collection. Clockwise from top left: A.L. 413-1, A.L. 427-1, A.L. 486-1, A.L. 417-1 (left lateral), A.L. 417-1 (right lateral); A.L. 442-1. In A.L. 417-1, note the strong contrast between the relatively vertical midfacial (“nasocanine” of Kimbel et al., 1984) and horizontal nasoalveolar contours. Scale = 2 cm.

sion of great vertical depth, lies behind the generally “hominin-like” appearance of the *A. afarensis* face, which is subsequently elaborated in structurally dissimilar ways in *Homo* and “robust” *Australopithecus* species.

In *A. afarensis* the zygomatic bones and processes are expansive, especially in their relative mediolateral breadth (compared to biorbital breadth, for example). The remarkably rugose masseter origin sites thicken and swell the inferior border of the zygomatics, but they

⁸Some adult mandibles of *A. africanus* show substantial absolute corpus depth (e.g., Sts 7, Sts. 36), but associations with well preserved crania are inconclusive. However, if Sts. 36 represents the same individual as Sts. 71, as hypothesized by Clarke (1994), then *A. africanus*, too, may share relatively high corpus depth in relation to facial height.

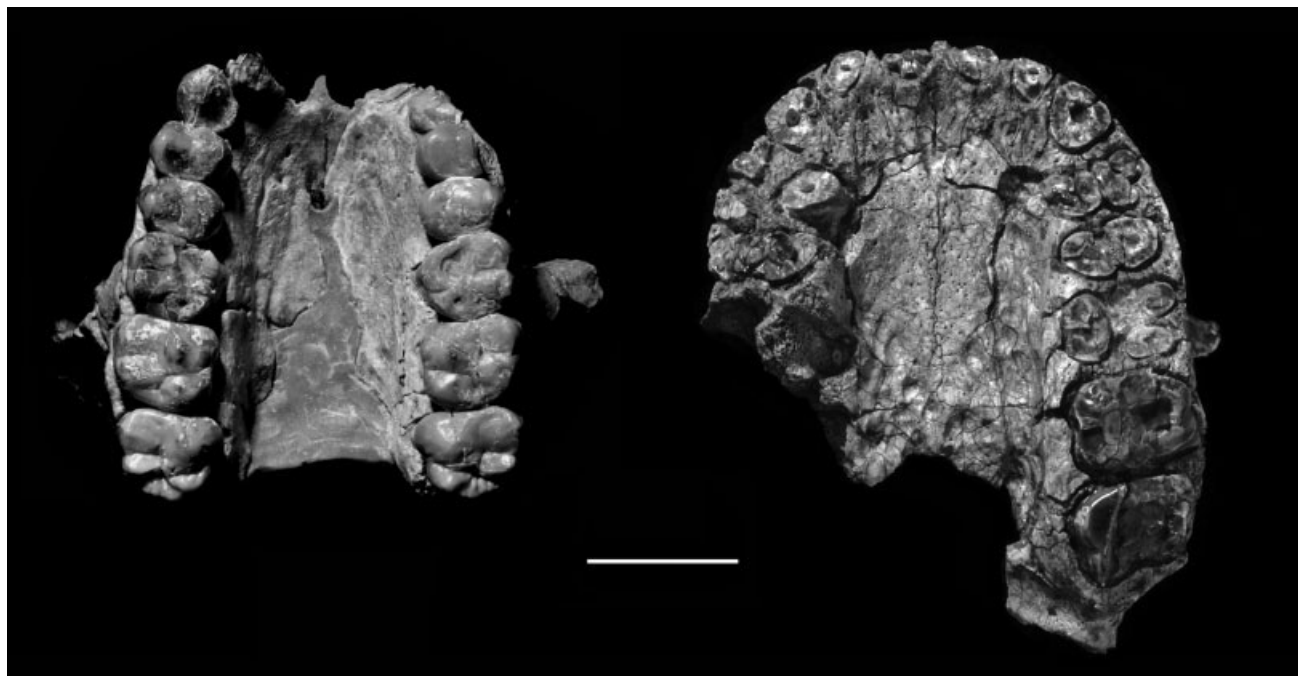


Fig. 9. Two palates from the 1990s Hadar collection. Left, A.L. 417-1; right, A.L. 427-1. The uniformly shallow palate of A.L. 427-1 is similar to that of many other Hadar maxillae, while the deeper palate of A.L. 417-1, seen in a few other smaller Hadar specimens, forecasts the derived condition common in subsequent hominin taxa. Scale = 2 cm.

are set well posterior in relation to the toothrow (over M^1 or P^4/M^1), providing the face with its generally prognathic appearance. Rak's (1983) indices of the masticatory apparatus confirm the strong forward extension of the palate (prosthion) relative to the masseter muscle's origin (at the zygomatic tubercle), a condition shared with *A. africanus* but not with *A. robustus* or *A. boisei*, in which forward advancement of the zygomatics and retraction of the palate brings the coronal planes on which the masseter origin and prosthion reside much closer together than in the more apelike faces of *A. afarensis* and *A. africanus* (Kimbel et al., 2004). *Australopithecus aethiopicus* (KNM-WT 17000) is also primitive in this index due to its strongly prognathic maxilla and in spite of its anteriorly shifted zygomatics. However, according to Rak's "index of overlap," a summary metric that expresses the extent to which the dental arcade length overlaps the distance between the articular eminence and the masseter origin, *A. afarensis* specimens A.L. 333-1 and A.L. 444-2 are the most apelike of any known australopith skull because of the combination of a posteriorly situated masseter origin and a highly prognathic maxilla (Kimbel et al., 2004: 55).

Although quantitative relationships within the *A. afarensis* masticatory apparatus point to the predicted ancestral state for all hominins, the face and mandible diverge from this condition in their relatively deep corpus, relatively vertical symphyseal and midfacial segments, and very broad zygomatics that anchored powerful masseter muscles. Among known australopith taxa, the upright symphysis is an innovation appearing first in *A. afarensis*; this morphological pattern is more clearly expressed in the Hadar than in the smaller Laetoli sample, while the vertical midface is already apparent in *A. anamensis*. The condition of the relative depth of the mandibular corpus and breadth of the zygomatic bones is unknown

before Hadar times, but deep corpora and expanded zygomatics are derived characters putatively linking *A. afarensis* to later hominins.

The palate. A shallow palate was listed as a diagnostic feature of the *A. afarensis* cranium by Johanson et al. (1978). Palate depth in this taxon has two aspects meriting attention: the absolute height of the palatine processes of the maxilla above the postcanine alveolar margins and the degree of inferior flexion of the premaxillary component (anterior to the incisive foramen) (see Fig. 9). In most *Australopithecus* species, the palate is deep in the postcanine region and the premaxilla is strongly inflected inferiorly such that the palatal roof is divided into two planes; in *A. afarensis* the palate is usually shallow in the postcanine region and the premaxilla is unflexed such that the entire palatal surface occupies a single plane. The Hadar maxilla A.L. 200-1a presents the classic example of this morphology, but many other specimens show it as well (including the Garusi I maxilla from Laetoli).

Olson (1981) argued that Hadar specimen A.L. 199-1 differed from the pattern described above for *A. afarensis* in the greater inferior angulation of the premaxillary plane, which aligned this specimen with *Homo* (which for Olson included *A. africanus*), but Kimbel et al. (1985) countered that the difference among the Hadar specimens was actually less than the degree of variation observed in the Sterkfontein sample of *A. africanus*: Sts. 5 and Sts. 52a had very deep palates with strongly inflected premaxillae, whereas Sts. 53 (a small female) was more similar to the modal Hadar pattern. However, more recently recovered Hadar specimens show that while *A. afarensis* palates remain, on average, shallower and flatter than those of other australopith species, some specimens show substantial depth and premaxillary

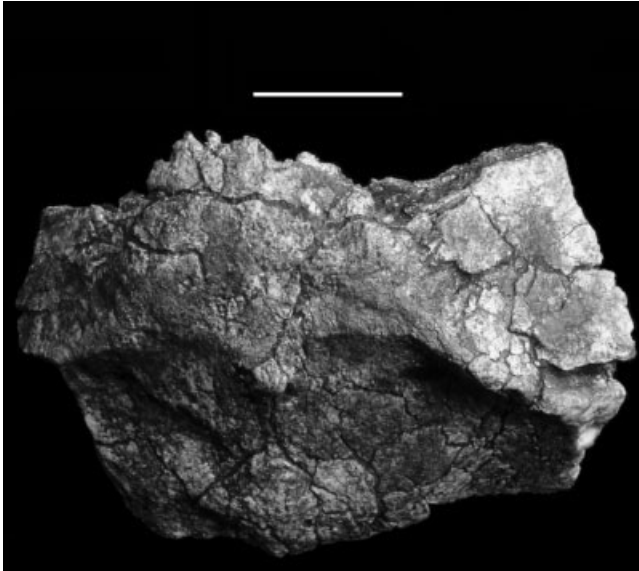


Fig. 10. A.L. 439-1, the largest occipital in the Hadar sample. Note the lambdoidal suture (at top, center), where the temporal lines are in near-contact; the massive compound temporal/nuchal crest on the right; the long, steep nuchal plane; and the high medial arc of the superior nuchal line, which reaches well above the biasterion line. Scale = 2 cm.

angulation of the palatal roof. The latter specimens (A.L. 417-1, A.L. 822-1) (see Fig. 9) are identified as female based on dental size and/or facial form (Kimbel et al., 2003, 2004) and have the narrowest dental arches in the Hadar sample. Perhaps increased palatal depth in these individuals compensated for the restricted oral cavity volume engendered by narrow dental arches, which, in turn, may reflect small cranial base widths in some smaller Hadar individuals. We wonder whether the impressive relative mandibular corpus depth in some Hadar individuals (including A.L. 417-1; see above)—with otherwise fairly generalized masticatory systems (in the australopith context)—may also be influenced by this relationship. With several more or less complete skulls now at hand, this is an aspect of skull form and function in *A. afarensis* worth exploring further.

The cranial vault. The cranial vault of *A. afarensis* encloses a generally small endocranial space (see section below on the endocranial cast), but appears quite large when the massive ectocranial structures are considered; these are related to extensive temporalis muscle origins, especially of the posterior fibers, and a high degree of pneumatization of the lateral cranial base, in both large and small individuals. Extensive pneumatization and expanded posterior temporalis origins are primitive character states for hominins that have been significantly modified—mainly reduced—during the course of human evolution.

A highly pneumatized cranial base is also encountered in the robust australopiths, although, in contrast to the great apes and *A. afarensis*, the degree to which mastoid cellularization expands superiorly and anteriorly into the temporal squama is reduced in the later species of this group, and the architectural and sutural details of the mastoid region itself differ diagnostically (Kimbel et al., 1984, 1985, 2004; Kimbel and Rak, 1985). The adult cranial sample of *A. africanus*, which, in light of

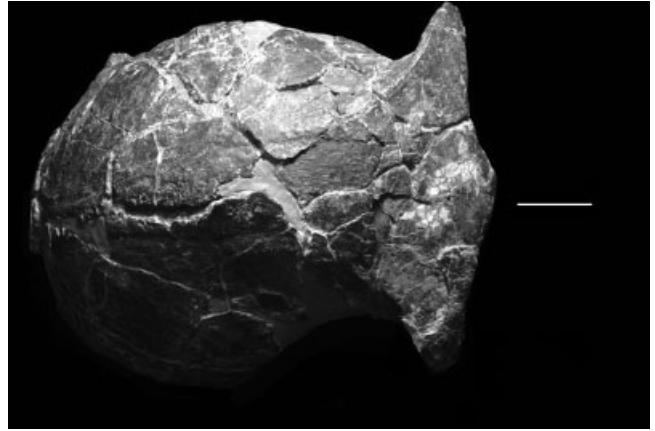


Fig. 11. The calotte of *A. afarensis* skull A.L. 822-1. Scale = 2 cm.

the large Stw. 505 specimen (Lockwood and Tobias, 1999) may be biased toward small female individuals, has less heavily pneumatized vaults—a derived condition shared with *Homo*—than the australopith species that precede or succeed it in time.

Judged by the disposition and size of the ectocranial crests, the emphasis on temporalis fibers migrated anteriorly in species subsequent to *A. afarensis*, although there is individual variation in each taxon. In *A. afarensis*, both large and small individuals (presumptive males and females, respectively) show closest approximation of the left and right temporal lines or compound sagittal crests in the posterior third of the bregma-lambda arc and compound temporal/nuchal crests occur frequently (six of eight adult individuals in which the feature can be evaluated; Fig. 10). With the exception of the *A. aethiopicus* cranium (KNM-WT 17000), which is similar to *A. afarensis* in this respect, all later hominin species typically show anteriorly approximated temporal lines and sagittal crests and reduced frequencies (if not elimination) of compound temporal/nuchal crests, whose occurrence is normally confined to the largest individuals.

The adult frontal bone of *A. afarensis* was almost completely unknown in the 1970s Hadar collection, but with new additions to the sample we can observe one of the most diagnostic areas of *A. afarensis* cranial anatomy (Kimbel et al., 2003, 2004; see Figs. 8 and 11).⁹ The supraorbital elements vertically thicken laterally and in superior view are coronally aligned, deviating slightly forward at their lateral extremities. In other australopiths, these structures are usually thickest medially and retreat backward from the coronal plane laterally. The postorbital distance across the frontal squama is large, absolutely and relative to facial breadths, and there is consequently a less constricted postorbital region than in robust australopiths and *A. africanus* (in both of which the postorbital distance is similar in absolute terms; thus, the perception of strong “postorbital constriction” in the robust group is a function of large facial breadths). It is difficult to assign polarity to these varia-

⁹The 3.8-myr-old partial frontal from Belohdelie shares some of this distinctive anatomy and therefore could represent the oldest known *A. afarensis* specimen (Asfaw, 1987; Kimbel et al., 2004). Because the frontal of *A. anamensis* is unknown, taxonomic attribution is tentative.

tions, as australopith supraorbital architecture differs fundamentally from that of extant African ape outgroup taxa, with their superiorly protruding tori bounded posteriorly by well developed supratoral sulci.

In *A. afarensis*, as in all australopith crania, the frontal squama rises directly from the supraorbital elements without interruption by a supratoral sulcus (see Fig. 8). The ascent of the frontal to bregma describes a flat or mildly convex path, and though there is sometimes a weak supraglabellar depression, a frontal trigone—basinlike and extending posteriorly to or beyond the postorbital plane—is absent, in contrast to morphology in the “robust” australopiths and (as reported by Asfaw et al., 1999) *A. garhi*. The morphology here in *A. afarensis* is similar to that observed in *A. africanus*, except that in *A. afarensis* the relative height of the vault at vertex [expressed, for example, by Le Gros Clark’s (1950) supraorbital height index] is less, a primitive characteristic shared with great apes, *A. aethiopicus* and *A. boisei* (and possibly with the Drimolen skull of *A. robustus*, based on images in Keyser, 2000).

Another distinctive area of the braincase in *A. afarensis* is the occipital bone (see Fig. 10), which was known mainly from three adult specimens in the 1970s Hadar sample (A.L. 162-28, A.L. 288-1, A.L. 333-45) plus a fragmentary but diagnostic specimen from the Tulu Bor member of the Koobi Fora Formation (KNM-ER 2602; Kimbel, 1988); additions since 1990 have increased this sample to eight, two of which are part of complete skulls (A.L. 444-2, A.L. 822-1). The shape of the occipital squama in *A. afarensis* is distinctive among hominin species, as, across the size range, the occipital plane of the squama (lambda-inion) is dominated by the nuchal plane (inion-opisthion), yielding an average index of lower to upper scale distances of about 117%. Although individual specimens (usually large males) in other australopith species occasionally display strong lower scale dominance (e.g., OH 5, MLD 1), species’ mean values average around 100% (the difference is dictated by the very low heights of the upper scale in *A. afarensis* occipitals: the la-i chord as a percentage of biasterionic breadth in *A. afarensis* is 36%; in *A. boisei* it is 41% and in *A. africanus* it is 45%).

The nuchal plane of the occipital bone is much steeper (in relation to the Frankfurt Horizontal) compared to other australopith species. This aspect of cranial morphology appears to be partly sexually dimorphic in *A. afarensis*. In two of three large (male) specimens, the nuchal plane is considerably more horizontal than any of the four smaller (female) specimens (Kimbel et al., 2004). Moreover, in one cranium we judge to be female (A.L. 822-1; Kimbel et al., 2003), nuchal plane steepness is associated with a very high position of the superior nuchal lines in relation to FH: in this specimen, Le Gros Clark’s (1950) nuchal area height index is ~23% (maximum height of the nuchal line above FH/height of vertex above FH), and while this is not as high a value as in chimpanzees (ca. 50%; Kimbel et al., 2004: 35), no other hominin cranium for which this index can reliably be computed has a value higher than about 12% (ms. in prep.). The high index value in A.L. 822-1 highlights the morphology of partial cranial vaults A.L. 439-1 (see Fig. 10) and KNM-ER 2602, which cannot be oriented on the FH with precision, but when positioned appropriately using a variety of preserved landmarks, suggests a similarly high nuchal line position. Specimens of *A. afarensis* with more horizontal nuchal planes have, not surpris-

ingly, lower nuchal lines/crests (A.L. 333-45, A.L. 444-2), the typical condition in other australopith species.

Traditional explanations for the transformation of the occipital region in hominins focus on the acquisition of upright posture and bipedality as the adaptive basis for the forward migration of the foramen magnum/occipital condyles, the lowering of the nuchal plane into alignment with the Frankfurt Horizontal, and the reduction or loss of compound temporal/nuchal cresting (e.g., Schultz, 1955; Robinson, 1958; Olson, 1981). However, while the foramen magnum and occipital condyles are located well forward on a sagittally short cranial base (Kimbel et al., 2004)—already expressed in the more basal hominin taxa *Ardipithecus ramidus* (White et al., 1994) and *Sahelanthropus tchadensis* (Guy et al., 2005)—steep nuchal planes, high superior nuchal lines, and compound crests in both males (4/4) and females (2/4) are more common than would be predicted by this model for an upright biped such as *A. afarensis*. This suggests that bipedality per se played a less central role in the modification of the posterior calvaria and that a more complex scenario involving locomotion-independent variation in head carriage, perhaps involving feeding behavior and posture, should be developed to explain these changes.

The cranial base. The central part of the *A. afarensis* cranial base, featuring reduced anteroposterior length and anteriorly positioned foramen magnum and occipital condyles (seen in A.L. 333-45, A.L. 444-2, A.L. 822-1), is morphologically more derived than the posterior (squamous occipital; see above) or lateral (temporal) portions. Among the most commonly cited apelike attributes of this species’ cranial base is the glenoid region of the temporal bone. Initial characterizations focused on the flat or “open” mandibular fossa, which is weakly bounded anteriorly by a low articular eminence, and the “tubular,” horizontally disposed tympanic situated entirely behind an enlarged (i.e., heavily pneumatized) postglenoid process; these features were clearly seen in the A.L. 166-9, A.L. 333-45, and A.L. 333-84 temporal bones (Kimbel et al., 1984). The more complete cranial specimens recovered since 1990 reaffirm the description of the fundamentally apelike anatomy in the basicranium of *A. afarensis*, with some qualification. For example, the newer specimens (A.L. 444-2, A.L. 822-1) show that, on average, articular eminence development is stronger, and hence mandibular fossa depth is greater (less apelike), with overlap between the ranges of variation for *A. afarensis* and *A. africanus* (e.g., TM 1511, Sts. 5; Kimbel et al., 2004). The mean fossa depth for *A. afarensis* remains shallow relative to other australopiths except *A. anamensis* ($n = 1$).

In later australopiths and *Homo* the semi- or completely vertical platelike tympanic forms more of the posterior “wall” of the mandibular fossa than the postglenoid process, which in great apes forms the greater part of this boundary, with the tympanic situated directly behind it (Weidenreich, 1943; Tobias, 1967). Even in the largest robust australopith crania the postglenoid process is much reduced compared to the large, inflated structure in the plesiomorphic glenoid region, and comes to occupy almost the same coronal plane as the tympanic itself. In *A. afarensis* the tympanic retains almost all of this symplesiomorphic feature set: it is horizontal, with anterior and posterior borders, rather than inferior and superior borders as in the vertical tympanic, the princi-

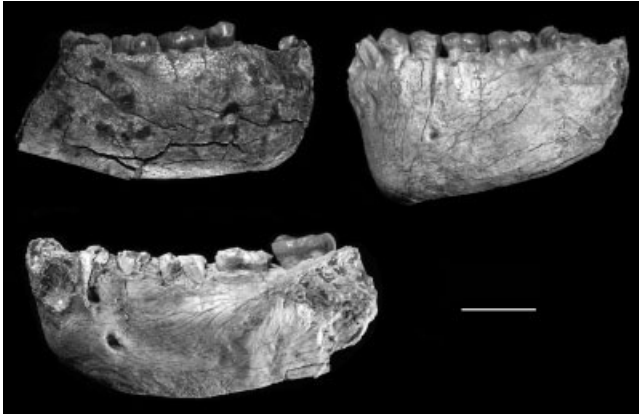


Fig. 12. Lateral views of Hadar mandibles A.L. 330-5 (upper left), A.L. 417-1 (upper right) and A.L. 620-1 (lower left). The A.L. 417-1 mandible is associated with the craniofacial portion of the skull shown in Figure 8. Note the high, posterior position of the ramal root in all three jaws. Scale = 2 cm.

pal inferior surface is convex or flat, and the attenuated “petrous crest” of the platelike configuration is weak or nonexistent. This anatomy is apparent, too, in the temporal bone fragment forming part of the type specimen of *A. anamensis* (Ward et al., 2001), but is modified to a greater or lesser degree in all hominins subsequent to *A. afarensis* (see Kimbel et al., 2004 for further details).

Neither the functional nor the adaptive basis for many of the evolutionary changes charted in the glenoid region of the hominin skull is well understood. Weidenreich (1943) thought that many of the distinctions of the human glenoid region could be traced to “transformation” of the cranial base (occipital rotation, forward migration of the foramen magnum, etc.) co-occurring with brain expansion, although he realized this could not be the whole story in light of the humanlike glenoid morphology in the small-brained type cranium of *A. robustus* (TM 1517). Subsequent discoveries of *Australopithecus* and early *Homo* show that morphological change in this region of the cranium has occurred outside the context of brain expansion or postural changes. These changes have been complex and mosaic in pattern (e.g., Kimbel et al., 2004; Terhune et al., 2007), raising potential links to dietary shifts as read in the record of dentognathic transformation (e.g., DuBrul, 1977); yet these links remain to be tested in explicit functional-adaptive and phylogenetic contexts.

The mandible. The mandible is the most common element other than teeth in the *A. afarensis* hypodigm: the Hadar sample alone includes 56 adult or near-adult mandibular specimens, some of which are spectacularly complete (Figs. 12–15). At Dikika, located just to the south of the Awash River from Hadar (see Fig. 1), a partial adult mandible was recovered from the Basal Member of the Hadar Formation (DIK-2-1, the first hominin fossil from this unit, which is poorly exposed at Hadar) (Alemseged et al., 2005) and at Maka (Middle Awash, Ethiopia) a nearly complete adult mandible of *A. afarensis* was recovered from sediments equivalent in age to lower Hadar Formation units (MAK-VP 1/12; White et al., 2000); both of these specimens are around 3.4 myr old. As noted above, preliminary descriptions of the Hadar and Laetoli hominins mentioned distinctive attributes of their mandibular corpus anatomy

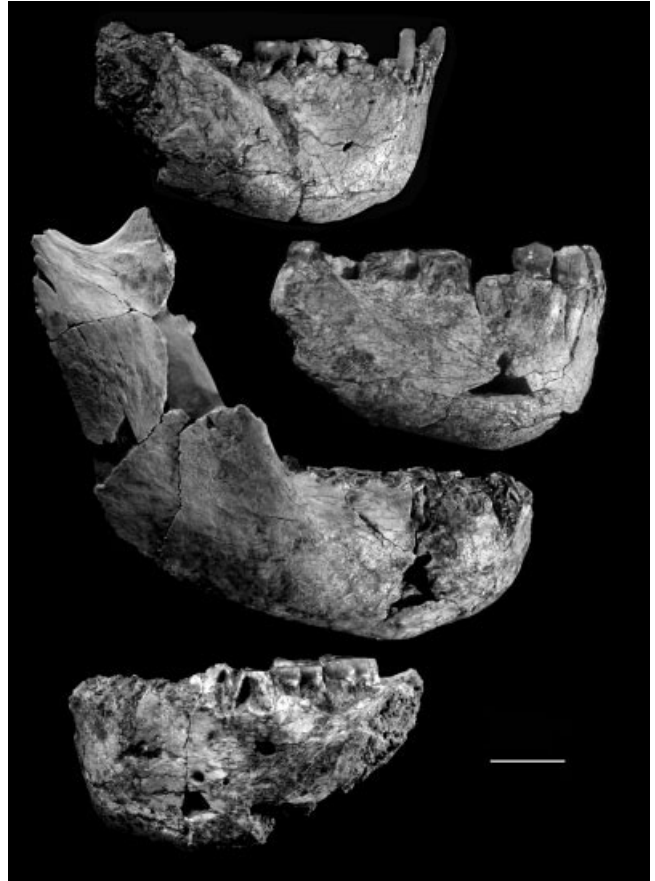


Fig. 13. Lateral views of Hadar mandibles, from top: A.L. 444-2, A.L. 437-2, A.L. 438-1, A.L. 437-1. All are from the youngest sediments (ca. 3.0 Ma) in the Hadar Formation known to contain *A. afarensis* and constitute a key part of the evidence for a size increase in the KH-2 submember (see also Fig. 15). Scale = 2 cm.



Fig. 14. Occlusal views of Hadar mandibles: A.L. 417-1 (left) and A.L. 330-5 (right), demonstrating variation in dental arch shape in *A. afarensis*. Scale = 2 cm.

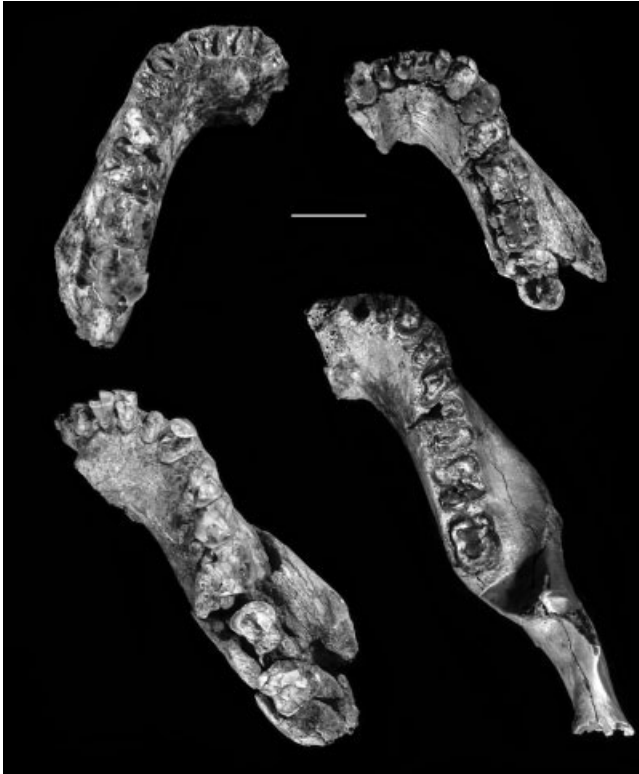


Fig. 15. Occlusal views of Hadar mandibles: clockwise from upper left, A.L. 437-1, A.L. 437-2, A.L. 438-1, A.L. 444-2. In the latter jaw, M2 and M3 are displaced laterally.

(Johanson and Taieb, 1976; Leakey et al., 1976), and mandible LH-4 exemplified these distinctions so thoroughly that it was selected as the type specimen of the species.

The *A. afarensis* mandible sample is impressively variable in size and shape. This variation surrounds an invariant core of diagnostic, mostly plesiomorphic, characters (Johnson et al., 1978; White et al., 2000; Kimbel et al., 2004):

- a posteriorly sloping, rounded, bulbous anterior corpus
- a weak to moderate superior transverse torus
- a low, rounded, basally set inferior transverse torus
- an inferiorly placed, anterosuperiorly opening mental foramen
- a hollowed lateral surface (superior and posterior to the mental foramen), defined anteriorly by a C/P₃ root bulge and posteriorly by a weak lateral prominence
- generally straight molar/premolar dental rows, but with variations from a slight lateral convexity to a slight lateral concavity
- ascending ramus arising high on the corpus to form a narrow extramolar sulcus

First examinations of metric variation in the *A. afarensis* mandibular corpus (Johanson and White, 1979; Kimbel and White, 1988b) found substantial amounts of size variation (as measured by the CV), but which did not exceed that found in the largest great apes (*Gorilla*) or *A. boisei* (the only other australopith species with an adequate sample size; see Silverman et al., 2001). With

the recently augmented Hadar mandible samples at hand, Lockwood et al. (2000) analyzed corpus size variation (breadth, height, geometric mean at M₁) using randomization tests to evaluate the significance of differences between coefficients of variation for *A. afarensis* and hominoid comparative samples. In this study, the null hypothesis that the *A. afarensis* mandible corpus is no more variable than that of samples of African great ape mandibles was rejected in five of six tests. In contrast, variation in the corpus shape index was found to be within the range for the comparative taxa. Lockwood et al. (2000) used nonparametric rank correlation and randomization tests to investigate whether anagenetic change within the *A. afarensis* lineage contributed significantly to the elevated levels of size variation in the mandible corpus. They discovered a pronounced temporal shift toward larger corpus size (especially corpus height) within the Hadar stratigraphic sequence, localized in the upper part of the Kada Hadar member (KH-2), from which A.L. 444-2, as well as three other large mandibles (A.L. 437-1, A.L. 437-2 and A.L. 438-1g), were recovered (Figs. 13 and 15). The mean corpus (at M₁) height and breadth for this late (ca. ≤ 3.0 Ma) sample are, respectively, 21 and 18% larger than for the older *A. afarensis* sample (ca. 3.2–3.4 Ma: sub-KH-2 Hadar, MAK-VP 12/1, DIK-2-1).¹⁰ When these four specimens are removed from the analysis, no significant size trend is detectable. Lockwood et al. (2000) concluded that the relatively high levels of variation in the *A. afarensis* mandible corpus were due mostly to change in size over time. There was no finding of temporally directed change in the corpus shape index; apparently, ancestral corpus proportions were preserved as the *A. afarensis* mandible grew larger over time.

In interspecific comparisons of early hominins, a transversely broad mandibular corpus has been interpreted as a functional response to high magnitude loading and axial twisting of the corpus during mastication (e.g., Hylander, 1979; but see Daegling and Hylander, 1998, for a cautionary note). For the entire Hadar *A. afarensis* sample, the mean shape index value is 57% ($n = 21$ Hadar specimens for which both variables can be measured; the addition of MAK-VP 1/12, LH-4 and DIK-2-1 does not change this value); in other australopiths the mean index value is between ca. 60 and 65%, increasing in the series *A. africanus*-*A. robustus*-*A. boisei*, meaning wider corpora (at M₁) relative to depth (Kimbel and White, 1988b). As in the great apes, often in *A. afarensis* larger (male) mandibles (e.g., A.L. 277-1, A.L. 437-1) have a more slender (i.e., relatively deep) corpus than do smaller (female) mandibles (Kimbel and White, 1988b; Lockwood et al., 2000), but this is not clearly associated with larger canine size in the sample as has sometimes been suggested.

A number of fossils added to the Hadar mandible series during since 1990 feature a more upright symphyseal axis than typical of the 1970s sample (A.L. 417-1a, A.L. 437-1, A.L. 437-2, A.L. 438-1g, A.L. 444-2, and A.L. 620-1). Although it remains true that few, if any, mandibles

¹⁰Canine crown and root size and/or associated cranial morphology suggest that all four late mandibles are male. The metric differences are 9 and 10%, respectively, when only the largest mandibles (confidently sexed as male; $n = 5$ of 20) in the older sample are used. These differences are likely to be underestimates, however, as some moderate-sized mandibles in the older sample that cannot confidently be sexed are undoubtedly male.

bles of *A. africanus* have symphyseal axes as inclined as those of A.L. 198-1, A.L. 277-1, A.L. 333w-60, or A.L. 400-1a, the degree of overlap between the mandibles of this species and those of *A. afarensis* is much greater than was previously documented. Thus, the inclination of the symphysis is quite variable in *A. afarensis*. In one of the largest Hadar mandibles, A.L. 444-2, and in one of the smallest, A.L. 288-1i, the mandibular symphysis is nearly vertical, but more posteriorly inclined symphyses are also encountered across the Hadar mandible size range (A.L. 207-13, small vs. A.L. 333w-60, large).

In terms of its symphyseal inclination, the *A. afarensis* type mandible LH-4 falls within the range for the Hadar sample, but differs from Hadar and Maka specimens in the external midsagittal contour of its anterior corpus. In the Laetoli specimen, the inferior part of the contour is not bulbous but is “cut away” to create a curved, continuously retreating profile, a configuration shared with mandibles of *A. anamensis* (Ward et al., 2001; Kimbel et al., 2006). The difference between the Laetoli specimen and those from Hadar does not appear to relate to the inclination of the symphyseal cross section per se, as Hadar mandibles with the symphysis inclined to a similar degree as LH-4’s maintain a straighter, more “filled out” external anterior profile (e.g., A.L. 400-1a). The departure of LH-4 from Hadar anterior corpus morphology is underscored by the similar differences between the Laetoli (LH-2) and Hadar-Dikika (A.L. 333n-1, A.L. 333-43, DIK-1-1) juvenile mandibles (Alemseged et al., 2006; Kimbel et al., 2006).

In their diagnosis of the Chadian species *Australopithecus bahrelghazali*, Brunet et al. (1996: 908) point to the “flat anterior corpus” as distinctive with respect to *A. afarensis* mandibles. However, the variation in Hadar mandibular anatomy comfortably accommodate the external anterior corpus form of the KT 12 holotype (Kimbel et al., 2004: 189). Indeed, Guy et al.’s (2008) recent detailed study of this mandibular region in the Chadian sample (now augmented by a second mandible, KT 40) does not appear to locate distinctive anatomy in this aspect of mandibular form (in contrast to the lingual surface of the anterior corpus).

In almost all *A. afarensis* mandibles, the ramus arises high on the corpus and defines a narrow extramolar sulcus (buccinator groove) (see Fig. 12). Neither the height nor the anterior extension of the ramus root on the corpus appears to covary with corpus size in the Hadar sample. In one large Hadar mandible, A.L. 437-2, the ramus root reaches inferiorly to approximately midcorpus level, as frequently seen in later *Australopithecus* species (White et al., 1981), while in A.L. 333w-60, A.L. 444-2, A.L. 438-1g and A.L. 437-1, also large specimens, the ramus origin sits high on the corpus, as in many other *A. afarensis* mandibles (see Fig. 13). The root of the ramus extends forward to the mesial M₁ level in A.L. 444-2 and A.L. 438-1g, as it does in the small female A.L. 288-1i. In most *A. afarensis* mandibles, the position of the ramal root ranges from middle (e.g., A.L. 128-23, A.L. 330-5, A.L. 333w-1) to distal M₁ (e.g., A.L. 277-1, A.L. 417-1a, A.L. 437-1, A.L. 620-1; MAK-VP 1/12). Even in those specimens with a relatively anterior extension of the ramal root, the characteristic hollowing of the lateral corpus beneath the premolars is still in evidence. This is a sharp distinction relative to the mandibles of later australopiths, including *A. africanus*, in which the ramal root often merges indistinguishably with the swollen lateral corpus under the premolars.

The form of the coronoid process and the adjacent mandibular notch varies among hominoid species according to the study by Rak et al. (2007), who pointed to a broad, posteriorly attenuated process and narrow notch as derived states cladistically linking *A. afarensis* and *A. robustus*. However, as these authors observe, *A. africanus* also appears to share these features, which would imply in their scheme that *all* australopith species (for which the mandibular ramus is known) are part of a deeply rooted “robust” hominin clade within which phylogenetic relationships remain poorly resolved. However, because this region of the ramus is unknown for early *Homo*, it is difficult to make reliable inferences about phylogeny based on the Rak et al. (2007) character analysis.¹¹

The hyoid bone. The only known hyoid bone of an australopith-grade hominin comes from the DIK-1-1 juvenile skeleton of *A. afarensis*. Preliminary study of this bone reveals strong affinities with African ape hyoids: “the exposed greater horn is slender, and the body is expanded anteriorly, forming a bulla that is deep relative to its breadth and height” (Alemseged et al., 2006: 298).

The endocranium. Holloway and Yuan (2004; Holloway et al., 2004) have summarized the state of knowledge regarding endocranial volume determinations for *A. afarensis*, and the methodological details need not be reiterated here. Four adult crania (A.L. 162-28, A.L. 333-45, A.L. 444-2, A.L. 822-1) yield some information about the internal capacity of the brain case, estimates of which range between ≤ 400 cc and ca. 550 cc (the endocranial cavity of A.L. 822-1 is still under reconstruction and study and a volume estimate is not yet available; on the basis of visible evidence and external dimensions, however, the volume can be predicted to fall near the lower limit of this range). The A.L. 444-2 volume is the largest in this range of estimates, exceeding the A.L. 333-45 volume by as much as 75 cc. Recall, however, that the A.L. 444-2 skull is from the latest *A. afarensis*-bearing portion of the Hadar Formation and constitutes part of the evidence for skull (and possibly body) size increase in the Hadar australopith lineage (Lockwood et al., 2000). It is therefore reasonable to think that the large endocranial volume determination for A.L. 444-2 may simply be a consequence of an increase in overall size, as opposed to an indication of encephalization within the lineage. Although endocranial volume estimates do not exist for *A. afarensis* skulls with firmly associated postcrania from which body size can be estimated (and they do not for any australopith species), the amassed sample suggests that brain:body size relationships within *A. afarensis* were not unusual for an australopith species, which is to say that encephalization may have modestly surpassed what is observed in the extant great apes. It is our impression that this relationship was essentially stable across all species of the australopith grade (not necessarily including species usually attributed to genus *Homo*, however).

The form of the *A. afarensis* brain endocast reveals a mixed pattern of affinities with respect to other hominin species (Holloway and Yuan, 2004). As in endocasts of *A. robustus* (i.e., SK 1585) and some *A. boisei* (OH 5 and KNM-ER 407, but not KNM-ER 23000), as well as some

¹¹Moreover, the morphology is present in *Gorilla* but not *Pan* or *Pongo*, raising questions about polarity and homoplasy.

of early *Homo* (e.g., OH 24), the position of the cerebellar lobes is apomorphic: tucked under and well forward of the occipital poles of the cerebrum. In *A. africanus*, as in chimpanzees, the occipital poles and the cerebellar lobes project posteriorly subequally, which is also the case in the KNM-WT 17000 endocast of *A. aethiopicus*. The form of the cerebellar lobes in A.L. 333-45 and A.L. 444-2 is also similar to that of robust australopiths—triangular in outline, with a flattened posterolateral face—but in relation to the rest of the endocast, cerebellar size (estimated volume) is much smaller than in any other australopith or even in African great apes (Holloway and Yuan, 2004).

Of the endocasts studied to date, only those of A.L. 444-2 and A.L. 438-1 (a frontal fragment associated with a mandible and partial upper limb skeleton; Drapeau et al., 2005) provide information on the shape of the frontal lobes. In contrast to the frontal lobe morphology of the robust australopiths, which features a unique, sharply tapering or “beaked” anterior contour (Falk et al., 2000), the front of the *A. afarensis* brain endocast is full and rounded, as in *A. africanus* and *Homo* (the plesiomorphic condition). The tapering frontal lobe in the robust australopiths likely is a reflection of the external form of the braincase, which (in superior view), from the plane of maximum calvarial width, narrows much more “rapidly” to the postorbital plane than in other australopiths, including *A. afarensis* (Kimbel et al., 2004).

The pattern of venous sinus grooves in the posterior endocranium of the *A. afarensis* skull is consistent with a dominant but asymmetrically developed (often unilateral) occipital-marginal sinus outflow track, another endocranial feature shared with robust australopiths (Falk and Conroy, 1983; Kimbel, 1984). To date, eight of nine specimens in which the pattern can be discerned unequivocally show occipital-marginal system dominance (it is not present in the LH-21 juvenile). Almost all the robust australopiths do as well (it is apparently absent in KGA 10-525; Suwa et al., 1997), but the most common human and great ape pattern of transverse-sigmoid sinus outflow is present in most *A. africanus* specimens (two of seven individuals, Taung and Stw. 187a, have a dominant occipital-marginal system; see Tobias and Falk, 1988; Kimbel et al., 2004).

The dentition of *Australopithecus afarensis*

The dental characters used initially to diagnose *A. afarensis*—principally associated with the canines and P₃ and their inferred function—were more apelike than in any other known hominin taxon and, consistent with its geological antiquity, this suite of primitive features supported the phylogenetic hypothesis that *A. afarensis* was the sister taxon to all other then known hominin species. Since the initial discoveries at Hadar and Laetoli, dental specimens attributable to *A. afarensis* have been found at Maka (White et al., 2000) and Dikika (Alemseged et al., 2005, 2006), in Ethiopia, and many additional specimens have been recovered from Hadar (see Table 1 and Kimbel et al., 2004). These new specimens reinforce the morphological pattern described initially for the Hadar and Laetoli series and add dental elements that were previously unknown (i.e., the di¹; Alemseged et al., 2006), so that, now, all dental positions, both deciduous and permanent, are represented for the species. The discovery of *A. anamensis*, *Ardipithecus*, *Orrorin tugenensis*, and *S. tchadensis*, which are geologically older than *A. afarensis*, reveals, not unex-

pectedly, a still more primitive dental configuration; however, dental morphology is still consistent with the hypothesis that *A. afarensis* is the sister taxon to all geologically younger hominin species.

Detailed descriptions and interspecific comparative analyses of the *A. afarensis* dentition are presented in White (1977b, 1980b), White et al. (1981, 2000), Johanson et al. (1982c), Grine (1985), Kimbel et al. (2004), and Alemseged et al. (2005, 2006). Here we summarize important aspects of *A. afarensis* dental morphology, function, and development.

The deciduous dentition. Comparisons of the *A. afarensis* deciduous anterior dentition are limited by small sample sizes for most hominin taxa. In the deciduous (and permanent) dentitions of *A. afarensis*, as in extant great apes, the maxillary central incisor is larger than the lateral incisor (Johanson et al., 1982c). Deciduous maxillary incisors are not represented in the *Ardipithecus* material so far published and the di¹ is not currently represented in the *A. anamensis* sample (Ward et al., 2001). Additionally, for Sterkfontein *A. africanus* the di² is unknown (Moggi-Cecchi et al., 2006); however, the Taung child has a di¹ that is only slightly longer MD than the di², suggesting that the degree of deciduous incisor heteromorphy is reduced in this taxon. The shape of the *A. afarensis* maxillary deciduous incisors is distinct from that of younger hominins. As in the extant African apes, both deciduous maxillary incisors of DIK-1-1 are MD long relative to their LaL breadth, giving them a fan-shape that differs from the cylindrical incisor crowns of the Taung child (Alemseged et al., 2006).

Paralleling changes in the permanent dentition, discussed below, the *A. afarensis* deciduous dentition displays a mixture of primitive and derived traits related to the loss of canine honing. Deciduous maxillary canines from Laetoli, Dikika, and Hadar are similar morphologically. The *A. afarensis* d^c is larger in basal dimensions than those of *Homo*, the robust australopiths, and *A. africanus* (White et al., 1981; Grine, 1985; White, 1985; Moggi-Cecchi et al., 1998; Alemseged et al., 2006). Though the *A. afarensis* d^c is reduced compared to that of extant apes, little can be said about the evolutionary pace of this reduction in hominins since the d^c is unknown for hominins geologically older than *A. afarensis*. The situation is better for the d_c, which is represented in *Ar. ramidus* and *A. anamensis*. Both absolutely and relative to deciduous molar size, the d_c of *A. afarensis* is larger than that of the robust australopiths and early *Homo* (Grine, 1985) but, relative to dm₁ size, the d_c of *A. afarensis* is reduced compared to *Ar. ramidus* (ARA-VP-1/129). The *Ar. ramidus* d_c, in fact, surpasses in relative size the d_c in *Pan troglodytes* and *Gorilla gorilla* (White et al., 1994).

In extant apes, which have a functional honing complex, the dm₁ resembles the permanent P₃: the dm₁ is elongated MD and is dominated occlusally by a large protoconid, which renders the crown nearly unicuspid. The mesial marginal ridge is weakly developed or absent; thus, the anterior fovea forms a tall, flat triangular face—when viewed lingually—which is “open” mesiolingually. Much of this plesiomorphic feature set is seen in the sparse record of dm₁s for taxa that antedate *A. afarensis* (the dm₁ is unknown for *Ar. kadabba*, *S. tchadensis*, and *O. tugenensis*). The *Ar. ramidus* dm₁ (ARA-VP-1/129) is the most ancient and primitive in the known hominin record. Relative to *A. afarensis*, ARA-VP-1/129 is smaller, more MD elongated relative to its

BL breadth, has a poorly developed talonid, and lacks a prominent metaconid and any development of the anterior fovea (White et al., 1994). Though not as exaggerated as in *Ar. ramidus*, the *A. anamensis* dm_1 (KNM-KP 34725) is also MD elongated relative to its BL breadth, and has a poorly developed talonid (Leakey et al., 1998).

Compared to *Ar. ramidus* and *A. anamensis*, the *A. afarensis* dm_1 is "molarized" and is similar in morphology to the dm_1 of *A. africanus*. In *A. afarensis* the dm_1 is multicuspid and the mesial marginal ridge is present, though poorly developed, contributing to the formation of the trigonid, which, as noted, is absent in the geologically older hominins (White, 1985; Alemseged et al., 2006). *Australopithecus afarensis* dm_1 s depart from the plesiomorphic configuration in shape: relative to its BL breadth, the *A. afarensis* dm_1 is less elongated MD than the geologically older hominins and approaches the shape seen in *A. africanus* (White et al., 1994; Leakey et al., 1998; Moggi-Cecchi et al., 2006), though White et al. (1981) noted that distal crown of *A. afarensis* is BL narrower than in *A. africanus*. The *A. afarensis* dm_1 retains plesiomorphic features that are reduced in geologically younger hominins. These include a disparity in cusp size (the protoconid is still the largest in area and the tallest cusp) and a disparity in the occlusal heights of the trigonid and talonid (the talonid is lower than the trigonid). These plesiomorphic disparities are reduced in *A. africanus* and even further reduced in the robust australopiths (White et al., 1981). For example, in the robust australopith dm_1 the two mesial cusps (protoconid and metaconid) are nearly aligned in the BL dimension and the trigonid is well developed and enclosed by the mesial marginal ridge (Grine, 1985). In contrast to the extant apes, which present significant heteromorphy and functional difference between the dm_1 and dm_2 , dm_1 molarization in *A. afarensis* results in a reduction in mandibular deciduous molar heteromorphy. This reduction in heteromorphy reflects abandonment of deciduous canine honing and functional similarity for the mandibular deciduous molars.

Though not as pronounced as with the dm_1 , the other *A. afarensis* deciduous molars present phylogenetically informative information as well. As with the dm_1 , the protoconid of the *A. afarensis* dm_2 is placed mesial to the metaconid and there is a marked difference in the occlusal heights of the two mesial cusps. The mesial cusps are asymmetrically placed in *A. africanus* as well, but there is less difference in the heights of the cusps; however, in the robust australopiths the two mesial cusps are approximately aligned BL. The *A. afarensis* dm_2 lacks accessory cusps, which are more prominent in *A. africanus* and the robust australopiths (White et al., 1981; Grine, 1985).

Maxillary deciduous molars are less distinctive than the mandibular. However, Grine (1985) noted a disparity in buccal cusp size in *A. africanus* and *A. afarensis* dm_1 s; both taxa have larger paracones than metacones, the plesiomorphic condition observed in *Pan* and *Gorilla*. The robust australopiths have expanded metacones, which yields similarly sized metacones and paracones and a more symmetric dm_1 crown.

The permanent incisors. The size and shape of the incisors distinguishes *A. afarensis* from other hominin taxa. *Australopithecus afarensis* can be distinguished from its probable ancestor, *A. anamensis*, in its absolutely smaller maxillary (I^1) and mandibular incisors (I_1 and I_2) (Ward et al., 2001). As in extant apes, in *A. afarensis* the lateral and central maxillary incisors are unequal in MD length, with the central incisor dominat-

ing the lateral (Table 2). The only known *A. anamensis* maxillary lateral incisor falls below the range of MD length observed in *A. afarensis*, which combined with the larger MD length of maxillary central incisors (noted above), suggests that heteromorphy in size was pronounced in *A. anamensis* as well. Maxillary incisal size heteromorphy is also present in *A. africanus*, though, it is reduced in *A. robustus*.

The permanent canines. The morphology and inferred function of the canines remains one of the most diagnostic aspects of *A. afarensis*. Studies of dental wear in *A. afarensis* indicate the absence of great apelike canine honing (Greenfield, 1990), although some aspects of canine wear still recall this plesiomorphic functional complex. For example, wear on the maxillary canines is not entirely apical, as an exposed strip of dentine developed distally as wear progressed on some *A. afarensis* dentitions (see Fig. 16) (e.g., A.L. 200-1, LH-5). In contrast, maxillary canine wear is almost entirely apical in *A. africanus*, the robust australopiths and *Homo* (Johanson and White, 1979; White et al., 1981). Similarly, the mandibular canine of *A. afarensis* exhibits a pattern of wear intermediate between those of great apes and later hominins; the *A. afarensis* mandibular canine M. 42323 has a distally exposed wear facet that was produced by contact with the maxillary canine, which is reminiscent of mandibular canine wear in some *Pan* females (White, 1980b, 1981). As noted by White (1981), it was the plesiomorphic nature of the morphology and wear of M. 42323, relative to geologically younger hominins, that precluded its recognition as a hominin upon its discovery by Louis Leakey in 1935.

When measured relative to the size of the postcanine dentition, canine size decreases in the series *Ar. ramidus*-*A. anamensis*-*A. afarensis*, with a further significant reduction in relative size occurring in the robust australopiths (Tables 2 and 3). In basal dimensions, the canine crowns of *A. anamensis*, *A. afarensis*, and *A. africanus* are similar in absolute size. Canine reduction began with the earliest known hominins—only moderate reduction is present in *Ar. kadabba* and *O. tugenensis*—and continued throughout *Australopithecus* evolution to reach its most derived state in the robust australopiths (White et al., 1994, 2006; Ward et al., 1999b, 2001; Haile-Selassie, 2001; Plavcan, 2001; Senut et al., 2001; Brunet et al., 2002; Haile-Selassie et al., 2004; Semaw et al., 2005). Although the holotype cranium of *A. garhi* has a maxillary canine that exceeds the size of any other specimen of *Australopithecus* (Asfaw et al., 1999; Table 2), in relation to its M^1 size, it is proportioned exactly as in *A. afarensis*.

As noted above, *A. anamensis* absolute maxillary and mandibular canine size does not differ appreciably from that of *A. afarensis*.¹² However, *A. anamensis* maxillary canine crowns are MD elongated in comparison to those of *A. afarensis* (Ward et al., 2001; White et al., 2006); this difference is even more pronounced when the Laetoli and Hadar samples are analyzed separately because, like those of *A. anamensis*, the Laetoli upper canines are MD long relative to Hadar homologs, which is consistent with the MD-elongated P_3 in *A. anamensis* and the Laetoli site-sample of *A. afarensis* (Kimbel et al., 2006). In addition, the maxillary canines of *A. anamensis* and *A. afarensis* can be distinguished by the position of the mesial

¹²Based on KNM-ER 20432, which preserves a mandibular canine alveolus, it has been suggested that the range of *A. anamensis* mandibular canine size would have exceeded that observed in *A. afarensis* (Ward et al., 2001).

TABLE 2. Comparative metrics of the australopith dentition: permanent upper teeth

		MD				B(La)L					
		N	Mean	s.d.	CV	Range	N	Mean	s.d.	CV	Range
I ¹	<i>A. anamensis</i>	3	11.3			10.5–12.4	4	8.8	0.46	5.21	8.2–9.3
	<i>A. afarensis</i>	7	10.6	0.80	7.30	9.0–11.8	9	8.3	0.80	9.90	7.0–9.7
	<i>A. africanus</i>	10	10.1	1.20	11.53	7.4–11.8	10	8.3	0.40	5.00	7.6–8.9
	<i>A. robustus</i>	11	8.6	1.08	12.58	7.1–10.8	7	7.4	0.31	4.17	6.8–7.7
	<i>A. boisei</i>	1	10.0				2	7.7			7.4–8.0
	<i>A. garhi</i>					1	9.2				
I ²	<i>A. anamensis</i>	1	5.8				2	6.5			
	<i>A. afarensis</i>	8	7.5	0.60	7.50	6.6–8.2	10	7.3	0.60	7.70	6.2–8.1
	<i>A. africanus</i>	10	6.8	0.60	8.70	5.9–7.7	8	6.8	0.63	9.12	5.6–7.7
	<i>A. robustus</i>	7	6.5	0.69	10.51	5.8–7.9	7	6.6	0.68	10.41	5.6–7.8
	<i>A. boisei</i>	2	7.0			6.9–7.0	2	7.0			6.4–7.5
	<i>A. garhi</i>	1	6.8			1	6.9				
C	<i>A. anamensis</i>	7	10.7	1.47	13.70	7.8–12.3	8	10.4	0.89	8.57	9.0–11.8
	<i>A. afarensis</i>	15	9.8	0.70	7.40	8.8–11.6	15	10.8	0.90	8.60	9.3–12.5
	<i>A. africanus</i>	11	9.9	0.60	5.71	8.8–10.8	11	10.4	1.00	9.24	8.7–12.0
	<i>A. robustus</i>	14	8.6	0.70	8.15	7.6–10.6	16	9.3	0.98	10.51	7.9–11.2
	<i>A. boisei</i>	8	8.6	1.18	13.75	6.5–10.8	4	8.9	1.11	12.54	7.5–9.9
	<i>A. garhi</i>	1	11.7			1	12.9				
P ³	<i>A. anamensis</i>	5	10.0	1.17	11.72	8.7–11.8	4	13.2	0.90	6.87	12.1–14.3
	<i>A. afarensis</i>	10	8.8	0.50	5.90	7.5–9.5	10	12.4	0.60	4.60	11.3–13.4
	<i>A. africanus</i>	18	9.1	0.30	3.08	8.7–9.6	16	12.7	0.70	5.79	11.7–14.1
	<i>A. robustus</i>	28	10.1	0.72	7.31	9.2–12.3	26	13.9	0.72	5.23	12.3–15.1
	<i>A. boisei</i>	6	10.6	0.88	8.32	9.5–11.8	5	15.2	1.35	8.89	13.8–17.0
	<i>A. garhi</i>	1	11.2			1	16.0				
P ⁴	<i>A. anamensis</i>	4	9.0	2.17	24.09	7.2–12.1	2	14.1			13.9–14.2
	<i>A. afarensis</i>	20	9.2	0.70	7.90	7.6–10.8	14	12.6	0.90	6.90	11.1–14.5
	<i>A. africanus</i>	25	9.4	0.57	6.55	8.0–10.8	18	13.4	1.10	8.10	10.7–15.2
	<i>A. robustus</i>	26	10.7	0.64	5.87	9.5–11.9	23	14.8	1.36	9.17	10.3–16.3
	<i>A. boisei</i>	4	12.1	0.30	2.48	11.7–12.4	4	16.2	1.56	9.61	14.2–17.6
	<i>A. garhi</i>	1	11.4			1	16.0				
M ¹	<i>A. anamensis</i>	11	11.8	1.17	9.95	10.0–12.9	9	13.3	1.49	11.18	11.7–14.1
	<i>A. afarensis</i>	17	12.0	1.00	8.30	10.5–13.8	14	13.5	0.90	6.60	12.0–15.0
	<i>A. africanus</i>	30	12.8	0.74	5.11	11.5–13.8	20	13.9	0.80	5.80	12.7–15.3
	<i>A. robustus</i>	26	13.3	0.75	5.64	11.4–15.6	20	14.6	0.88	6.04	13.0–16.8
	<i>A. boisei</i>	5	15.0	0.89	5.95	13.4–15.6	5	16.2	1.03	6.37	14.9–17.7
	<i>A. garhi</i>	1	14.4			1	16.5				
	<i>K. platyops</i>	1	10.5			1	12.0				
M ²	<i>A. anamensis</i>	8	12.8	0.93	7.26	11.4–14.2	9	14.6	1.16	7.90	12.9–16.3
	<i>A. afarensis</i>	12	13.0	0.60	4.30	12.1–14.1	13	14.8	0.60	4.00	13.4–15.8
	<i>A. africanus</i>	27	14.3	1.00	7.27	12.8–16.4	27	15.9	1.20	7.81	13.7–18.3
	<i>A. robustus</i>	28	14.5	1.20	7.30	12.8–18.6	23	15.6	1.10	6.76	13.1–16.9
	<i>A. boisei</i>	3	16.5			15.6–17.2	3	18.8			17.1–21.0
	<i>A. garhi</i>	1	14.4			1	17.7				
	<i>K. platyops</i>	1	11.4			1	12.4				
M ³	<i>A. anamensis</i>	8	12.1	0.78	6.50	11.1–12.7	7	14.1	0.96	6.83	13.0–15.7
	<i>A. afarensis</i>	14	12.5	1.20	9.20	10.9–14.8	14	14.4	1.00	7.00	13.0–16.3
	<i>A. africanus</i>	30	13.7	1.40	9.93	11.1–16.9	22	15.5	1.30	8.62	13.1–17.9
	<i>A. robustus</i>	21	14.8	1.10	7.35	12.5–17.1	24	16.7	0.80	5.02	14.8–18.2
	<i>A. boisei</i>	4	16.9	0.44	2.60	16.3–17.3	3	18.6			17.4–20.5
	<i>A. garhi</i>	1	15.2			1	16.9				

Sources: *A. anamensis* Ward et al., 2001; White et al., 2006; *A. afarensis* Kimbel et al. 2004 with additions through 2007; *A. africanus* Authors + Moggi-Checci et al., 2005; *A. robustus* Authors; *A. boisei* Authors; *A. garhi* Asfaw et al., 1999; *K. platyops* Leakey et al., 2001.

and distal shoulders of the crown. *Australopithecus anamensis* maxillary canines from Kanapoi have shoulders placed at similar levels below the cervix, giving the crown a symmetrical triangular shape when viewed lingually (this morphology can not be adequately assessed on the only maxillary canine from Allia Bay, KNM-ER 30744). In *A. afarensis* the crown shoulders are placed more apically, but unlike the condition observed in the Laetoli sample, Hadar canine crowns tend to be asymmetric in their shoulder position, with the mesial shoulder placed more apically than the distal (see Fig. 17). Symmetric canine

crowns—as in the Kanapoi sample of *A. anamensis*—are plesiomorphic (Kimbel et al., 2006), though White et al. (2006) noted that the shoulders of the Asa Issie and Aramis specimens they assigned to *A. anamensis* are not as cervically positioned as in those from Kanapoi. In *Ardipithecus* the maxillary canine shoulders are placed at similar levels, but in *Ar. kadabba* they are more cervically positioned than in *Ar. ramidus* (White et al., 1994; Haile-Selassie et al., 2004; Semaw et al., 2005).

Mandibular canines of *A. afarensis* can be distinguished from the Kanapoi, but not the Allia Bay, sample



Fig. 16. Lingual view of the upper right canine of *A. afarensis* maxilla A.L. 200-1. Note apical wear and exposed dentine strip distally. Scale = 0.5 cm.

of *A. anamensis*. The Kanapoi canines express a prominent basal tubercle (see Fig. 18) (Ward et al., 2001; referred to as the “distal basal heel or cingulum” in Kimbel et al., 2006), which is reduced in the younger Allia Bay (i.e., KNM-ER 30750, KNM-ER 30731) and *A. afarensis* canines.¹³

Despite reduced canine crowns, diastemata are frequently observed adjacent to *A. afarensis* canines. A diastema is observed between the I² and maxillary canine (e.g., A.L. 200-1, A.L. 444-2) and between the mandibular canine and the P₃ (e.g., A.L. 333w-58, MAK-VP-1/12; M. 42323) (White et al., 1981, 2000; Johanson et al., 1982c; Kimbel et al., 2004). Of 10 *A. afarensis* specimens for which the presence/absence of a maxillary diastema can be judged, five specimens possess a diastema (Kimbel et al., 2004). White et al. (1981) reported that of 20 individuals known at the time, nine have a C/P₃ diastema. In contrast, only one of 12 *A. africanus* and no *A. robustus* individuals were reported to have a mandibular diastema. Diastemata are present in other hominin taxa, but the wide separation between the I² and upper canine observed in A.L. 200-1, for example, is not observed in *A. africanus*, *A. boisei*, *A. robustus*, or early *Homo* (White et al., 1981). Not surprisingly, diastemata are observed in *A. anamensis* as well (e.g., KNM-KP 29287) (Ward et al., 2001), though frequency comparisons with *A. afarensis* are limited by small sample sizes for the older taxon.

¹³The Fejej mandibular canine, FJ-4-SB-1, which is approximately synchronic with the *A. anamensis* sample (Fleagle et al., 1991; Kappelman et al., 1996), also lacks a prominent tubercle. Grine et al. (2006b) stated that the lack of a prominent tubercle indicates morphological affinities of the Fejej hominins with the *A. afarensis* sample; however, the absence of a prominent tubercle is shared with Allia Bay *A. anamensis* as well as *A. afarensis*. We are not convinced that the preserved morphology on the mostly heavily worn Fejej crowns is diagnostic.

The permanent premolars. The evolution of the hominin canine honing complex is reflected in P₃ morphology. Occlusally, African ape P₃s are characterized by a distolingually oriented transverse crest (extending from the protoconid and dividing the posterior and anterior foveae); a single tall cusp (protoconid), which is situated distal to the MD midpoint of the crown; a weakly developed or absent mesial marginal ridge, resulting in a large, “open” anterior fovea; and an expansive mesiobuccal face that hones the upper canine. The major axis of the *Pan* and *Gorilla* P₃ crown runs from the distolingual corner through this expansive mesiobuccal surface, creating a crown that is obliquely oriented relative to the other postcanine teeth. *Ardipithecus* and *A. anamensis* share many components of this plesiomorphic feature set with the great apes (e.g., an open anterior fovea, minimally developed mesial marginal ridge, obliquely oriented transverse crest, tall protoconid, marked crown obliquity), yet the early stages of loss of apelike functional shearing is already apparent in these taxa (White et al., 1994; Ward et al., 2001; Haile-Selassie et al., 2004; Brunet et al., 2005; Semaw et al., 2005; Kimbel et al., 2006; Delezené and Kimbel, in prep.).

Several aspects of *A. afarensis* P₃ morphology significantly depart from the plesiomorphic configuration and reflect abandonment of C/P₃ shearing function. In extant ape P₃s the mesial portion of the crown (trigonid) dominates the distal (talonid). In contrast, in *A. afarensis* the talonid dominates the occlusal surface. Talonid expansion occurs as the result of several independent changes: the mesiobuccal face is reduced and the protoconid is centered on, or slightly mesial to, the MD midpoint of the tooth; the transverse crest often forms a right angle with the mesial protoconid crest (as opposed to its distolingual orientation in apes and basal hominins), which reduces the size of the anterior fovea; the crests of the *A. afarensis* crown are more developed than in *Ardipithecus* or *A. anamensis* and a prominent mesial marginal ridge often encloses the reduced anterior fovea. In addition to the shift toward talonid dominance, the *A. afarensis* P₃ sample includes teeth with the earliest known fully bicuspid configuration. Lingual cusp (metaconid) expression ranges from absent (e.g., A.L. 128-23; A.L. 277-1; A.L. 288-1, A.L. 417-1a), which is the primitive state, to well developed and distinctly separated from the protoconid (see Fig. 19) (e.g., A.L. 333w-1; LH-3), with many specimens showing an intermediate condition (White, 1977b, 1980b, Johanson et al., 1982c; Leonard and Hegmon, 1987; Suwa, 1990; White et al., 2000). A similar pattern is observed in the closure of the anterior fovea. Though the crests that enclose the anterior fovea (mesial marginal ridge and transverse crest) are generally more developed than in geologically older hominins (Kimbel et al., 2006), the anterior fovea of *A. afarensis* is still occasionally “open” mesially; open foveae occur in the unicuspid teeth. Finally, some *A. afarensis* P₃s retain significant crown obliquity in the tooth row, while others do not, though this positioning does not appear to correlate with variation in occlusal form. These P₃ polymorphisms have been used to argue for multiple species within the *A. afarensis* hypodigm (Coppens, 1977; Olson, 1985) or to be the result of sexual dimorphism (Leonard and Hegmon, 1987). In fact, neither hypothesis is robustly supported by the observed variation, which cuts across proposed groupings by taxon (Kimbel et al., 1985; White, 1985) and sex (Kimbel et al., 1994). The alternative hypothesis posits that the variation is phylogeneti-

TABLE 3. Comparative metrics of the australopith dentition: permanent lower teeth

		MD				B(La)L					
		N	Mean	s.d.	CV	Range	N	Mean	s.d.	CV	Range
I ₁	<i>A. anamensis</i>	3	7.0	0.30	4.38	6.8–7.3	2	8.0		0.00	7.4–8.5
	<i>A. afarensis</i>	6	6.5	0.90	14.30	5.6–8.0	6	7.4	0.30	4.00	6.9–7.7
	<i>A. africanus</i>	11	6.1	0.65	10.73	4.7–6.9	11	6.7	0.65	9.80	5.8–7.9
	<i>A. robustus</i>	7	5.3	0.26	4.87	4.9–5.6	6	6.0	0.46	7.79	5.2–6.5
	<i>A. boisei</i>	5	5.4	0.68	12.69	4.2–5.9	4	6.3	0.67	10.68	5.9–7.3
I ₂	<i>A. anamensis</i>	4	7.8	0.94	11.94	6.6–8.7	3	8.3	0.38	4.54	7.9–8.6
	<i>A. afarensis</i>	8	6.5	0.90	13.20	5.0–7.4	8	8.0	0.70	8.40	6.7–8.8
	<i>A. africanus</i>	9	7.2	0.79	10.94	5.3–8.1	10	8.1	0.59	7.32	7.0–9.2
	<i>A. robustus</i>	4	6.3	0.48	7.67	5.7–6.7	4	7.2	0.50	6.90	6.7–7.8
	<i>A. boisei</i>	4	6.3	0.26	4.10	6.0–6.6	4	7.3	0.89	12.21	6.4–8.2
C	<i>A. anamensis</i>	5	8.8	1.46	16.63	6.6–10.4	5	10.4	0.99	9.55	9.2–11.4
	<i>A. afarensis</i>	13	9.0	1.10	12.20	7.5–11.7	16	10.5	1.10	10.20	8.8–12.4
	<i>A. africanus</i>	26	9.5	0.61	6.41	8.5–11.0	30	10.1	0.85	8.47	8.7–12.0
	<i>A. robustus</i>	11	7.8	0.59	7.59	7.0–8.7	9	8.5	0.96	11.26	7.5–10.5
	<i>A. boisei</i>	5	7.8	0.47	6.05	7.2–8.5	2	8.7			8.3–9.1
P ₃	<i>A. anamensis</i>	6	9.9	0.60	6.06	9.3–10.9	5	10.9	1.00	9.17	9.5–12.0
	<i>A. afarensis</i>	29	9.5	1.00	10.90	7.9–12.6	29	10.7	1.10	9.90	8.9–13.6
	<i>A. africanus</i>	18	9.7	0.74	7.66	8.4–11.2	17	11.4	1.17	10.28	9.2–13.9
	<i>A. robustus</i>	20	10.2	0.61	6.01	9.0–11.4	19	11.6	1.14	9.88	9.0–13.7
	<i>A. boisei</i>	5	11.1	1.66	14.95	8.9–13.0	5	13.0	0.93	7.16	11.4–13.7
P ₄	<i>A. anamensis</i>	6	9.0	0.95	10.52	7.4–9.8	7	10.6	0.84	7.94	9.6–11.9
	<i>A. afarensis</i>	26	9.8	1.00	10.30	7.7–11.4	22	11.0	0.80	7.10	9.8–11.8
	<i>A. africanus</i>	24	10.4	0.76	7.33	9.3–12.3	20	11.6	0.90	7.81	10.3–13.4
	<i>A. robustus</i>	17	11.5	0.62	5.38	10.6–12.6	16	13.1	1.11	8.45	11.5–14.8
	<i>A. boisei</i>	9	13.5	1.76	13.02	10.1–15.6	9	14.3	1.28	8.96	12.3–16.5
M ₁	<i>A. anamensis</i>	8	12.6	0.87	6.90	11.6–13.7	8	11.7	1.10	9.37	10.2–13.3
	<i>A. afarensis</i>	31	13.1	0.90	7.10	10.1–14.8	24	12.6	0.80	6.00	11.0–13.9
	<i>A. africanus</i>	32	13.9	1.07	7.72	12.4–15.8	30	13.2	0.90	6.81	10.8–15.1
	<i>A. robustus</i>	24	14.7	0.77	5.22	13.2–16.5	18	13.7	0.85	6.24	11.8–15.0
	<i>A. boisei</i>	10	16.5	0.97	5.89	15.4–18.6	6	15.5	1.17	7.56	14.4–17.6
M ₂	<i>A. anamensis</i>	7	14.3	0.92	6.48	13.0–15.9	7	13.5	0.88	6.55	12.3–14.9
	<i>A. afarensis</i>	33	14.3	1.20	8.60	12.1–16.5	31	13.5	1.00	7.20	11.1–15.2
	<i>A. africanus</i>	37	15.7	0.98	6.22	14.0–17.8	40	14.4	0.99	6.90	12.7–16.8
	<i>A. robustus</i>	20	16.3	0.90	5.49	14.8–17.9	20	14.7	0.84	5.71	12.8–16.3
	<i>A. boisei</i>	8	18.2	1.33	7.32	16.4–20.0	6	16.9	1.11	6.56	15.8–18.6
M ₃	<i>A. anamensis</i>	7	15.0	1.17	7.83	13.7–17.0	7	13.2	0.66	5.05	12.1–13.7
	<i>A. afarensis</i>	26	15.2	1.30	8.30	13.4–18.1	23	13.4	1.00	7.20	11.3–15.3
	<i>A. africanus</i>	34	16.1	1.10	6.86	12.9–18.5	31	14.5	1.08	7.42	12.1–16.8
	<i>A. robustus</i>	22	17.1	1.38	8.05	15.1–20.5	21	14.5	1.14	7.87	12.6–17.0
	<i>A. boisei</i>	9	16.4	1.56	9.49	14.7–19.2	12	20.0	1.71	8.56	17.6–22.4

Sources: *A. anamensis* Ward et al., 2001; White et al., 2006; *A. afarensis* Kimbel et al. 2004 with additions through 2007; *A. africanus* Authors + Moggi-Checci et al., 2005; *A. robustus* Authors; *A. boisei* Authors.

cally meaningful, capturing a dental complex in the process of structural and functional transition within an early hominin lineage (Kimbel et al., 2004, 2006; White et al., 2006).

Australopithecus afarensis P₃s are also polymorphic in root number and configuration. Some specimens possess a Tomes’ root, a single root with two root canals, which gives the root a “dumbbell” shape in cross section (e.g., A.L. 145-35, A.L. 288-1, A.L. 400-1a). Most specimens possess two distinct roots, a mesiobuccal root that is circular in cross section and a smaller, platelike distolingual root (Ward et al., 1982) [see Fig. 1 in Wood et al. (1988) for a depiction of these root shapes]. The Maka P₃ (MAK-VP-1/12) has distinct platelike mesial and distal roots (White et al., 2000) and the LH-24 P₃ has three roots (separate mesial and distal roots, the latter of which is divided into two segments), which is the configuration in KT 12/H1, the holotype of *A. bahrelghazali* (White, 1980b; Brunet et al., 1995; White et al., 2000). The two-rooted form (mesiobuccal and distal) is also the form most commonly observed in extant great apes and

is reconstructed as plesiomorphic for the hominin clade (Wood et al., 1988; Wood, 1993).

Wood et al. (1988) identified two trends in hominin P₃ root evolution. One leads from the primitive form (two roots: mesiobuccal and distal) to a single rooted form, characteristic of *A. africanus* and *Homo*—though some early *Homo* specimens from Koobi Fora have two well developed P₃ roots (see Table 13 in Wood, 1993)—while the other leads from the primitive condition to a form characterized by mesial and distal platelike roots, similar to what is seen in mandibular molars, which is typical of robust australopiths. The *A. afarensis* hypodigm contains examples of all of these configurations, with the “primitive” form of Wood et al. (1988) being the most common; thus, *A. afarensis* provides a reasonable ancestral pool from which to derive both the reduced and molarized P₃ root configurations characteristic of geologically younger hominins. This polymorphism may extend into geologically older periods. Three P₃ roots are reported for *A. anamensis* specimen KNM-KP 29281 (Ward et al., 2001), a Tomes’ root characterizes *Ar. rami-*



Fig. 17. Lingual views of *A. afarensis* left maxillary canines A.L. 763-1 (left) and A.L. 333x-3 (right), showing sexual dimorphism in crown and root size. Note the asymmetric placement of the mesial and distal crown shoulders. Scale = 1 cm.



Fig. 18. Lingual views of right mandibular canines: *A. anamensis*, Kanapoi, (left); *A. anamensis*, Allia Bay, (right); *A. afarensis*, Laetoli, (right). Note reduced heel distally on the Allia Bay and Laetoli canines. (Courtesy C. Ward.)

dus specimen GWM5SW/P56 (Semaw et al., 2005), and the primitive platelike distal and rounded mesiobuccal root is present in *S. tchadensis* (Brunet et al., 2005). In *Pan* P_3 root polymorphism may be an expression of sexual dimorphism: 20% of males and 46% of females were reported to have a single root (Wood, 1993; see also Kupczik et al., 2005). Sexual dimorphism could explain some of the polymorphism observed in *A. afarensis* P_3 roots, though this has not so far been investigated.

Variation in *A. afarensis* maxillary premolars is also phylogenetically important. Already in early accounts, the relative size of the Garusi I P^3 , in relation to the P^4 , and the P^3 mesiobuccal enamel extension were recognized as distinct from other species of *Australopithecus* (Remane, 1951, 1954; Senyürek, 1955; see also White et al., 1981). In addition, the P^3 crown is asymmetric, with the buccal cusp (paracone) dominating the lingual (protocone) in area and MD length. When viewed occlusally, this yields a crown with a short, tightly convex lingual profile and a longer, flatter buccal profile (e.g., A.L. 199-1, A.L. 200-1, A.L. 486-1, A.L. 822-1). White et al. (1981) contrasted this morphological pattern with that observed in robust australopiths in which protocone and paracone are more equal in size, yielding a more sym-

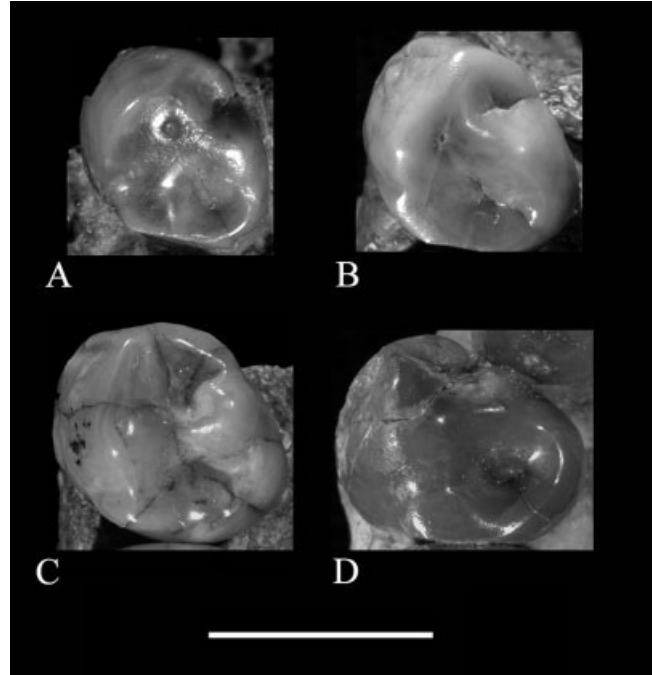


Fig. 19. Variation in P_3 form in Hadar *A. afarensis* sample. **A**, A.L. 207-13; **B**, A.L. 266-1 (image flipped); **C**, A.L. 333w-1; **D**, A.L. 417-1. See text for details. Scale = 1 cm.

metric, ovoid crown. *Australopithecus africanus* is intermediate between *A. afarensis* and the robust australopiths in these features. As clearly expressed in A.L. 199-1 and A.L. 200-1, there is a marked asymmetry in occlusal wear, with a steeply angled facet mesial to the paracone and a planar facet distal to the paracone.

The sizes of the premolars, as measured by BL and MD crown diameters, do little to distinguish among *A. anamensis*, *A. afarensis*, and *A. africanus*; however, the robust australopiths and *A. garhi* have larger premolars in both dimensions. *Australopithecus boisei* and *A. garhi* have the largest maxillary premolars of any hominin species (Table 2); the huge premolars of *A. garhi* are exceeded in size only by those of *A. boisei* (in the case of the P^3 *A. garhi* is larger). The evolution of postcanine tooth size is discussed in more detail with the permanent molars (see below).

The “canine step”. We noted above that the *A. afarensis* dental mechanism was distinctive in that the lower canine crowns remained relatively unscathed in the face of advanced postcanine occlusal wear (see, e.g., A.L. 198-1 in Fig. 20). In the moderately worn dentition of the Maka mandible MAK-VP 1/12, there is a sharp topographic step-down from the elevation of the incisors and canine apex to the level of the canine’s distal basal tubercle and P_3 occlusal surface along a steep planar wear facet on the canine’s distal edge (matching the mesial edge of the upper canine) (White et al., 2000, p 56; Fig. 20). White et al. (2000) referred to this topographical change as the “canine step” and noted the intermediate position of *A. afarensis* between the great apes, in which the canine crown projects above both the incisors and the postcanine teeth, and modern humans, in which the canine apex wears to the same level as the incisor and postcanine occlusal surfaces. As in modern humans, in *A. africanus* and other fossil hominin species subsequent to *A. afaren-*

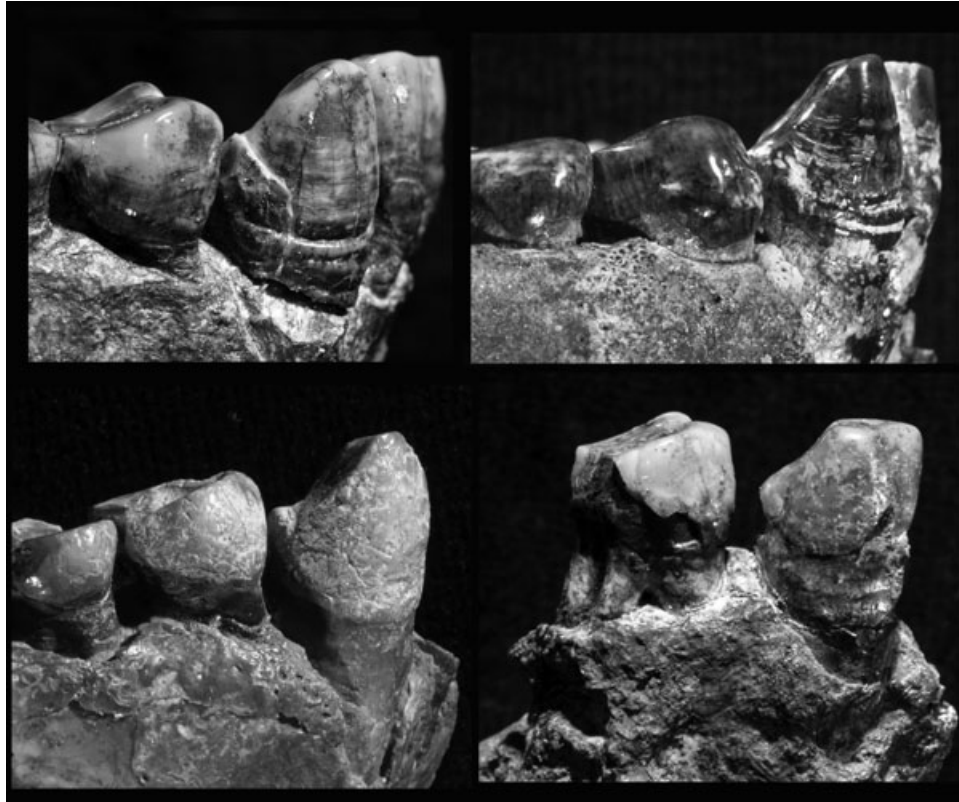


Fig. 20. The “canine step” in mandibles of *A. afarensis*. Clockwise from upper left: A.L. 822-1, MAK-VP 1/12 (image flipped), A.L. 440-1, A.L. 198-1 (image flipped). All scaled to same canine crown length (A.L. 440-1 = 1.5× natural size). See text for details.

sis lower canines typically wore down to the level of the postcanine occlusal plane as wear progressed.

The canine step is well seen in Hadar mandibles such as A.L. 440-1 and A.L. 822-1 (see Fig. 20). However, in these specimens, which feature more advanced occlusal wear than the Maka jaw, the dramatic topographical break is between *mesial* P₃ and the adjacent postcanine occlusal plane (including *distal* P₃). White et al. (2000) hypothesized that the canine step functioned to “protect” the canine and P₃ crowns from heavy occlusal wear (fostering a strong posterior to anterior wear gradient that is distinctive of *A. afarensis*; White et al., 1981). However, given the strong discrepancy in wear across the P₃, the marked asymmetry of the upper canine—recall that the distal shoulder of the crown, which occludes with the the P₃ trigonid, is more cervically positioned than the mesial shoulder (see Fig. 17)—may determine how the P₃ crown transforms with wear: the more elevated distal crown shoulder may leave the mesial part of P₃ occlusal surface less marked by wear compared to the distal, which, as part of the postcanine battery, would wear more heavily via occlusion with the P³. This discrepancy would be expected to endure until the latest stages of wear (e.g., A.L. 198-1). It is significant in this context that although they broadly overlap the *A. afarensis* size range, the upper canines of *A. africanus* are more symmetrical in shoulder position and the occlusal wear discrepancy across the P₃ crown is weak or absent.

The permanent molars. In spite of differences in measurement technique among investigators, documented variation across a tooth’s surface (e.g., Schwartz, 2000;

Kono, 2004), and metameric variation among postcanine teeth (e.g., Smith et al., 2008), all species of *Australopithecus* have thick molar enamel relative to extant African apes. Enamel thickness in *Ardipithecus* is described as thinner than in *Australopithecus* (e.g., White et al., 1994; Haile-Selassie, 2001), whereas *O. tugenensis* has been reported to have thicker enamel than *Ardipithecus* (Senut et al., 2001), which makes it unclear which is the more likely primitive state for the hominin clade. Thickened enamel may be a derived feature of *Australopithecus* or it may be a plesiomorphic feature shared with thickly enameled Miocene hominoids (e.g., Lucas et al., 2008), which would imply that thin enamel is derived (and/or homoplastic) in *Pan*, *Gorilla*, and *Ardipithecus*. To date, enamel thickness variation has not been studied systematically in *A. afarensis*.

All species of *Australopithecus* can be distinguished from *Sahelanthropus*, *Orrorin*, and *Ardipithecus* by their large (absolutely and relative to estimated body size) postcanine teeth (e.g., McHenry, 1984; White et al., 1994, 2006; Haile-Selassie, 2001; Ward et al., 2001; Haile-Selassie et al., 2004; Semaw et al., 2005). Based on current evidence, postcanine megadontia appeared with the earliest species of the *Australopithecus* grade. Size distinctions between the postcanine teeth of robust australopiths and *A. afarensis* are well established (e.g., White et al., 1981; Suwa et al., 1996), of course, and these are of the same order of importance as those perceived by Robinson (1956) in his pioneering comparisons of *A. africanus* and *A. robustus* dentitions based on samples amassed through the mid-1950s. Overall, the molars of *A. afarensis* and *A. anamensis* are similar in size

(Ward et al., 2001; Tables 2 and 3). *Australopithecus africanus* exceeds *A. afarensis* in mean MD length and BL breadth for all molar positions, especially for the M2 and M3 in both the mandible and maxilla, in which crown size closely approaches or even matches that of *A. robustus*. East African *A. garhi* also exceeds *A. afarensis* in most measures of postcanine dental size, though this comparison is derived from a single (holotype) specimen for *A. garhi*. In light of the discovery of *A. afarensis*, *A. africanus* was argued to be more megadont than expected for a species conventionally accorded the role of an ancestor of *Homo* (assuming approximately equal body size estimates for the relevant australopith taxa, which is a reasonable inference on present though imperfect evidence) (Johanson and White, 1979; White et al., 1981; Suwa et al., 1994; see above), an argument that has not lost strength with the augmented sample size for Sterkfontein *A. africanus* (Moggi-Cecchi et al., 2006). Given the discoveries of *A. aethiopicus* and *A. garhi*, it now appears that the later mid-Pliocene (≤ 2.7 Ma) saw the emergence of several megadont hominin species with strikingly dissimilar craniofacial configurations, any or all of which could plausibly have been derived from a species dentally similar to the more plesiomorphic *A. afarensis*. This mix of characters makes teasing out relationships to potential descendants a daunting task.

The recently discovered *Kenyanthropus platyops* has provided the strongest evidence for taxonomic diversity in east Africa before 3.0 Ma (Leakey et al., 2001). The *K. platyops* holotype (KNM-WT 40000) preserves only a single complete crown, the RM², which is smaller than the smallest known *A. afarensis* specimen (A.L. 199-1). The *K. platyops* paratype maxilla KNM-WT 38350 contains a RM¹ that is only matched by the smallest *A. afarensis* specimens (A.L. 651-1 for length; A.L. 199-1 for breadth) (Table 2). Leakey et al. (2001) were cautious about characterizing *K. platyops* as a small-toothed species, relative to *A. afarensis*, and they suggested that the holotype and paratype may represent females of a dentally sexually dimorphic species. Among the several other hominin teeth from Lomekwi, which are not attributed to *K. platyops*, some (i.e., KNM-WT 38337) are similar in size to the *K. platyops* holotype, while others (i.e., KNM-WT 38362, KNM-WT 8556) are much larger (Brown et al., 2001; Leakey et al., 2001), falling within the range for *A. afarensis*.

Nonmetric features of the molars distinguish *A. afarensis* from other species of *Australopithecus*. For example, the protostylid is not a common feature in the mandibular molars of *A. afarensis* and when present, it is not prominent. This contrasts with the condition observed in robust australopiths, where the protostylid is more frequent and more prominent, and in *A. africanus*, where the protostylid is more common and has a wider range of expression (Wood and Abbott, 1983; Hlusko, 2004). Protostylids are also a common feature on the molars of *A. anamensis* (Ward et al., 2001; Hlusko, 2004). If the presence of a protostylid, as in *A. anamensis*, is the plesiomorphic state, then their rarity in *A. afarensis* would be autapomorphic; a more thorough comparison to extant apes would be useful in this regard. Hlusko (2004) documented metameric differences in the frequency of the protostylid in *A. afarensis* molars: M₂s have a higher frequency of expression than either M₁s or M₃s.

An accessory cusp of the mandibular molars, the C6, has been argued to be phylogenetically informative. The

presence of a well developed C6 has been described as a derived feature of robust australopiths (e.g., Wood and Abbott, 1983; Suwa et al., 1994, 1996). However, Guatelli-Steinberg and Irish (2005) reported that C6 is present on the molars of *A. afarensis* at a similar frequency to that observed in *A. robustus* and *A. boisei*. [The frequencies reported by Guatelli-Steinberg and Irish contrast with those of Suwa et al. (1994), which might be explained by differences in the methods used to define the presence of a C6.] Regardless of the similarity of frequency, the morphology of the C6 distinguishes *A. afarensis* from the robust australopiths. *Australopithecus afarensis* M₃s often express a "double" C6, which is not observed in robust australopith or *Homo* M₃s. In contrast, the double C6 is not present on either the M₁ or M₂ of *A. afarensis*, but is observed rarely on robust australopith M₁s and M₂s (Bailey and Wood, 2007). The C6 of *A. afarensis* is usually smaller, relative to the size of other cusps, than in robust australopith taxa (Suwa et al., 1994), which increases the likelihood that C6 frequency is not a synapomorphy linking *A. afarensis* exclusively with the robust australopiths. Ward et al. (2001) reported that the C6 is frequently present on *A. anamensis* molars. Metameric variation is present in the expression of a C6, with the feature being more common on *A. afarensis* M₃s than M₁s or M₂s (Suwa et al., 1994).

Australopithecus afarensis mandibular molar roots are characterized by a "serrate" pattern: there are two roots, mesial and distal, and the mesial root is usually larger and more vertically inclined than the distal root, which angles buccally (Ward et al., 1982; Ward and Hill, 1987; White et al., 1993). This pattern of root morphology is shared with geologically older hominins such as *A. anamensis*, *Ar. ramidus*, the Tabarin mandible (KNM-TH 13150), and the Lothagam mandible (KNM-LT 329), but is lacking in many Omo-Shungura Formation "non-robust" specimens (Ward and Hill, 1987; Hill and Ward, 1988; Hill et al., 1992; White et al., 1994; Leakey et al., 1995; Suwa et al., 1996). Thus, mandibular molar root morphology apparently shifted in taxa geologically younger than *A. afarensis*.

Temporal trends in dental size. Lockwood et al. (2000) found that some features of dental size and shape show statistically significant directional change over the temporal span of *A. afarensis*, principally between the two temporally disjunct site-samples of Hadar (3.0–3.4 Ma) and Laetoli (3.5–3.7 Ma): BL and MD M³ dimensions increased; crown area and MD length of P₃ decreased; and the mandibular canine became LaL broader without a significant increase in overall crown size. The trend in M³ size increase potentially reflects a bias toward small M³s in the very small Laetoli sample (White, 1985), but compared to those from Hadar, the P₃s from Laetoli are MD elongated relative to BL breadth, which is nearly identical in the two samples (Kimbel et al., 2004). The P₃ of *A. anamensis* is MD longer than in *A. afarensis*, suggesting that this trend has deeper historical roots (Kimbel et al., 2006). The DIK-2-1 specimen, from the Basal Member of the Hadar Formation at Dikika (≤ 3.4 Ma) is among the largest in the *A. afarensis* sample, but is proportioned exactly as are the P₃s in the Hadar site-sample (Alemseged et al., 2005).

Dietary reconstructions and occlusal wear. Molar microwear in *A. afarensis* can be distinguished from that of extant hard-object feeders (i.e., *Cebus apella* and *Cercocebus albigena*). In fact, the high incidence of scratches

on *A. afarensis* molars is most similar to that of *Gorilla gorilla beringei*, which mostly consumes soft fruits and leaves. This microwear pattern is consistent across time and inferred paleohabitat (Grine et al., 2006b). A similar pattern of microwear was described for the molars of *A. anamensis* (Grine et al., 2006a), suggesting that neither taxon regularly consumed hard objects. Indeed, the results of molar microwear analyses for *A. afarensis* and *A. anamensis* are not surprising given the finding that neither *A. africanus* nor even *A. boisei* evinces a microwear pattern that matches those of extant primate hard-object feeders (Grine and Kay, 1988; Ungar et al., 2008). The only early hominin species with a microwear pattern that has been reported to be consistent with at least occasional hard-object feeding is *A. robustus* (Grine and Kay, 1988; Scott et al., 2005).

The idea that *A. afarensis* did not consume hard dietary items is at odds with the common inference that relatively large, thickly enameled, low-cusped postcanine teeth, as well as musculoskeletal indicators of powerful bite force generation (see above) are adaptations to the consumption of hard objects (reviewed in Lucas et al., 2008; see also Strait et al., 2009). If hard objects were a fallback resource for *A. afarensis*, rather than the main component of its diet, then this might explain the discordant signals given by anatomy and microwear (Grine et al., 2006b). However, if hard-object foods were consumed in high stress periods with (presumably) high mortality, then at least *some* fossils should be expected to show evidence of hard-object feeding; it would be a taphonomic anomaly that none do. It has also been proposed that grit in the diet, and not the primary foods consumed, may be responsible for the wear striae observed on *A. afarensis* molars (Grine et al., 2006b). This hypothesis is consistent with microwear on the anterior dentition (Ryan and Johanson, 1989), which shows a mixed pattern of fine wear striae and “microflakes” that suggest *A. afarensis* used its incisors to strip plant parts that contained grit. At any rate, resolving the apparently conflicting evidence on diet—or, more properly, the mechanical properties of dietary items—from micro- vs. macroscopic data sources should be an important target of research in paleoanthropology.

Dental development. Incremental markers of growth are evident in dental tissues; for example, in enamel there are circadian cross striations and longer period striae of Retzius, which are visible externally on imbricational enamel as perikymata (e.g., Dean, 1987a; FitzGerald, 1998; Smith, 2006, 2008). The periodicity of these structures permits investigations of the time required to complete various aspects of dental development. Stria of Retzius periodicity is variable across taxa as well as within and among populations. In extant *H. sapiens* the periodicity ranges from 6 to 12 days with a modal value of 8 days (e.g., FitzGerald, 1998; Reid and Dean, 2006; Smith et al., 2007; Smith, 2008). The modal value for early *Homo* is also reported to be 8 days (Lacruz et al., 2006, 2008). *Pan troglodytes*, on the other hand, has a periodicity of 6–9 days, with a modal periodicity of 6 (Reid et al., 1998; Schwartz et al., 2001; Smith et al., 2007; Smith, 2008). Based on small samples, periodicity in *Australopithecus*, including *A. afarensis*, is thought to be 7 days (Lacruz et al., 2008); thus, *Australopithecus* lies comfortably within the ranges observed for both *Pan* and *Homo*.

Australopithecus afarensis has figured prominently in studies of hominin dental development. Reconstructions of the age at death for the juvenile *A. afarensis* individual LH-2, based on perikymata counts of the unerupted I₁, demonstrated that the anterior teeth of *Australopithecus* have shorter crown formation times than extant *H. sapiens* (Bromage and Dean, 1985). There is variation among *Australopithecus* taxa in this feature; in robust australopiths, which possess relatively and absolutely smaller anterior teeth than other australopith species, the incisor crowns developed more rapidly (Bromage and Dean, 1985; Bromage, 1987; Dean, 1987a; Beynon and Dean, 1988; Dean and Reid, 2001; Dean et al., 2001).

Similarly rapid crown formation times are observed for the *A. afarensis* postcanine teeth (Beynon and Dean, 1988). All species of *Australopithecus* are characterized by relatively large postcanine teeth with thick enamel, which yields larger absolute enamel volumes than in *Pan*, *Gorilla*, or *Homo*. Despite this, postcanine crown formation times are generally shorter in *Australopithecus* than in *H. sapiens* and are similar to that observed in *Pan* and *Gorilla* (e.g., Beynon and Dean, 1987; Beynon and Wood, 1987; Dean, 1987b, Dean et al., 1993, 2001; Smith, 2008). Rapid crown formation was accomplished in *Australopithecus* by elevating the daily enamel secretion rates (DSRs) of ameloblasts above those observed in *Pan*, *Gorilla*, and *Homo* (Dean et al., 2001; Lacruz and Bromage, 2006; Macchiarelli et al., 2006; Smith, 2008). Among hominins, the DSR appears to be correlated with relative postcanine tooth size—as measured by the megadontia quotient (e.g., McHenry, 1984, 1988)—with robust australopiths having the highest DSRs; *A. afarensis* and *A. anamensis* have similar DSRs, which are lower than in the more megadont *A. africanus* (Lacruz et al., 2008). Thus, based on limited evidence, the DSR of *A. afarensis* is derived relative to *Pan*, but is plesiomorphic relative to geologically younger species of *Australopithecus*. Interspecific differences in the DSR point to a transformation series coincident with that of postcanine tooth size, with the DSR of robust australopiths being the most derived.

In addition to crown formation times, attention has been focused on the sequence of permanent tooth eruption. In *A. afarensis* and *A. africanus*, the M1 erupts prior to the eruption of the I1. In robust australopiths, the I1 and M1 erupt in near synchrony. The robust eruption pattern resembles that of extant *Homo*, while that of nonrobust australopiths is more apelike (e.g., Bromage, 1987; Beynon and Dean, 1988).

Though dental development is not a determinant of life history (*sensu* Robson and Wood, 2008), it is often the most abundant evidence from which to investigate life history in fossil primates. The relationship between dental development and life history is complex in hominins (e.g., Smith, 1986, 1987, 1994; Smith and Tompkins, 1995; Smith et al., 1995) and it is not our goal here to provide a thorough review of this issue (for recent reviews, see Dean, 2006; Robson and Wood, 2008). Australopiths and early *Homo* devoted a shorter amount of time to dental development and erupted their teeth at earlier chronological ages than in *H. sapiens* (see Table 3 in T. Smith, 2008 for a summary of estimated chronological age at deaths for several juvenile fossil hominoids). Thus, *Australopithecus* and early *Homo* did not significantly depart from the dental developmental schedule present in the *Pan-Homo* last common ancestor (e.g., Beynon and Wood, 1987; Robson and Wood, 2008). This

finding is line with those derived from the relationship between brain size and many aspects of life history (Smith, 1989). Given estimates for cranial capacity in *A. afarensis* that slightly exceed those of *Pan*, then an apelike dental developmental trajectory is not surprising. As Smith et al. (1995) noted, “if it is true that these fossil hominids did have maturation ages similar to extant *H. sapiens*, it is evident that they would have had a relationship between cranial capacity and M₁ eruption age unlike any living primate for which data are known thus far.” Currently, there is little evidence—and little reason to suspect—that *A. afarensis* departed from a *Pan*-like pace of life-history (e.g., Dean et al., 2001; Dean, 2006).

In addition to studies of dental development, studies of deciduous dental macrowear may provide insight into the life history of *A. afarensis*. Aiello et al. (1991) noted that relative to *A. africanus* and the robust australopiths, the deciduous dentition of *A. afarensis* wore at a slower rate. The observed degree of difference in hominin deciduous dental attrition is of the same order of magnitude as that observed between *Pan* and *Gorilla*. The hominin pattern could be explained by either a later chronological weaning age for *A. afarensis*—also implying a longer interbirth interval—or a less abrasive diet (Dean, 1987, 2006; Aiello et al., 1991). Given the expanded hominin deciduous dental samples of *A. afarensis* and *A. robustus* (i.e., DIK-1-1 and DNH 44 and 47, respectively) (Keyser et al., 2000; Alemseged et al., 2006) and the discovery of deciduous teeth for *A. anamensis* (Ward et al., 2001) and *Ar. ramidus* (White et al., 1994), this would be an important topic to revisit.

The postcranium of *Australopithecus afarensis*

The *A. afarensis* postcranial sample is important not only because it is abundant—most parts of the limb and axial skeletons are represented—but also because it is directly associated with taxonomically unequivocal craniodental material, which is uncommon for east African early hominins. At the time of their initial discovery in 1973, the Hadar postcranial remains were the oldest skeletal evidence for striding bipedalism in the hominin clade. Since the discovery of the lower limb elements from A.L. 128 and A.L. 129, significant additions have been made to the *A. afarensis* postcranial sample, including the adult partial skeletons A.L. 288-1 (Johanson et al., 1982a) and A.L. 438-1 (Kimbel et al., 1994; Drapeau et al., 2005) from Hadar and the juvenile partial skeletons LH-21 from Laetoli (White, 1980b) and DIK-1-1 from Dikika (Alemseged et al., 2006). In addition, the A.L. 333 collection includes an abundant and diverse array of postcrania (Bush et al., 1982; Latimer et al., 1982; Lovejoy et al., 1982a,b,c), though it is difficult to assign isolated elements to particular individuals from this locality (e.g., Behrensmeyer et al., 2003). The Laetoli hominin footprints add further information on the bipedal locomotion of *A. afarensis* (e.g., White, 1980a; Charteris et al., 1981; Leakey, 1987; Tuttle, 1987; White and Suwa, 1987; Tuttle et al., 1991; Raichlen et al., 2008).

Body proportions. The *A. afarensis* humerofemoral index, only calculable for A.L. 288-1, is Ca. 85, which is intermediate between small-bodied modern human pygmies (ca. 74) and *P. paniscus* (ca. 98), the smallest-bodied great ape. Because of the way Lucy's limb bone lengths deviate from the scaling relationships in modern humans and apes, her humerofemoral index is not the product of

a simple transformation of apelike proportions to modern-humanlike ones. Lucy's humerus is significantly shorter than a bonobo's and within the range for human pygmies, but her femur is within the range for bonobos and much shorter than a pygmy's. Therefore, her intermediate humerofemoral index is due to an apelike short femur rather than an apelike long humerus (Jungers, 1982; Jungers and Stern, 1983). Lucy indicates that humeral reduction preceded femoral elongation in hominin evolution.

It has been debated whether the evolution of postcranial proportions in *Australopithecus* involved reversals of character states in that limb length ratios may have been more apelike in *A. africanus* and *H. habilis* than in *A. afarensis* (e.g., Hartwig-Scherer and Martin, 1991; McHenry and Berger, 1998; Dobson, 2005; Reno et al., 2005a; Green et al., 2007; see also Ruff, 2009). This would imply either a reversal of limb proportions—assuming an *A. afarensis*-like ancestral limb proportion for *A. africanus* or that the ancestor(s) of *A. africanus* and *H. habilis* possessed more primitive limb proportions than *A. afarensis*, which would count as evidence against *A. afarensis* as an ancestor of these taxa. By and large, the evidence upon which these estimates are made is scant and often requires rough estimates from very few and incomplete specimens; thus, the true pattern of limb proportion evolution remains obscure (Reno et al., 2005a).

Using the fragmentary but substantially complete radius of A.L. 288-1, a brachial index of ca. 91 has been estimated (Kimbel et al., 1994; Asfaw et al., 1999; Reno et al., 2005a), which is more like values for extant apes (mean of 92 for *P. troglodytes*, 81 for *G. gorilla*, and 101 for *Pongo pygmaeus*) than for *H. sapiens* (mean of 75) (Reno et al., 2005a). Based on two Hadar specimens, a nearly complete humeral shaft from the Sidi Hakoma member (A.L. 137-50) and a complete ulna from the Kada Hadar member (A.L. 438-1), Kimbel et al. (1994) estimated a “composite” brachial index of 91-92.5. Although it agrees with the index from the Lucy skeleton, the composite estimate did not take into account the subsequently inferred body size increase in *A. afarensis* in the upper part of the Kadar Hadar Member (Lockwood et al., 2000), from which the A.L. 438 partial skeleton comes, so its validity is questionable.

Relative to a skeletal size surrogate derived from metrics of the proximal ulna, A.L. 438-1 ulnar length is intermediate between those of *Pan* and *H. sapiens*. The A.L. 438-1 partial skeleton is the only known Pliocene hominin specimen for which forearm/metacarpal proportions can be assessed. In relation to ulnar length and a skeletal size surrogate, *A. afarensis*, *H. sapiens*, and *G. gorilla* are similar in relative metacarpal length; in contrast, those of *P. troglodytes* and *Pan paniscus* are relatively longer (Drapeau et al., 2005). *Pan* appears specialized in its extreme relative metacarpal lengths, a topic that will be revisited below.

The axial skeleton. Ribs of *A. afarensis* are present in the A.L. 288-1 (Johanson et al., 1982a) and DIK-1-1 (Alemseged et al., 2006) partial skeletons and are represented by isolated specimens from A.L. 333 (see Table 1 in Lovejoy et al., 1982a). The Hadar *A. afarensis* ribs are mostly fragmentary and not identifiable to rib number, while those of DIK-1-1 are largely anatomically in situ but await full preparation and description; thus, the costal skeleton of *A. afarensis* remains poorly character-

ized in a comparative context. The one exception is the first rib, which is represented by A.L. 288-1ax and A.L. 333-118 (Johanson et al., 1982a; Lovejoy et al., 1982a). Ohman (1986) demonstrated that, as in *H. sapiens*, the *A. afarensis* first rib has a single articulation with the first thoracic vertebra, as opposed to a “bivertebral” articulation, with the superior portion of the first thoracic centrum and the inferior portion of the seventh cervical centrum, as is observed in all nonhuman primates. The functional—and potential selective—advantages of this articulation are unclear (Ohman, 1986; Stern and Jungers, 1990). Clearly, this derived feature of hominins deserves further inquiry.

Australopithecus afarensis vertebrae are rare, although they are more plentifully represented than for any other australopith species except perhaps *A. africanus*. Significant specimens include several partial or complete thoracic and lumbar vertebrae associated with A.L. 288-1 (Johanson et al., 1982a), an atlas (A.L. 333-83), an axis (A.L. 333-101), and additional cervical, thoracic, and/or lumbar vertebrae from A.L. 333 and A.L. 444 (Lovejoy et al., 1982a; Ward et al., in prep.). Notably, the best represented individual adult spine is that of A.L. 288-1, which is characterized by a pathology (Johanson et al., 1982a) that Cook et al. (1983) likened to Scheuermann disease [see Appendix 1 in Johanson et al. (1982a) for a description of the pathology]. The most complete spinal series is represented by the DIK-1-1 partial immature skeleton, which preserves the entire cervical and thoracic series, as well as the first two lumbar vertebrae (Alemseged et al., 2006).

Reflecting the paucity of extinct hominin cervical vertebral remains, little comparative work has been done to characterize the *A. afarensis* cervical vertebral morphology, except the lack of articulation of the C7 with the first rib, discussed above. Lovejoy et al. (1982a) noted that lower cervical vertebra (C6) A.L. 333-106 has very small centrum, and a long, straight (not inferiorly angulated) spinous process. These attributes create an apelike appearance for this specimen. The atlas (A.L. 333-83) features a strongly concave articular surface for the occipital condyle, which in adult Hadar crania bears a reciprocally convex articulation comprising two distinct surfaces for C1 (A.L. 333-45, A.L. 822-1); this, too, is an apelike attribute of *A. afarensis* head and neck anatomy that remains relatively unexplored.

In comparison to great apes, *H. sapiens* has a higher modal number of lumbar vertebra (typically five in *H. sapiens* and four in apes) and the lumbar vertebral bodies exhibit dorsal wedging (i.e., a centrum that is taller anteriorly than posteriorly). These features help to create lumbar lordosis, the dorsal concavity of the lower spinal column that results in an overall S-shaped column. Such a configuration is biomechanically advantageous for a biped, because it aligns the support of the spine directly beneath the upper body and head and over the hips (e.g., Lovejoy, 2005a). Mobility in the lumbar region is enhanced in *H. sapiens* by a reduction in iliac height, which reduces the “lumbar entrapment” present in great apes. In addition, the *H. sapiens* lumbar vertebrae demonstrate a progressive widening of the zygapophyseal facets, which is related to the relatively broader sacrum in *H. sapiens* (discussed below with the pelvis) (reviewed in Lovejoy, 2005a).

Evidence for modern humanlike aspects of the lumbar series is limited in *A. afarensis* due to the paucity of lumbar remains. For example, dorsal wedging is

observed in A.L. 333-73, but not in A.L. 288-1aa/ak/al (Sanders, 1998), though the absence of dorsal wedging in A.L. 288-1aa/ak/al, which is identified as L3 (Johanson et al., 1982a), should not be seen as evidence for the absence of lumbar lordosis in the A.L. 288-1 spine because dorsal wedging is absent in upper lumbar vertebrae of other hominin skeletons that display wedging and lordosis in the lower part of the lumbar series (e.g., the *A. africanus* partial skeleton Stw. 8 and the *Homo erectus* partial skeleton KNM-WT 15000; Sanders, 1998). A complete lumbar series is not present in the *A. afarensis* sample, so the number of lumbar elements is unknown. It is expected that, like other known hominin skeletons, the lumbar region of *A. afarensis* would be elongated relative to those of extant apes. There is disagreement about the modal number of lumbar vertebrae present in the early hominin skeletons that do preserve a complete lumbar series (e.g., Robinson, 1972; Latimer and Ward, 1993; Häeusler et al., 2002); however, all early *Homo* and *Australopithecus* skeletons that preserve a lumbar vertebral series have more lumbar elements than the modal condition in extant apes (Lovejoy, 2005a). The humanlike progressive inferior expansion of lumbar zygapophyseal spacing is present in A.L. 288-1 and other species of *Australopithecus* (Sanders, 1998; Lovejoy, 2005a). Thus, based on available evidence, lumbar lordosis was present in *A. afarensis*, but the evidence for other humanlike attributes is limited.

The pectoral girdle. The scapula of *A. afarensis* is represented by a well preserved juvenile specimen DIK-1-1 (Alemseged et al., 2006) and a fragment (glenoid and part of the lateral border) associated with the A.L. 288-1 partial skeleton (Johanson et al., 1982a). Much has been made of primitive aspects of the *A. afarensis* scapula (e.g., Stern and Susman, 1983; Alemseged et al., 2006). Although the cranial orientation of the A.L. 288-1 glenoid fossa has been hailed as apelike in morphology and function (Stern and Susman, 1983), Inouye and Shea (1997), using an ontogenetic allometric approach, demonstrated that at small body sizes the glenoid orientation of *H. sapiens* and apes overlaps [see Stern (2000) for a counter-argument]. The virtually complete scapulae associated with immature DIK-1-1 skeleton are visibly and morphometrically intermediate between those of juvenile *Gorilla* and *H. sapiens* scapulae (Alemseged et al., 2006: Fig. 5): DIK-1-1 is similar to *Gorilla* in the moderate cranial orientation of the glenoid fossa, the diagonal orientation of the spine, and the wide supraspinous fossa, whereas it is more like *H. sapiens* in having a relatively large axillo-spinal angle (see Larson, 2007). *Pan* scapulae are much more generalized in form than those of either *Gorilla* or *H. sapiens*.

The clavicle of *A. afarensis* is represented by several partial specimens (A.L. 288-1; A.L. 333-94; A.L. 333-6/9; A.L. 438-1), which are similar to one another morphologically (Johanson et al., 1982a; Lovejoy et al., 1982a; Drapeau et al., 2005). The clavicle of the juvenile DIK-1-1 is also preserved, but has not been described (Alemseged et al., 2006). In the adult specimens, the deltoid origin is prominent and the conoid tubercle is weakly expressed, but located on the inferior surface of the clavicle, as in *H. sapiens* (Johanson et al., 1982a; Lovejoy et al., 1982a; Ohman, 1986; Drapeau et al., 2005). The morphology of the *A. afarensis* clavicle—and indeed of other known *Australopithecus* clavicles—contrasts with that of the *Australopithecus* sp. clavicle (Stw. 606) from



Fig. 21. The *A. afarensis* humerus A.L. 137-50. Scale = 2 cm.

the Jacovec Cavern, Sterkfontein, which is reported to have a well developed and posteriorly projecting conoid tubercle that is reminiscent of the condition in *Pan* (Partridge et al., 2003).

The humerus. The humerus of *A. afarensis* is represented by adult specimens at Hadar and Maka as well as by the juvenile specimen DIK-1-1 (see Fig. 21) (Johanson et al., 1982a; Lovejoy et al., 1982b; White et al., 1993; Kimbel et al., 1994; Alemseged et al., 2006). The head of the humerus is elliptical, as opposed to the spherical condition in the great apes, and the bicipital groove tends to be shallower than in African apes (*Pongo* differs from the African apes in the latter regard) (Lovejoy et al., 1982b; Larson, 2007). These two features are also observed in *Ar. ramidus* (White et al., 1994). As in other humeri of *Australopithecus*, as well as those of *H. erectus* and *H. floresiensis*, the *A. afarensis* humeral head displays modest torsion compared to extant *H. sapiens* and the African apes (Larson, 1996, 2007).

The humerus bears strong muscle scars, including a well developed lateral supracondylar crest (the origin of the brachioradialis muscle) and a prominent insertion for the pectoralis major along the lateral crest of the bicipital groove (Lovejoy et al., 1982b; White et al., 1993; Drapeau et al., 2005; Crompton et al., 2008), which suggests that the *A. afarensis* arm was heavily muscled. As discussed above, relative to body size, the humerus of A.L. 288-1 is shorter than is observed in extant apes and in this it is similar to *H. sapiens* (Jungers, 1982; Jungers and Stern, 1983).

The radius. The *A. afarensis* radius is represented by A.L. 288-1, A.L. 333-98, and A.L. 333w-33 (Johanson et al., 1982a; Lovejoy et al., 1982b). The distal radius of A.L. 288-1 presents a larger lunate than scaphoid articular surface. In both extant African apes and humans the scaphoid articular surface occupies a larger area on the distal radius. *Pongo*, like *A. afarensis*, has a larger lunate articular surface (Heinrich et al., 1993; Richmond

and Strait, 2000), the functional significance of which is unclear. The dorsal ridge of the radiocarpal articular surface is more projecting in *A. afarensis* than it is in *H. sapiens*. The distal radius of *A. anamensis*, KNM-ER 20419, resembles A.L. 288-1p in both the proportion of carpal articular areas and the projection of the dorsal ridge (Heinrich et al., 1993; Richmond and Strait, 2000), though Crompton and Thorpe (2007) suggested that the projection of the dorsal ridge in *A. anamensis* is an artifact resulting from a broken styloid process and the reconstruction of the region performed by Richmond and Strait (2000). The projecting dorsal ridge in *Pan* and *Gorilla* probably limits dorsiflexion at the wrist during knuckle-walking (Tuttle, 1967; Richmond and Strait, 2000; Orr, 2005). However, Corruccini and McHenry (2001) found more overlap in metric features of the distal radius among the apes than did Richmond and Strait (2000) and argued that *Australopithecus* is better characterized as having a generalized ape wrist. Because *Australopithecus* species did not knuckle-walk, if the distinctiveness of the dorsal ridge is confirmed for knuckle-walkers, the presence of a pronounced ridge in the australopiths must be either a primitive retention from a knuckle-walking ancestor or evidence of a novel function.

The ulna. Relatively complete ulnae of *A. afarensis* are represented in the partial skeletons A.L. 438-1 (Drapeau et al., 2005) and A.L. 288-1 (Johanson et al., 1982a), while A.L. 137-48b and several specimens from A.L. 333 are more fragmentary (Lovejoy et al., 1982b). The *A. afarensis* ulna retains some apelike features, but significantly deviates toward the *H. sapiens* condition in others. The diaphysis of A.L. 438-1 is more curved than is typical for *H. sapiens*; however, that of the smaller A.L. 288-1 is not (see Fig. 22) (Drapeau et al., 2005). In African apes the olecranon process projects more posteriorly than in *H. sapiens*, maximizing the lever arm of *m. triceps brachii* in extended arm postures. The *A. afarensis* olecranon process projects proximally, resembling the modern human condition. To Drapeau et al. (2005; Drapeau, 2004, 2008), hominin olecranon morphology signals a reduction of the use of the arm in extended postures, as occurs in suspensory contexts, as well as in knuckle-walking. Drapeau et al. argue that the hominin configuration might be associated with manipulative behaviors that occur when the forearm is flexed at $\sim 90^\circ$. The *A. afarensis* ulna is also derived in the orientation of the trochlear notch, which faces more anteriorly and lacks the heavy keeling in the African apes. These modern-humanlike ulnar features are also observed in *Ar. ramidus* (White et al., 1994).

The hand. Most elements of the *A. afarensis* hand are preserved in the extensive A.L. 333 sample and a few other specimens from Hadar (Bush et al., 1982); the South Turkwel (Kenya) manual remains possibly represent *A. afarensis* as well (Ward et al., 1999a). The hand of *A. afarensis* presents a mixture of primitive and derived features. Primitive features include curved manual phalanges with prominent ridges on the palmar surface marking the insertion of the digital flexor musculature, the lack of a styloid process on the third metacarpal, a laterally "waisted" capitate, a dorsally placed trapezoid articulation on the capitate, and an elongated pisiform coupled with a prominent hamulus on the hamate, the latter feature suggesting a well developed flexor retinaculum and/or *m. flexor carpi ulnaris* (Tuttle,

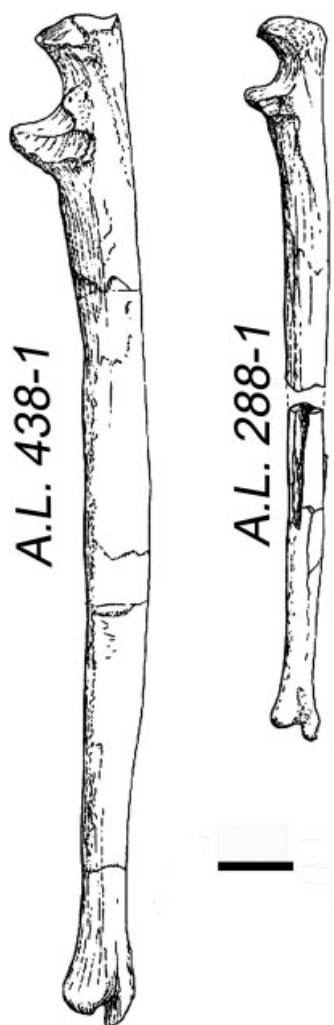


Fig. 22. Artist's renderings of *A. afarensis* ulnae in lateral view. (Drawings by Susan Alta Martin, reproduced from Drapeau MSM, Ward CV, Kimbel WH, Johanson DC, Rak Y. Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *Journal of Human Evolution* 48:593–642. © 2005 with permission from Elsevier). Scale = 2 cm.

1981; Bush et al., 1982; Johanson et al., 1982a; Stern and Susman, 1983; Ward et al., 1999a; Drapeau et al., 2005; Tocheri et al., 2007).¹⁴ The morphology of the hand is poorly represented in geologically older hominins, but curved manual phalanges are also observed in *Ardipithecus* and *Orrorin* (Haile-Selassie, 2001; Senut et al., 2001; Tocheri et al., 2007). Carpal bones are almost unknown in geologically older hominin taxa, but a capitate referred to *A. anamensis* displays the primitive radio-ulnar articulation for the MC2 base, unlike the more humanlike, distolateral orientation observed in *A. afarensis* (Leakey et al., 1998; Ward et al., 2001; Tocheri et al., 2007, 2008).

Relative to *Pan* and *Gorilla*, the *A. afarensis* hand possesses a number of derived features shared with *H. sapi-*

ens. Metacarpals 2–5 tend to be short, relative to both the first metacarpal and estimated body size (Latimer, 1991; Alba et al., 2003; Drapeau et al., 2005). Similar metacarpal proportions are also observed in *A. africanus* (Green and Gordon, 2008), the only other early hominin in which they can be estimated reliably. Thus, the proportions of the manual rays are similar in *Australopithecus* and *Homo* and unlike those of extant apes in which the first metacarpal is short compared to the others. It should be noted that, relative to body size and ulnar length, the metacarpal 2–5 elongation observed in *Pan* is likely autapomorphic (Drapeau and Ward, 2007), which has led some investigators to argue that derived manual proportions in *Australopithecus* were achieved by shortening rays 2–5 and not by elongating the first (e.g., Latimer, 1991; Alba et al., 2003; Green and Gordon, 2008). Though like *Homo* in relative metacarpal proportions, the metacarpal bases of *Australopithecus* are relatively gracile (Green and Gordon, 2008) and the first metacarpal of *A. afarensis* is relatively slender and not robust as in geologically younger australopiths and *Homo* (Susman, 1994). On the metacarpal heads, African apes display a transversely oriented dorsal ridge, which limits dorsiflexion of the metacarpophalangeal joint during knuckle-walking. This ridge is absent from the *A. afarensis* metacarpals (Lovejoy et al., 1982b; Stern and Susman, 1983).

The pelvis. As is well established, the pelvis of *H. sapiens* is highly derived morphologically and functionally relative to the great apes. Derived features include a relatively broad sacrum, enlarged auricular surfaces of the sacroiliac joint, and a superoinferiorly short and anteroposteriorly broad iliac blade that is rotated into the sagittal plane. This derived pelvic morphology affects the action of the muscles that assist in bipedal locomotion. Most importantly, the gluteus medius and minimus muscles, which originate from the lateral iliac surface, function as hip abductors (i.e., trunk stabilizers during stance phase of bipedalism) in *H. sapiens*, whereas they function as hip extensors in extant apes.

The *A. afarensis* partial skeleton A.L. 288-1 provides the best evidence for early hominin pelvic morphology (Johanson et al., 1982a; Lovejoy, 1988, 2005b). It shares many features with *H. sapiens*, but is, nevertheless, morphologically distinct. The A.L. 288-1 ilium is short, broad and sagittally rotated, which indicates the presence of the derived role for the gluteal muscles (see also Häusel et al., 2002, for maps of gluteal muscle origins on the *Australopithecus* pelvis) and a reduction in lumbar entrapment (Lovejoy, 2005b). A well developed iliac pillar and an expanded sacrum (Abitbol, 1987) indicate enhanced adaptation to weight transfer through the sacrum. The A.L. 288-1 pelvis has a well developed anterior inferior iliac spine, which Lovejoy (2005b) argues arose from independent ossification center as in *H. sapiens*. But unlike in *H. sapiens*, the A.L. 288-1 pelvis is more strongly flared laterally (e.g., Rak, 1991; Lovejoy, 2005b; Simpson et al., 2008).¹⁵ This would have placed the hip abductors in a position of mechanical disadvantage since their origin would be directly above their insertion on the greater trochanter; however, *Australopithecus*

¹⁴The waisted capitate morphology is also observed in *H. floresiensis*, apparently a tool-making hominin, suggesting that derived features of the manus and carpus in *H. sapiens* did not evolve in the context of stone tool manufacture (Tocheri et al., 2007).

¹⁵It should be noted that widely flared ilia are also found in pelvises attributed to *Homo*, including the female *H. erectus* pelvis BSN49/P27 (Simpson et al., 2008) and the female *H. floresiensis* pelvis LB 1 (Brown et al., 2004; Morwood et al., 2005), suggesting that evolution of pelvic morphology was strongly mosaic within the genus *Homo*.



Fig. 23. Relatively complete femora of *A. afarensis*, in anterior view: A.L. 288-1 (left), A.L. 827-1 (right). Scale = 5 cm.

appears to have maintained significant mechanical advantage for these muscles by elongating the femoral neck, so that the insertion is still lateral to the origin, as observed in *H. sapiens* (Heiple and Lovejoy, 1971; Lovejoy, 1988, 2005b).

Primitive aspects of the A.L. 288-1 pelvis have been used to argue for the lack of fully obligate bipedalism in *A. afarensis*. These include a relatively small anterior portion of the acetabular articular surface (implying less habitual weight transfer through this joint), hamstring moment arms that are greater than in *H. sapiens* (implying significant ability to extend the thigh in arboreal contexts), underdeveloped upper lateral angles on the sacrum (implying weak sacroiliac ligaments), and an apelike lumbosacral angle (Stern and Susman, 1983; Abitbol, 1987). Others have argued that the pelvis of A.L. 288-1 is fully adapted to bipedalism and that the differences between the pelves of *H. sapiens* and *Australopithecus* are due to obstetric adaptations that appeared later in the *Homo* lineage, in which relatively large infant heads posed an obstetric risk (Tague and Lovejoy, 1986; Lovejoy, 2005b). We summarize arguments concerning locomotion in *A. afarensis* below.

The femur. The femur of *A. afarensis* (Figs. 23 and 24) is represented by 15 specimens from Hadar and single



Fig. 24. Variation in *A. afarensis* proximal femoral size: A.L. 333-3 (left), A.L. 152-2 (center), A.L. 288-1 (right). Scale = 2 cm.

specimens from Laetoli (LH-21; juvenile), Maka (MAK-VP 1/1; adult), and Dikika (DIK-1-1; juvenile) (Johanson and Coppens, 1976; Johanson and Taieb, 1976; Johanson et al., 1982a; Lovejoy et al., 1982c, 2002; White et al., 1993; Harmon, 2005). These femora display a complex of features consistent with humanlike striding bipedalism; however, the femur is morphologically distinct from those of *H. sapiens*. Bipedal features of the *A. afarensis* femur include the presence of a bicondylar angle in both adults and juvenile specimens (Johanson and Taieb, 1976; Lovejoy et al., 1982c; Alemseged et al., 2006), which, as in other species of *Australopithecus*, is higher than is observed on average in *H. sapiens* (Heiple and Lovejoy, 1971; Johanson and Taieb, 1976); a prominent lateral patellar lip (Johanson and Taieb, 1976; Lovejoy, 2007); flattened, ellipsoid femoral condyles (Johanson and Taieb, 1976; Tardieu et al., 2006; Lovejoy, 2007); the (at least occasional) presence of an obturator externus groove (Lovejoy et al., 1982c, 2002); an elongated femoral neck (Lovejoy et al., 2002; Harmon, 2005); reduced height of the greater trochanter (Lovejoy et al., 2002); a prominent intertrochanteric line in some individuals (e.g., A.L. 333-3), indicating a strong iliofemoral ligament (Lovejoy et al., 1982c; Stern and Susman, 1983); and low neck shaft angle (Lovejoy et al., 2002; Harmon, 2005). This package of derived features is also observed in other fossil hominins (e.g., *A. africanus*, *A. anamensis*, *O. tugenensis*) (Heiple and Lovejoy, 1971; Lovejoy and Heiple, 1972; Pickford et al., 2002; Galik et al., 2004; White et al., 2006; Richmond and Jungers, 2008). The presence of a bicondylar angle in both juvenile (e.g., DIK-1-1; Alemseged et al., 2006) and adult specimens is of particular importance since the feature develops as an ontogenetic response to the adoption of bipedal behavior (e.g., Tardieu and Damsin, 1997; Shefelbine et al., 2002).

Another important indicator of bipedalism is the distribution of cortical bone in the femoral neck. Lovejoy (1988, 2005b) argued that the femoral neck acts as a cantilevered beam during bipedal locomotion and that

the combined action of body weight and hip abductor muscle force during single-limb support phase subjects the inferior aspect of the femoral neck to very high compressive loads, resulting in the development of an especially thickened band of cortical bone in this part of the neck. This contrasts with other extant hominoids in which cortical bone is more uniform in its thickness across the femoral neck cross section. *Australopithecus afarensis* and all other hominins have the asymmetric humanlike pattern of cortical bone distribution in the femoral neck (Ohman et al., 1997; Lovejoy et al., 2002). Although the importance of the distribution of cortical bone in the proximal femur as an indicator of bipedalism has been questioned (Stern, 2000), among hominoids this pattern is only observed in hominins. To Lovejoy (1988, 2005b), the hominin pattern of cortical bone distribution arises because a portion of the gluteal muscle force is directed medially, pushing the femoral head into the acetabulum. This reduces tension superiorly and produces a gradient of strain that is lowest superiorly and highest inferiorly (see Fig. 2 in Lovejoy, 2005b). Thus, if the modern humanlike pattern of strain and cortical bone distribution reflects an effective hip-stabilizing role for the gluteal muscles, as argued by Lovejoy, then it provides circumstantial evidence supporting the hypothesis that the elongated femoral necks of *Australopithecus* maintain a significant lever arm for the gluteal muscles, despite the fact that the ilium is more flared laterally than is typical of *H. sapiens* (Lovejoy, 1988, 2005b).

Some aspects of the *A. afarensis* femur are not humanlike. For example, there is often a well developed insertion of the gluteus maximus, forming a prominent “third trochanter” (e.g., MAK-VP-1/1, A.L. 333-95) (Lovejoy et al., 2002). Additionally, the linea aspera is often not well developed (e.g., A.L. 288-1). A minimally developed linea aspera is also observed in *A. anamensis* and *O. tugenensis* femora (White et al., 2006; Richmond and Jungers, 2008). The femoral heads of *Australopithecus* are small, relative to equivalently sized *H. sapiens* femora, and the femur is not as elongated, relative to body size, as it is in *H. sapiens* (Heiple and Lovejoy, 1971; Jungers, 1982; Jungers and Stern, 1983; Harmon, 2005; Lovejoy, 2005b; Richmond and Jungers, 2008).

There is a wide range of femoral size in the *A. afarensis* hypodigm, though this size range is not excessive compared to highly dimorphic apes (see Fig. 23) (e.g., Lague, 2002; Harmon, 2006). Early analyses of *A. afarensis* femoral morphology suggested that significant morphological differences existed between small and large individuals, which might imply biomechanical differences in locomotion between sexes (e.g., Tardieu, 1981, 1983; Stern and Susman, 1983). Recent statistical analyses of proximal (Harmon, 2006) and distal femur (Lague, 2002) geomorphometry fail to support this contention.

The tibia. The tibia of *A. afarensis* expresses derived morphology consistent with bipedalism. Relative to extant apes, the proximal shaft is mediolaterally expanded below the tibial plateau. Distally, the talar articular surface is orthogonal to the diaphyseal long-axis, unlike the superolaterally canted diaphysis in extant great apes; this articular orientation produces an axis of plantar- and dorsiflexion that allows the diaphysis of the tibia to pass directly over the talus in the sagittal plane (Latimer et al., 1987; Latimer, 1991; Alemseged et al., 2006). *Australopithecus anamensis* is represented by a fragmentary tibia (KNM-KP 29285) that, as

in *A. afarensis*, shows the distinctively modern humanlike proximal shaft expansion and orthogonally disposed talar facet (Ward et al., 1999b). In *A. afarensis* tibiae the malleolar groove is well developed, which along with a well developed peroneal groove on the fibula, suggests powerful musculature to evert and invert the foot (Stern and Susman, 1983).

Though otherwise demonstrating adaptations to bipedalism, proximally the *A. afarensis* tibia presents some primitive features. For example, there is no osteological indication of a doubled attachment for the lateral meniscus (Tardieu, 1983; Senut and Tardieu, 1985; see also Organ and Ward, 2006) as is observed in modern humans, which suggests to some that the knee of *A. afarensis*—and that of other species of *Australopithecus* (Berger and Tobias, 1996)—would have been more mobile than the human knee. In addition, Organ and Ward (2006) noted that the *A. afarensis* tibial plateau is more curved sagittally than is typical of modern humans.

The fibula. The fibula of *A. afarensis* is represented by several partial specimens from Hadar (Lovejoy et al., 1982c). The right distal fibula, in association with the distal tibia and talus of A.L. 288-1 (Johanson et al., 1982a), permits a reconstruction of the *A. afarensis* talocrural joint. Stern and Susman (1983) claimed that the distal fibula of *A. afarensis* reflects a “plantarflexion set” to the talocrural joint, as opposed to the neutral position observed in *H. sapiens*. They interpreted this to reflect a greater range of plantarflexion, compared to humans, which would have been useful in arboreal contexts. This plantarflexion set is partially indicated by the shape of the distal articular facet of the fibula. In modern humans the proximal portion of this facet is perpendicular to the fibular shaft; however, in apes and *A. afarensis* the proximal portion of the facet is obliquely oriented (see Fig. 11 in Stern and Susman, 1983 and Fig. 1 in Stern, 2000). Though they did agree that the A.L. 288-1 talocrural joint was capable of a greater range of motion than the human joint, Latimer et al. (1987) concluded that this resulted from increased dorsiflexion rather than plantarflexion as argued by Stern and Susman (1983).

The *A. afarensis* fibula bears a deep peroneal groove (Lovejoy et al., 1982c; Stern and Susman, 1983), which implies powerful peroneal muscles. Stern and Susman (1983) provided two hypotheses to explain the prominent peroneal muscles in *A. afarensis*. If the peroneal muscles were used during terrestrial bipedalism, then *A. afarensis* may have relied more heavily on these muscles to stabilize the foot as weight was transferred from the heel to the hallux during the stance phase of bipedalism. Alternatively, the peroneal muscles may have been recruited to evert the foot during arboreal activities, as occurs in *Pan*. Stern and Susman (1983) preferred the second hypothesis.

The foot. The *A. afarensis* foot skeleton is well represented, especially in the A.L. 333 sample (Johanson et al., 1982a; Latimer et al., 1982). Multiple skeletal features of the *A. afarensis* foot support the inference of bipedal locomotion. The trochlea of the *A. afarensis* talus is flatter than is observed in apes (Latimer et al., 1987; Harcourt-Smith and Aiello, 2004; Gebo and Schwarz, 2006) and the talocrural axis of rotation is perpendicular to the tibial shaft (Lovejoy et al., 1982c; Latimer et al., 1987). In apes the lateral trochlear ridge of the talus is longer than the medial ridge, which gives the trochlea a

conical shape, whereas in *A. afarensis*, as in modern humans, the medial and lateral ridges are nearly equal in length, lending the trochlea a symmetrical shape (Latimer et al., 1987). The *A. afarensis* calcaneus shares with humans an expanded posterior portion and a salient lateral plantar process (Latimer et al., 1982; Latimer and Lovejoy, 1989; but see Stern and Susman, 1983; Stern, 2000). The calcaneus also has a prominent peroneal tubercle on its lateral surface. The peroneal tubercle is the site of attachment for the inferior peroneal retinaculum and supports the conclusion—along with the deep peroneal groove on the fibula—that the peroneal muscles were relatively large (Latimer et al., 1982; Stern and Susman, 1983; Latimer and Lovejoy, 1989), which Stern and Susman (1983) suggested may indicate a unique role, relative to *H. sapiens*, for stabilizing the ankle during bipedal locomotion. In line with the Stern and Susman findings, Gebo and Schwarz (2006) inferred that the subtalar joint of *A. afarensis* would have required more muscular effort to limit mobility than is observed in geologically younger hominins.

In *A. afarensis*, the metatarsophalangeal joints display an articulation that emphasizes dorsiflexion during toe-off. The metatarsal heads are expanded dorsally, and evince a sulcus superiorly where the articular surface meets the shaft. Such dorsally expanded heads are typical of modern humans, but not apes, which emphasize plantarflexion at the metatarsophalangeal joints. On the reciprocal joint surface, the proximal articular surface of the proximal pedal phalanx, the articular surface is canted dorsally, increasing the capacity for dorsiflexion relative to the ape condition (Latimer et al., 1982; Latimer and Lovejoy, 1990b; see also Duncan et al., 1994). This pedal phalangeal morphology is also observed in a 5.2-myr-old phalanx attributed to *Ar. kadabba*, which is the sole evidence for bipedalism in that taxon (Haile-Selassie, 2001).

Proximal pedal phalanges of *A. afarensis* display more longitudinal curvature than is typical of modern humans; however, the degree of curvature is most pronounced in the first pedal phalanx and decreases in the lateral rays (e.g., the A.L. 333-115 partial foot), as in modern humans (Latimer et al., 1982; Stern and Susman, 1983). The hallux of the *A. afarensis* foot—and for all species of *Australopithecus* for that matter—appears to have been permanently adducted, as in modern humans (Latimer and Lovejoy, 1990a; McHenry and Jones, 2006, *contra* Clarke and Tobias, 1995). Additionally, as in humans, the hallux is robust and has an enlarged head and the pedal phalanges are shorter, relative to body size, than in extant apes (Latimer et al., 1982). These features are related to a modern humanlike load transfer mechanism at toe-off.

The morphology of the bony foot is broadly confirmed by the 3.5-myr-old Laetoli footprint trails (e.g., Leakey and Hay, 1979; White, 1980a; Leakey, 1987). Though there are limitations to the inferences that can be made from the footprint trail (White and Suwa, 1987), a convincing argument can be made that the trails were made by individuals with a bipedal stride that is fundamentally humanlike. This is evidenced by a distinct heel strike and lateral-to-medial force transfer across the metatarsal heads, as well as by the adducted hallux (e.g., Day and Wickens, 1980; White, 1980a; Robbins, 1987; White and Suwa, 1987). However, it has been argued that the foot of Hadar *A. afarensis* was morphologically incompatible with the Laetoli footprint trail.

For example, Harcourt-Smith and Aiello (2004) noted that *A. afarensis* has a large, proximodistally oriented navicular tuberosity (see also Latimer et al., 1982), which they suggested was weight-bearing and indicative of the lack of a medial longitudinal arch. This is an interesting observation given that a medial longitudinal arch is present in the Laetoli footprints. Tuttle et al. (1987, 1991; Tuttle, 1981) argued that the Hadar pedal phalanges were too long and curved to create the more humanlike Laetoli trail. In the views of Tuttle et al. (1991) and Harcourt-Smith and Aiello (2004), the geologically younger Hadar fossils evince a more primitive pedal morphology than is expressed in the older Laetoli footprint trail.

Debate about locomotion in *Australopithecus afarensis*

Functional-adaptive interpretations of the *A. afarensis* postcranial skeleton have tended to divide paleoanthropologists into two camps. One, whose members appeal to derived (humanlike) pelvic, lower limb, foot (and footprint) morphology, thinks that *A. afarensis* was a fully committed terrestrial biped with humanlike striding gait (e.g., Latimer et al., 1987; Lovejoy, 1988; Latimer and Lovejoy, 1990a,b; Latimer, 1991; Lovejoy et al., 2002). The other includes those who think that the species retained aspects of ancestral arboreal behavior and/or practiced a form of bipedality distinct from that of modern humans—based mainly on skeletal features that differ from human anatomy and tend to resemble that of extant African apes (e.g., Stern and Susman, 1983, 1991; Susman et al., 1984, 1985; Stern, 2000). Compared to the polarized positions these camps occupy in the locomotion debate, there are surprisingly few disagreements about fossil morphology. As reviewed by Ward (2002), at the center of the debate are sharp differences about how to reconstruct function from morphology and relate function to behavior.

It is abundantly clear that the *A. afarensis* postcranium expresses derived features related to habitual striding bipedalism. These features include, but are not limited to, lumbar column lordosis; a short, broad, sagittally rotated ilium; a valgus, fully extendable knee; an adducted, robust hallux; a talar facet on the distal tibia oriented orthogonal to the tibial shaft; a lateral plantar process on the calcaneus; and a medial longitudinal arch of the foot. These derived features are found in combination with primitive features, such as long forearms; short femora; a single tibial attachment for the lateral meniscus; a superiorly oriented scapular glenoid fossa; a prominent brachioradialis origin; and curved pedal and manual phalanges. Additionally, though clearly derived in the human direction, departures from human morphology in the pelvis and femur of *A. afarensis* have led some workers to conclude that bipedalism in this species was biomechanically less efficient than in humans and so giving the impression of a “partly arboreal, funny-walking biped” (Stern, 2000, p 125). In contrast, Lovejoy has argued that *Australopithecus* was an efficient biped and that the morphological differences in the lower pelvis and femur observed between humans and *A. afarensis* are related to later obstetric adaptations in *Homo*. As he writes: “modern humans, however, are not simply bipeds: *they are bipeds with relatively enormous brains*” (Lovejoy, 2005b; italics original). Others have argued that, relative to extant apes, the *direction* of character

change in hominins signifies an abandonment of significant arboreal behaviors; that is, selection for terrestrial bipedalism negatively impacted arboreal climbing performance. According to this argument, retained primitive features of the postcranium are merely evolutionary baggage without “current” utility or selective value (e.g., Latimer, 1991). However, much of the mix of primitive and derived morphology in *A. afarensis* is found in hominin taxa that both predate and postdate it, which nourishes the idea that they formed a stable functional complex maintained by selection (Ward, 2002). The presence of postcranial features prominent in the *A. afarensis* locomotion debate in the 11-kyr-old bipedal skeleton of *H. floresiensis* (Brown et al., 2004; Morwood et al., 2005; Tocheri et al., 2007) is sure to raise anew questions about the reconstruction of function from form in the fossil record of the hominin locomotor apparatus.

Resolution of the debate about locomotion in *A. afarensis* will not likely come from further scrutiny of the known fossils in the context of the human-chimpanzee functional-morphological dichotomy. It will, rather, more likely arise from discovery, descriptions and analyses of still earlier, potentially ancestral, hominin taxa, which will reveal how the “stable complex” observed already in *A. afarensis* was built from more plesiomorphic patterns.

Sexual dimorphism in *Australopithecus afarensis*

In catarrhines, the degree of dimorphism in body size and canine size is principally related to the frequency and intensity of intrasexual competition in males and females (e.g., Kay et al., 1988; Plavcan, 1993, 1998; Plavcan et al., 1995). Dimorphism in both aspects of the phenotype is often used to infer social behavior in fossil taxa. Typically, in extant anthropoid primates, those taxa characterized by intense and frequent male–male competition express dimorphism in both canine size and body size. Monogamous taxa are characterized by low degrees of canine and body size dimorphism, though both males and females may both have canines that are large relative to body size (Plavcan, 2001). Extant humans are usually monogamous and have low levels of male–male competition; body size and canine size dimorphism are predictably minimal in *H. sapiens*. No other primate displays such low levels of both body-size and canine-size dimorphism.

Most analysts have concluded that *A. afarensis* possesses a degree of postcranial skeletal size dimorphism matched or exceeded only by the most dimorphic of extant great apes (i.e., *Pongo* and *Gorilla*) (e.g., Johanson and White, 1979; McHenry, 1986, 1991; Kimbel and White, 1988b; Richmond and Jungers, 1995; Lockwood et al., 1996; Plavcan et al., 2005; Harmon, 2006; Gordon et al., 2008).¹⁶ This finding arose originally from simple comparisons of extant hominoid and (limited) fossil hominin sample maximum/minimum ratios and coefficients of variation, but has been reinforced recently by bootstrapping procedures applied to CVs and range-based

statistics. Reno et al. (2003, 2005b) have questioned the common finding of high skeletal size dimorphism in *A. afarensis*, arguing that dimorphism in this taxon is most similar to that of *H. sapiens*. Responses to Reno et al.’s (2003, 2005b) interpretation have focused on methodological differences from other studies and on the apparent size bias against small adults in the A.L. 333 postcranial sample, upon which their analyses were based (e.g., Plavcan et al., 2005; Scott and Stroik, 2006; Gordon et al., 2008).

High levels of skeletal size dimorphism in *A. afarensis* contrast strikingly with the relatively small amount of canine sexual dimorphism—at least as inferred from the coefficient of variation and an apparently nonbimodal distribution of crown size (Kimbel et al., 1985; Leutenegger and Shell, 1987; Kimbel and White, 1988b). The coefficient of variation of extant anthropoid canine dimensions is strongly correlated with the index of sexual dimorphism (i.e., the ratio of mean male to mean female size) (e.g., Fleagle et al., 1980; Kay, 1982). Using this relationship, Leutenegger and Shell (1987) reported levels of sexual dimorphism for the canines in *A. afarensis* that are lower than those of *Gorilla*, *Pongo*, and *P. troglodytes*, but similar to that of *P. paniscus*. The sample of *A. afarensis* canines has been augmented since the Leutenegger and Shell study and the CVs for the current sample of *A. afarensis* canine metrics are, except for the MD length of the lower canine, all lower than those reported for *P. paniscus* by Leutenegger and Shell (1987).

The height of the canine crown, rather than the basal dimensions of the crown, shows the strongest correlation with male–male competition levels in extant anthropoids, which reflects the importance of crown height in weapon-related use (Plavcan and van Schaik, 1997; Plavcan, 2001). Canine height also tends to be more dimorphic than basal dimensions in extant anthropoids (Plavcan, 2001). Because *A. afarensis* canines wear apically, there are many fewer specimens (e.g., A.L. 763-1 and A.L. 333x-3; Fig. 17) from which this dimension can be estimated than for the basal dimensions; however, canine height in *A. afarensis* is also reduced in both relative size and dimorphism compared to extant hominoids (Plavcan and van Schaik, 1997).

Reduced canine size dimorphism in *A. afarensis*, relative to the presumed ancestral condition exemplified by the extant and fossil great apes, implies that male–male competition was reduced, but the high degree of skeletal size dimorphism implies that it was not (Plavcan and van Schaik, 1997; Plavcan, 2001). There appears to be no appropriate extant analog among anthropoids for understanding the pattern of sexual dimorphism in canine size and postcranial skeletal size expressed by *A. afarensis*, which makes inferences about social behavior difficult from a comparative perspective (Plavcan, 2000). Given the relatively small sample sizes for basal hominins, it is unclear if the degree of dimorphism in *A. afarensis* canine size and body size is similar to or reduced relative to these geologically older taxa.

Investigations of intraspecific variation in paleontological contexts are often complicated by lumping individuals across time and space to achieve adequate samples for statistical analyses. This is thought to produce an exaggerated estimate of variation in a single population, which is especially problematic when inferences to fossil samples are drawn from comparisons with skeletal or dental samples of extant primate taxa (mitigated somewhat by the practice creating comparative samples com-

¹⁶“Body size” typically refers to body mass (kg). Skeletal size, however measured, may not display the same degree of dimorphism as body mass. For example, while *H. sapiens* has greater skeletal size dimorphism than *P. troglodytes*, *P. troglodytes* displays greater body mass dimorphism. Given the uncertainty of the scaling relationships between body mass and most skeletal elements in fossil taxa (Plavcan, 2003), skeletal size is normally used for comparisons of size dimorphism in place of eliminated body mass.

prising mixtures of subspecies, on the theory that axes of geographical and temporal variation will be approximately equal). *Australopithecus afarensis* presents a prime example of how temporal variation can bias analyses of variation in a fossil taxon. Initial examinations of variation in mandibular corpus dimensions suggested that *A. afarensis* was as variable as *G. gorilla* in this respect (Kimbel and White, 1988b); this inference was reinforced with the addition in the 1990s of new specimens from Hadar (Lockwood et al., 1996). In a subsequent study, however, Lockwood et al. (2000) identified a temporal change in mandibular corpus size in the Hadar sample, with a series of large, late (KH-2 submember) specimens responsible for the elevated variation in corpus dimensions in comparison to extant African apes. Lockwood et al. (2000) surmised that the increase in mandibular corpus size reflected an increase in body size, but it is presently unclear whether the size increase involved both males and females or males only. Additional discoveries from sediments dated to ca. 3.0 Ma may show whether the degree of sexual dimorphism in *A. afarensis* also shifted late in Hadar Formation times.

The paleoenvironmental context of *A. afarensis*

Early paleoenvironmental interpretations of the Hadar site drew on the evidently cyclical sequence of fluvial (extensive sand bodies and pedogenic silts/silty clays) and lacustrine (principally clays and laminated silts) sediments (Taieb and Tiercelin, 1979; Aronson and Taieb, 1981; Johanson et al., 1982b; Tiercelin, 1986). Aronson and Taieb (1981) provided the most detailed rendition of this early model, which envisioned an extensive system comprising a large, meandering river and braided streams flowing from the western Ethiopian escarpment across a broad, flat plain in the central Hadar area toward a large lake to the east. Periodically (upper Basal Member, upper Sidi Hakoma-lowermost Denen Dora Members, lower Kada Hadar Member) the lake transgressed into the central Hadar area, resulting in the deposition of the lacustrine clays, which contain abundant ostracods, gastropods and other aquatic invertebrates (see also Tiercelin, 1986). The fossil-rich silts and silty clays, which by Aronson and Taieb's estimate constitute roughly 70% of the total sedimentary thickness at Hadar, were understood to be overbank deposits, the product of stream-channel flooding. These flood-plain deposits were subject to seasonal desiccation, promoting soil formation and the development of vegetation cover. Subsequent detailed work by Yemane (1997) and Campisano (2007; Campisano and Feibel, 2008) has validated the major points of this scheme. Campisano, however, has identified as many as seven lacustrine transgressions (some minor) in the Hadar sedimentary sequence, in part due to intensive study of fossil-bearing deposits in the upper section of the Kada Hadar Member, which was not well studied during the 1970s field work. The last major lake transgression recorded at Hadar occurred around 2.95 Ma (the age of the BKT-2 tephra). Above BKT-2 an unconformity surface divides the Hadar Formation from the overlying Busidima Formation, which contains early *Homo* and Oldowan tools (Kimbel et al., 1996; Semaw et al., 1997; Quade et al., 2004). A still incompletely understood interplay between tectonically induced basin subsidence and climatic forcing exerted the main control on the cyclicity of the depositional re-

gime at Hadar (Bonnefille et al., 2004; Campisano and Feibel, 2007).

The great majority of Hadar fossil vertebrate, including hominin, remains come from the fluvial sands and associated floodplain silts. Campisano (2007; Campisano and Feibel, 2008) has explained this as a taphonomic bias against preservation in finer-grained deposits, particularly floodplain vertisols (due to pedogenic processes, which tends to disturb or destroy bones), rather than as "representing the original distribution of faunal remains across the paleolandscape."

Mammalian paleontological indicators of Hadar environments are broadly consistent with the fluvial-lacustrine depositional regime recorded in Hadar Formation sediments (Johanson et al., 1978; Gray, 1980; Reed, 1997, 2008). Pliocene Hadar was, of course, a well-watered place, and early reconstructions (e.g., Johanson, 1976) emphasized relatively luxuriant riparian forests as a favored hominin habitat. Although the Hadar paleoenvironment was modally much less arid than many "savanna" models of early human evolution would have envisioned for a 3.0+ myr-old east African locale, conditions at the site were not environmentally static over the ca. 400 kyr captured by the deposition of the Hadar Formation. Reed's (1997, 2008) macromammalian community reconstructions indicate habitats fluctuating between more open and closed conditions around a modal woodlands theme, but with a mixture of wet grasslands and shrub across the well watered landscape at most times. The habitat reconstruction for the lowest part of the Sidi Hakoma Member (SH-1; ≤ 3.42 Ma) emerges as the most closed (with high rainfall and relatively low seasonality), with depositional environments representing near-lake shore and delta plain conditions (Campisano and Feibel, 2008). In contrast, the fauna from the upper Kada Hadar Member (KH-2; ca. 3.12–2.96 Ma) implies the most arid, open conditions of the Hadar Formation: KH-2 times—locally at least—witnessed a sharp proportional increase in the abundance of open-adapted antilopine bovids and the addition of at least 10 macromammalian taxa undocumented in lower parts of the section, including the only known camel species from Hadar. Notwithstanding the observation that the oldest Sidi Hakoma submember assemblage indicates the most closed conditions and the young Kada Hadar submember fauna the most open, neither geological nor paleontological findings support a continuous trend across time from closed to open conditions at the Hadar site (Campisano and Feibel, 2008; Reed, 2008). Rather, conditions in the central Hadar basin oscillated in tune with the proximity of the lake, which was driven by tectonic and/or regional and global climatic variables, and overall precipitation patterns (Campisano and Feibel, 2007).

Australopithecus afarensis was one of a handful of macromammalian taxa to persist through the entire Hadar Formation (including the Basal Member at Dikika), which has led to the conclusion that this hominin species was eurytopic (White et al., 1993; Kimbel et al., 1994; Reed, 2008). This idea has been reinforced by the impression from the absence of aquatic taxa and the abundance of alcelaphine bovids in the upper Laetoli Beds that *A. afarensis* was equally at home in dry, open grassland-savanna and in lush riverine forests (compare the artist's reconstruction in Leakey, 1979, with that in Johanson, 1976; but see Su and Harrison, 2007, 2008). However, as reviewed by Reed (2008, p 21;

see also Harris, 1987, and Su and Harrison, 2007), elements of the Laetoli faunal collection (e.g., colobines, galagines) argue for nearby tree cover, albeit not of the riverine variety. In addition, Kingston and Harrison (2007) have shown that isotopic dietary reconstruction of the Laetoli faunal assemblage indicates a predominance of mixed feeders and browsers. Su and Harrison (2007, p 303) summarize the ecological conditions of the Upper Laetoli Beds thusly: “... a mosaic habitat comprising open woodland, grassland, and shrubland, as well as closed woodland along seasonal river courses.” Although the Laetoli paleoenvironment was not the same as those common in fluvio-lacustrine settings, such as at Hadar, the differences between the two sites in terms of habitats available to hominins was probably not as strongly marked as early reconstructions indicated—though as Hay (1987; see also Su and Harrison, 2007) suggested, the frequency of volcanic eruptions must have had a periodically depressing effect on the local vegetation (the upper Laetoli Beds comprise mainly air-fall and aeolian tuffs).

This, of course, does not contradict the notion that *A. afarensis* was an ecologically generalized species, and the fact that dentognathic structure in the Hadar lineage shows no signs of adaptive change in the face of environmental fluctuation through the ca. 150-m thick Hadar Formation is at least consistent with eurytopy. The consistency of dental microwear in *A. afarensis* post-canine teeth across time (Grine et al., 2006b) may mean either that these hominins were able to track their preferred dietary resources in the face of relatively subtle changes in the environment or that environmentally induced shifts in diet did not involve changes in mechanical properties of the foods typically consumed. If the increase in jaw and cranial size in the KH-2 submember is a sign of enlarged body size in the latest samples of *A. afarensis* at Hadar (as suggested by Lockwood et al., 2000; see above), then questions about potential ecological causes arise (see Millien et al., 2006, for a review). A within-lineage response to environmental factors would reinforce the image of *A. afarensis* as an adaptively flexible species—one in which ecological change did not, as far as can be told, induce vicariance and speciation in what is today the central Afar—but knowledge of this part of the fossil record is not yet adequate to proffer causal explanations for the observed size changes.

SUMMARY AND CONCLUSIONS

More than 30 years of discovery and analysis of *Australopithecus afarensis* have filled a near one-million-year temporal interval with rich insights on hominin evolution. The 1970s discoveries pushed the time span of the hominin record back beyond 3.0 Ma just as molecular biology was propelling the date of chimpanzee-human lineage divergence forward in time to ca. 5.0–7.0 Ma. As the (up to then) oldest and most apelike hominin species, *A. afarensis* was neatly accommodated in this narrowed temporal and phylogenetic window. Subsequent field work in the late Miocene-early Pliocene of eastern and northern Africa has further reduced this gap and so while *A. afarensis* remains neither the oldest nor most apelike hominin species, it continues to be a principal record of transformation of major structural-functional systems in hominin evolution, including locomotion, the canine/P₃ complex, the masticatory system, and the brain. The insights on these transformations are independent

of the inference that *A. afarensis* was actually the ancestor (as opposed to a sister-species) of subsequent hominins, including early *Homo* (Kimbel et al., 2004). However, the record of mid-Pliocene hominin evolution is now sufficiently dense to infer with confidence that, at least in its dentognathic anatomy, *A. afarensis* evinces the outcome of phyletic (within-lineage) evolution of an earlier Pliocene ancestor, the nominal species *A. anamensis*. Within *A. afarensis* temporally vectored change has been documented between the older Laetoli and younger Hadar site-samples and within the Hadar sample itself, but whereas the former appears (in part) to be continuations of changes in the canine/P₃, mandible and maxilla initiated within *A. anamensis*, the latter, occurring within the latest samples of the species in the Hadar Formation, is size-related and does not, on current evidence, involve transformation of craniodental characters that have been used to differentially diagnose the species or are implicated in subsequent hominin adaptive evolution. This last observation is of considerable interest because of the temporal placement of the large and variable Hadar sample just prior to the period in which cladogenesis and diet-related adaptive differentiation are first documented unequivocally in the hominin fossil record. Changes within the ca. 0.40 myr Hadar time-series of *A. afarensis* yield no hint of the particular evolutionary innovations to come in the Plio-Pleistocene.

The value of the large sample of *A. afarensis* fossils extends beyond being able to pin the species to a particular position on the phylogenetic tree. With close to 400 specimens now known, paleoanthropologists are able to ask fairly refined questions about this early hominin species’ paleobiology. Some questions, including those pertaining to locomotor repertoire, sexual dimorphism and social behavior, and diet appear to be resistant to solution—or are at least ongoing subjects of polarized debate. These areas of research on *A. afarensis* are prime for fresh perspectives on research design.

The question of locomotion is particularly problematic because of the way the debate has been framed. As far as we are concerned, the case has been successfully made that the mechanical environments of the *A. afarensis* hip, knee and foot were fundamentally those of living humans. However, the conclusion that *A. afarensis* walked exactly as extant humans do, or was restricted to terrestrial locomotor behaviors, is not an ineluctable correlate of this observation in the context of a dichotomous chimpanzee-human comparative framework. However impressive the departures from human postcranial morphology and body form may be, it is unclear how conclusive as to function and adaptation these deviations are in the context of extant African great apes, whose own postdivergence fossil record of locomotor evolution is completely unknown. *Australopithecus afarensis* was in no evolutionary sense *intermediate* between chimpanzees and humans and there are simply no reasonable analogs to human striding bipedality elsewhere in the animal kingdom from which to draw lessons as to cause. Therefore, to understand this species’ locomotor adaptations is tantamount to having a fuller understanding of its own singular evolutionary history. This implies that their key pieces of evidence bearing on how “Lucy” walked (or climbed) reside in the still undocumented temporal sequence and pattern of locomotor skeletal change in hominin species that predate *A. afarensis*: *A. anamensis*, *Ar. ramidus*, and so forth. If the proposal that modifications of the lower spine and pelvis essential for terres-

trial bipedality imply correlated functional–morphological changes in the hip and, presumably, knee is valid, as the proponents of the argument that *A. afarensis* was a committed terrestrial biped have asserted, then we should expect to see a pattern of correlated morphological and functional change in axial, pelvic and lower limb anatomy leading up to *A. afarensis*; and we would then agree that these anatomically widespread changes probably precluded significant amounts of habitual nonbipedal locomotion by the time of *A. afarensis*. If, however, the changes in the spine, hip, knee, and so forth, evolved in a piecemeal fashion—manifested as a disjunct pattern of first appearances across taxa nearer than *A. afarensis* to the base of the hominin clade—then we would be less ready to conclude that their conjunction in *A. afarensis* should necessarily rule out reference to the more apelike aspects of this taxon’s postcranial anatomy in reconstructing its locomotion. Whatever the outcome, the earlier fossil record—rather than further debate about where *A. afarensis* resides on a modern chimpanzee–human continuum—is likely to be the final arbiter of the debate over Lucy’s locomotion.

The issue of sexual dimorphism in *A. afarensis* is similarly vexed. Despite variation in methodological approach, there is a consensus that *A. afarensis* was strongly dimorphic in skeletal size. However, the relationship between body size (i.e., mass) dimorphism and skeletal size dimorphism, on which basis the former is usually inferred, is not straightforward, and while most studies conclude that the species’ body size dimorphism registers between that of chimpanzees and the larger great apes, these estimates remain necessarily imprecise. But assuming the inference of strong body size dimorphism is valid, *A. afarensis* presents something of a paradox among catarrhines because of its drastically reduced canine crowns and crown-size dimorphism. As Plavcan and van Schaik (1997) have discussed, maxillary canine crown height dimorphism and body mass dimorphism are the most predictive variables for estimating the intensity of inter-male competition (and hence the inference of polygyny) among anthropoids, and so, for *A. afarensis*: “dimorphism of one character (canines or inferred body weight) can only be used as evidence of behavior if dimorphism in the other character is assumed to reflect some unusual mechanism operating in hominids” (Plavcan and van Schaik, 1997, p 365). The early australopiths exhibit canine crown heights that overlap those of female chimpanzees (Plavcan et al., 2009), but this similarity belies a critical distinction between early hominins and any great ape regardless of canine size, which is the transformation of the canine from a honing to a nonhoning crown—a fundamental functional-morphological shift already evident in Mio-Pliocene hominins such as *S. tchadensis* and *Ar. ramidus*. Hominins are indeed unique among catarrhines in this attribute, and we suggest that one key to the solution of the apparently paradoxical relationship between high body size dimorphism and low canine size dimorphism in *A. afarensis* will come from a better understanding of the adaptive basis for the *loss of canine honing*, the maintenance of which in adults is a *sine qua non* of catarrhine inter-male competition, as opposed to canine crown *reduction* alone, which has tended to be the focus of most investigations. Again, it will be the earlier fossil record that provides the evidence for the pathway along which the otherwise universal catarrhine sectorial C/P₃ complex was disintegrated and refashioned in

the hominin clade; no extant primate can serve as a model for this transformation.

Studies of likely diets in *A. afarensis* have reached something of an impasse because of the (so far) difficult task of integrating analyses carried out at different scales of resolution. At the gross anatomical level, the *A. afarensis* craniodental remains have many attributes conventionally associated with “heavy mastication” (however imprecisely defined) compared to extant great apes: thickly enameled, low-crowned and megadont cheek teeth; molarized premolars; deep mandibular corpora; tall, vertical mandibular rami; broad, robustly constructed zygomatic bones; deep, thick zygomatic arches; and expansive and rugose areas for the origins and insertions of *m. temporalis* and *m. masseter*. Teaford and Ungar (2000; Ungar, 2004) found many of these attributes to be consistent with a diet that included (but was not necessarily limited to) hard, brittle foods that would have required substantial “crushing” force to comminute. However, microwear of the molar occlusal surfaces is notably dissimilar to that of extant primate hard-object feeders, aligning instead with that of mountain gorillas (Grine et al., 2006b), which focus on tough, fracture-resistant plant foods. Moreover, the pattern of molar microwear in *A. afarensis* is uniform across the species’ known temporal and paleoenvironmental ranges and is the same as that in its likely ancestor, *A. anamensis* (Grine et al., 2006a), which, as we have reviewed here, differs diagnostically from *A. afarensis* in gnathic form, dental arch shape and aspects of molar crown topography. The disjunct between macro- and micro-perspectives on dietary material properties has led to the idea that the design features of the *A. afarensis* (and, by extension, *A. anamensis*) masticatory apparatus point to a “fallback” adaptation to hard, brittle foods during times of preferred resource scarcity and environmental stress (i.e., dry season)—while microwear consistently yields the “unstressed” dietary signal (we have already [above] noted the improbability of the taphonomic pattern implied by this explanation). We do not doubt the concept of fallback foods as a critical factor in the design of the primate masticatory apparatus—we take it as axiomatic that species frequently respond adaptively to the most stressful rather than merely the most common resource challenges—but from a hypothesis-testing perspective we are concerned that the “fallback foods” interpretation has become an ad hoc solution of last resort to account for discrepant paleontological datasets. Notwithstanding the high value of extant analog taxa for establishing the scientific credibility of inferences as to the “cause” of suspected adaptations among extinct species, the living primates will not yield up suitable models for the diet of *A. afarensis*. With Grine et al. (2006b, p 314), we think that strategies designed to vertically integrate scales of analysis (from stable dietary isotopes and microwear to occlusal design and craniofacial biomechanics) will lead to resolution of conflicts from the disparate approaches taken individually. The plentiful and complete remains of *A. afarensis* should provide an excellent opportunity to apply such integration to a paleontological case.

Our review has shown that while studies of *A. afarensis* have filled important gaps in knowledge of Pliocene hominin evolution, there yet remain many opportunities for strategic research on this taxon. Research to date has brought us to a better understanding of key paleobiological issues regarding phylogeny, locomotion, diet

and sexual dimorphism, if not to final answers to some of the significant questions arising from them. The species' extensive representation of the skull, dentition and postcranial skeleton during a period of hominin evolution when several major structural complexes had already undergone significant transformation provides one of the richest sources from which to draw fossil data as paleoanthropologists continue to narrow the search for these solutions.

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LITERATURE CITED

- Abitbol MM. 1987. Evolution of the lumbosacral angle. *Am J Phys Anthropol* 72:361–372.
- Aiello LC, Montgomery C, Dean C. 1991. The natural history of deciduous tooth attrition in hominoids. *J Hum Evol* 21:397–412.
- Alba DM, Moyà-Solà S, Köhler M. 2003. Morphological affinities of the *Australopithecus afarensis* hand on the basis of manual proportions and relative thumb length. *J Hum Evol* 44:225–254.
- Alemseged Z, Spoor F, Kimbel WH, Bobe R, Geraads D, Reed D, Wynn JG. 2006. A juvenile early hominin skeleton from Dikika, Ethiopia. *Nature* 443:296–301.
- Alemseged Z, Wynn JG, Kimbel WH, Reed D, Geraads D, Bobe R. 2005. A new hominin from the Basal Member of the Hadar Formation, Dikika, Ethiopia, and its geological context. *J Hum Evol* 49:499–514.
- Aronson JA, Schmitt TJ, Walter RC, Taieb M, Tiercelin J-J, Johanson DC, Naeser CV, Nairn AEM. 1977. New geochronologic and paleomagnetic data for the hominid-bearing Hadar Formation, Ethiopia. *Nature* 267:323–327.
- Aronson JA, Taieb M. 1981. Geology and paleogeography of the Hadar hominid site, Ethiopia. In: Rapp G, Vondra CF, editors. *Hominid sites: their geologic setting*. Boulder: Westview Press. p 165–195.
- Asfaw B. 1987. The Belohdelie frontal—new evidence of early hominid cranial morphology from the Afar of Ethiopia. *J Hum Evol* 16:611–624.
- Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. 1999. *Australopithecus garhi*: a new species of early hominid from Ethiopia. *Science* 284:629–635.
- Bailey SE, Wood BA. 2007. Trends in postcanine occlusal morphology within the hominin clade: the case of *Paranthropus*. In: Bailey SE, Hublin J-J, editors. *Dental perspectives on human evolution: state of the art research in Dental Paleoanthropology*. Dordrecht, Netherlands: Springer. p 33–52.
- Behrensmeyer K, Harmon EH, Kimbel WH. 2003. Environmental context and taphonomy of the first family hominid locality, Hadar, Ethiopia. *J Vert Paleo* 3:33A.
- Berger LR, Tobias PV. 1996. A chimpanzee-like tibia from Sterkfontein, South Africa and its implications for the interpretation of bipedalism in *Australopithecus africanus*. *J Hum Evol* 30:343–348.
- Beynon AD, Dean MC. 1987. Crown-formation time of a fossil hominin premolar tooth. *Arch Oral Biol* 32:773–780.
- Beynon AD, Dean MC. 1988. Distinct dental development patterns in early fossil hominids. *Nature* 335:509–514.
- Beynon AD, Wood BA. 1987. Patterns and rates of enamel growth in the molar teeth of early hominids. *Nature* 326:493–496.
- Bonnefille R, Potts R, Chalié F, Jolly D, Peyron O. 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. *Proc Natl Acad Sci USA* 101:12125–12129.
- Bromage TG. 1987. The biological and chronological maturation of early hominids. *J Hum Evol* 16:257–272.
- Bromage TG, Dean MC. 1985. Re-evaluation of the age at death of immature fossil hominids. *Nature* 317:525–527.
- Brown B, Brown FH, Walker A. 2001. New hominids from the Lake Turkana basin, Kenya. *J Hum Evol* 41:29–44.
- Brown FH. 1982. Tulu Bor Tuff at Koobi Fora correlated with the Sidi Hakoma Tuff at Hadar. *Nature* 300:631–635.
- Brown FH, Cerling TE. 1982. Stratigraphical significance of the Tulu Bor Tuff of the Koobi Fora Formation. *Nature* 300:212–215.
- Brown P, Sutikna T, Morwood MJ, Soejono RP, Jatmiko, Saptomo EW, Due RA. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431:1055–1061.
- Brunet M, Beauvilain A, Coppens Y, Heintz E, Moutaye AHE, Pilbeam D. 1995. The first australopithecine 2,500 kilometres west of the Rift Valley (Chad). *Nature* 378:273–275.
- Brunet M, Beauvilain A, Coppens Y, Heintz E, Moutaye AHE, Pilbeam D. 1996. *Australopithecus bahrelgazali*, une nouvelle espèce d'Hominidé ancien de la région de Koro Tor (Tchad). *C R Acad Sci IIa* 322:907–913.
- Brunet M, Guy F, Pilbeam D, Lieberman DE, Likius A, Mackaye HT, Ponce de León MS, Zollikofer CPE, Vignaud P. 2005. New material of the earliest hominid from the Upper Miocene of Chad. *Nature* 434:752–755.
- Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, Beauvilain A, Blondel C, Bocherens H, Boisserie JR, De Bonis L, Coppens Y, Dejax J, Denys C, Drustringer P, Eisenmann VR, Fanone G, Fronty P, Geraads D, Lehmann T, Lihoreau F, Louchart A, Mahamat A, Merceron G, Mouchelin G, Otero O, Campomanes PP, De Leon MP, Rage JC, Sapanet M, Schuster M, Sudre J, Tassy P, Valentin X, Vignaud P, Viriot L, Zazze A, Zellerkefer C. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418:145–151.
- Bush ME, Lovejoy CO, Johanson DC, Coppens Y. 1982. Hominid carpal, metacarpal, and phalangeal bones recovered from the Hadar Formation: 1974–1977 collections. *Am J Phys Anthropol* 57:651–677.
- Campisano CJ. 2007. Tephrostratigraphy and hominin paleoenvironments of the Hadar Formation, Afar Depression, Ethiopia. Ph.D. Dissertation, Rutgers University.
- Campisano CJ, Feibel CS. 2007. Connecting local environmental sequences to global climate patterns. Evidence from the hominin-bearing Hadar Formation, Ethiopia. *J Hum Evol* 53:515–527.
- Campisano CJ, Feibel CS. 2008. Depositional environments and stratigraphic summary of the Pliocene Hadar Formation at Hadar, Afar Depression, Ethiopia. *GSA Special Paper* 446:179–201.
- Charteris J, Wall JC, Nottrodt JW. 1981. Functional reconstruction of gait from the Pliocene hominid footprints at Laetoli, northern Tanzania. *Nature* 290:496–498.
- Clarke RJ. 1988. A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. In: Grine FE, editor. *Evolutionary history of the “Robust” Australopithecines*. New York: Aldine de Gruyter. p 285–292.

- Clarke RJ. 1994. Advances in understanding the craniofacial anatomy of South African early hominids. In: Corruccini RS, Ciochon RL, editors. Integrative paths to the past: paleoanthropological advances in honor of F. Clark Howell. New York: Prentice Hall. p 205–222.
- Clarke RJ, Tobias PV. 1995. Sterkfontein Member 2 foot bones of the oldest South Africa hominid. *Science* 269:521–524.
- Coffing K, Feibel C, Leakey M, Walker A. 1994. 4-million-year-old hominids from East Lake Turkana, Kenya. *Am J Phys Anthropol* 93:55–65.
- Collard M, Wood B. 2001. Homoplasy and the early hominid masticatory system: inferences from analyses of extant hominoids and papionins. *J Hum Evol* 41:167–194.
- Cook DC, Buikstra JE, DeRousseau CJ, Johanson DC. 1983. Vertebral pathology in the Afar Australopithecines. *Am J Phys Anthropol* 60:83–101.
- Coppens Y. 1977. Evolution morphologique de la première prémolaire inférieure chez certains Primates supérieurs. *C R Acad Sci D* 285:1299–1302.
- Corruccini RS, McHenry HM. 2001. Knuckle-walking hominid ancestors. *J Hum Evol* 40:507–511.
- Crompton RH, Thorpe SKS. 2007. Response to comment on “origin of human bipedalism as an adaptation for locomotion on flexible branches.” *Science* 318:1066.
- Crompton RH, Vereecke EE, Thorpe SKS. 2008. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. *J Anat* 212:501–543.
- Daegling DJ, Hylander WL. 1998. Biomechanics of torsion in the human mandible. *Am J Phys Anthropol* 105:73–87.
- Day MH, Wickens EH. 1980. Laetoli Pliocene hominid footprints and bipedalism. *Nature* 286:385–387.
- Dean C, Leakey MG, Reid D, Schrenk F, Schwartz GT, Stringer C, Walker A. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature* 414:628–631.
- Dean MC. 1987a. Growth layers and incremental markings in hard tissues; a review of the literature and some preliminary observations about enamel structure in *Paranthropus boisei*. *J Hum Evol* 16:157–172.
- Dean MC. 1987b. The dental developmental status of six East African juvenile fossil hominids. *J Hum Evol* 16:197–213.
- Dean MC. 2006. Tooth microstructure tracks the pace of human life-history evolution. *Proc R Soc Lond B Biol Sci* 273:2799–2808.
- Dean MC, Beynon AD, Thackeray JF, Macho GA. 1993. Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus* specimen, SK 63, from Swartkrans, South Africa. *Am J Phys Anthropol* 91:401–419.
- Dean MC, Reid DJ. 2001. Perikymata spacing and distribution on hominid anterior teeth. *Am J Phys Anthropol* 116:209–215.
- Delson E, Eldredge N, Tattersall I. 1977. Reconstruction of hominid phylogeny—testable framework based on cladistic analysis. *J Hum Evol* 6:263–278.
- Dobson SD. 2005. Are the differences between Stw 431 (*Australopithecus africanus*) and A.L. 288–1 (*A. afarensis*) significant? *J Hum Evol* 49:143–154.
- Drake R, Curtis GH. 1987. K-Ar geochronology of the Laetoli fossil localities. In: Leakey MD, Harris JM, editors. *Laetoli: a Pliocene site in Northern Tanzania*. Oxford: Clarendon Press. p 48–52.
- Drapeau MSM. 2004. Functional anatomy of the olecranon process in hominoids and Plio-Pleistocene hominins. *Am J Phys Anthropol* 124:297–314.
- Drapeau MSM. 2008. Articular morphology of the proximal ulna in extant and fossil hominoids and hominins. *J Hum Evol* 55:86–102.
- Drapeau MSM, Ward CV. 2007. Forelimb segment length proportions in extant hominoids and *Australopithecus afarensis*. *Am J Phys Anthropol* 132:327–343.
- Drapeau MSM, Ward CV, Kimbel WH, Johanson DC, Rak Y. 2005. Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *J Hum Evol* 48:593–642.
- DuBrul EL. 1977. Early hominid feeding mechanisms. *Am J Phys Anthropol* 47:305–320.
- Duncan AS, Kappelman J, Shapiro LJ. 1994. Metatarsophalangeal joint function and positional behavior in *Australopithecus afarensis*. *Am J Phys Anthropol* 93:67–81.
- Eldredge N, Tattersall I. 1975. Evolutionary models, phylogenetic reconstruction, and another look at hominid phylogeny. In: Szalay FS, editor. *Approaches to Primate Paleobiology*. Basel: Karger. p 218–242.
- Falk D, Conroy GC. 1983. The cranial venous sinus system in *Australopithecus afarensis*. *Nature* 306:779–781.
- Falk D, Gage TB, Dudek B, Olson TR. 1995. Did more than one species of hominid coexist before 3.0 Ma?: evidence from blood and teeth. *J Hum Evol* 29:591–600.
- Falk D, Redmond JC, Guyer J, Conroy C, Recheis W, Weber GW, Seidler H. 2000. Early hominid brain evolution: a new look at old endocasts. *J Hum Evol* 38:695–717.
- FitzGerald CM. 1998. Do enamel microstructures have regular time dependency? Conclusion from the literature and a large-scale study. *J Hum Evol* 35:371–386.
- Fleagle JG, Kay RF, Simons EL. 1980. Sexual dimorphism in early anthropoids. *Nature* 287:328–330.
- Fleagle JG, Rasmussen DT, Yirga S, Bown TM, Grine FE. 1991. New hominid fossils from Fejej, Southern Ethiopia. *J Hum Evol* 21:145–152.
- Galik K, Senut B, Pickford M, Gommery D, Treil J, Kuperavage AJ, Eckhardt RB. 2004. External and internal morphology of the BAR 1002' 00 *Orrorin tugenensis* femur. *Science* 305:1450–1453.
- Gebo DL, Schwarz GT. 2006. Foot bones from Omo: implications for hominid evolution. *Am J Phys Anthropol* 129:499–511.
- Gordon AD, Green DJ, Richmond BG. 2008. Strong postcranial size dimorphism in *Australopithecus afarensis*: results from two new resampling methods for multivariate data sets with missing data. *Am J Phys Anthropol* 135:311–328.
- Gray BT. 1980. Environmental reconstruction of the Hadar Formation (Afar, Ethiopia). Ph.D. Dissertation, Case Western Reserve University.
- Green DJ, Gordon AD. 2008. Metacarpal proportions in *Australopithecus africanus*. *J Hum Evol* 54:705–719.
- Green DJ, Gordon AD, Richmond BG. 2007. Limb-size proportions in *Australopithecus afarensis* and *Australopithecus africanus*. *J Hum Evol* 52:187–200.
- Greenfield LO. 1979. On the adaptive pattern of “*Ramapithecus*”. *Am J Phys Anthropol* 50:527–548.
- Greenfield LO. 1990. Canine “honing” in *Australopithecus afarensis*. *Am J Phys Anthropol* 82:135–143.
- Grine FE. 1985. Australopithecine evolution: the deciduous dental evidence. In: Delson E, editor. *Ancestors: the hard evidence*. New York: Liss. p 138–152.
- Grine FE, Kay RF. 1988. Early hominid diets from quantitative image analysis of dental microwear. *Nature* 333:765–768.
- Grine FE, Ungar PS, Teaford MF. 2006a. Was the early Pliocene hominin ‘*Australopithecus anamensis*’ a hard object feeder? *S Afr J Sci* 102:301–310.
- Grine FE, Ungar PS, Teaford MF, El-Zaatari S. 2006b. Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. *J Hum Evol* 51:297–319.
- Groves CP. 1999. Nomenclature of African Plio-Pleistocene hominins. *J Hum Evol* 37:869–872.
- Guatelli-Steinberg D, Irish JD. 2005. Brief Communication: early hominin variability in first molar dental trait frequencies. *Am J Phys Anthropol* 128:477–484.
- Guy F, Hassane-Taïso M, Likius A, Vignaud P, Schmittbuhl M, Brunet M. 2008. Symphyseal shape variation in extant and fossil hominoids, and the symphysis of *Australopithecus bahrelghazali*. *J Hum Evol* 55:37–47.
- Guy F, Lieberman DE, Pilbeam D, de Leon MP, Likius A, MacKay HT, Vignaud P, Zollikofer C, Brunet M. 2005. Morphological affinities of the Sahelanthropus tchadensis (Late Miocene hominid from Chad) cranium. *PNAS* 102:18836–18841.
- Häeusler M, Martelli SA, Boeni T. 2002. Vertebrae numbers of the early hominid lumbar spine. *J Hum Evol* 43:621–643.

- Haile-Selassie Y. 2001. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* 412:178–181.
- Haile-Selassie Y, Suwa G, White TD. 2004. Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science* 303:1503–1505.
- Harcourt-Smith WEH, Aiello LC. 2004. Fossils, feet and the evolution of human bipedal locomotion. *J Anat* 204:403–416.
- Harmon EH. 2005. A comparative analysis of femoral morphology in *Australopithecus afarensis*: implications for the evolution of bipedal locomotion. Ph.D. dissertation, Arizona State University.
- Harmon EH. 2006. Size and shape variation in *Australopithecus afarensis* proximal femora. *J Hum Evol* 51:217–227.
- Harris JM. 1987. Summary. In: Leakey MD, Harris JM, editors. *Laetoli: a Pliocene site in Northern Tanzania*. Oxford: Oxford University Press. p 524–532.
- Harrison T. 2002. The first record of fossil hominins from the Ndolanya Beds, Laetoli, Tanzania. *Am J Phys Anthropol Suppl* 34:83.
- Hartwig-Scherer S, Martin RD. 1991. Was “Lucy” more human than her “child”? Observations on early hominid postcranial skeletons. *J Hum Evol* 21:439–449.
- Hay RL. 1987. Geology of the Laetoli area. In: Leakey MD, Harris JM, editors. *Laetoli: a Pliocene site in Northern Tanzania*. Oxford: Clarendon Press. p 23–47.
- Heinrich RE, Rose MD, Leakey RE, Walker AC. 1993. Hominid radius from the Middle Pliocene of Lake Turkana, Kenya. *Am J Phys Anthropol* 92:139–148.
- Heiple KG, Lovejoy CO. 1971. The distal femoral anatomy of *Australopithecus*. *Am J Phys Anthropol* 35:75–84.
- Henning E. 1948. Quatärfaunen und Urgeschichte Ostafriacas. *Naturwiss Rdsch Jahrg* 12:212–217.
- Hill A, Ward S. 1988. Origin of the Hominidae: the record of African large hominoid evolution from between 14 My and 4 My. *Yearb Phys Anthropol* 31:49–83.
- Hill A, Ward S, Deino A, Curtis G. 1992. Earliest *Homo*. *Nature* 355:719–722.
- Hlusko LJ. 2004. Protostylid variation in *Australopithecus*. *J Hum Evol* 46:579–594.
- Holloway RL, Broadfield DC, Yuan MS. 2004. The human fossil record. Volume 3. Brain endocasts: the paleoneurological evidence. Hoboken: John Wiley and Sons, Inc.
- Holloway RL, Yuan MS. 2004. Endocranial morphology of A.L. 444–2. In: Kimbel WH, Rak Y, Johanson DC, editors. *The skull of Australopithecus afarensis*. New York: Oxford University Press. p 123–135.
- Howell FC. 1978. Hominidae. In: Maglio VJ, Cooke HBS, editors. *Evolution of African mammals*. Cambridge, MA: Harvard University Press. p 154–248.
- Howell FC, Coppens Y. 1976. An overview of the Hominidae from the Omo succession, Ethiopia. In: Coppens Y, Howell FC, Isaac G, Leakey REF, editors. *Earliest man and environments in the Lake Rudolf Basin*. Chicago: University of Chicago Press. p 522–532.
- Hylander WL. 1979. Functional significance of primate mandibular form. *J Morphol* 160:223–239.
- Inouye SE, Shea BT. 1997. What’s your angle? Size correction and bar-glenoid orientation in “Lucy” (A.L. 288–1). *Int J Primatol* 18:629–650.
- Johanson DC. 1976. Ethiopia yields 1st family of early man. *Natl Geogr* 150:790–811.
- Johanson DC. 1980. A provisional interpretation of the Hadar hominids. *Proc 8th Pan-african Congr Prehist Quat Studies* 157–168.
- Johanson DC, Coppens Y. 1976. A preliminary anatomical diagnosis of the first Plio/Pleistocene hominid discoveries in the Central Afar, Ethiopia. *Am J Phys Anthropol* 45:217–234.
- Johanson DC, Edey MA. 1981. Lucy: the beginnings of humankind. N.Y.: Simon and Schuster.
- Johanson DC, Lovejoy CO, Kimbel WH, White TD, Ward SC, Bush ME, Latimer BM, Yves Coppens. 1982a. Morphology of the Pliocene partial hominid skeleton (A.L. 288–1) from the Hadar Formation. *Am J Phys Anthropol* 57:403–451.
- Johanson DC, Taieb M. 1976. Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. *Nature* 260:293–297.
- Johanson DC, Taieb M, Coppens Y. 1982b. Pliocene hominids from the Hadar Formation, Ethiopia (1973–1977): stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematics. *Am J Phys Anthropol* 57:373–402.
- Johanson DC, Taieb M, Gray BT, Coppens Y. 1978. Geological framework of the Pliocene Hadar Formation (Afar, Ethiopia) with notes on paleontology including hominids. In: Bishop WW, editor. *Geological background to fossil man*. Edinburgh: Scottish Academic Press. p 549–564.
- Johanson DC, White TD. 1979. A systematic assessment of early African hominids. *Science* 203:321–330.
- Johanson DC, White TD, Coppens Y. 1978. A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa. *Kirtlandia* 28:1–14.
- Johanson DC, White TD, Coppens Y. 1982c. Dental remains from the Hadar Formation, Ethiopia: 1974–1977 collections. *Am J Phys Anthropol* 57:545–603.
- Jungers WL. 1982. Lucy’s limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature* 297:676–678.
- Jungers WL, Stern JT. 1983. Body proportion, skeletal allometry and locomotion in the Hadar hominids—a reply. *J Hum Evol* 12:673–684.
- Kapplerman J, Swisher III CC, Fleagle JG, Yirga S, Bown TM, Feseha M. 1996. Age of *Australopithecus afarensis* from Fejej, Ethiopia. *J Hum Evol* 30:139–146.
- Kay RF. 1982. Sexual dimorphism in Ramapithecinae. *Proc Natl Acad Sci USA* 79:209–212.
- Kay RF, Plavcan JM, Glander KE, Wright PC. 1988. Sexual selection and canine dimorphism in New World monkeys. *Am J Phys Anthropol* 77:385–397.
- Keyser AW. 2000. The Drimolen skull: the most complete australopithecine cranium and mandible to date. *S Afr J Sci* 96:189–193.
- Keyser AW, Menter CG, Moggi-Cecchi J, Pickering TR, Berger LR. 2000. Drimolen: a new hominid-bearing site in Gauteng, South Africa. *S Afr J Sci* 96:193–197.
- Kimbel WH. 1984. Variation in the pattern of cranial venous sinuses and hominid phylogeny. *Am J Phys Anthropol* 63:243–263.
- Kimbel WH. 1988. Identification of a partial cranium of *Australopithecus afarensis* from the Koobi Fora Formation, Kenya. *J Hum Evol* 17:647–656.
- Kimbel WH, Johanson DC, Rak Y. 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature* 368:449–451.
- Kimbel WH, Lockwood CA, Ward CV, Leakey MG, Rak Y, Johanson DC. 2006. Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record. *J Hum Evol* 51:134–152.
- Kimbel WH, Rak Y. 1985. Functional morphology of the asterionic region in extant hominoids and fossil hominins. *Am J Phys Anthropol* 66:31–54.
- Kimbel WH, Rak Y, Johanson DC. 2003. A new hominin skull from Hadar: implications for cranial sexual dimorphism in *Australopithecus afarensis*. *Am J Phys Anthropol Suppl* 36:129.
- Kimbel WH, Rak Y, Johanson DC. 2004. The skull of *Australopithecus afarensis*. New York: Oxford University Press.
- Kimbel WH, Walter RC, Johanson DC, Reed KE, Aronson JL, Assefa Z, Marean CW, Eck GG, Bobe R, Hovers E, Rak Y, Vondra C, Yemane T, York D, Chen Y, Evensen NM, Smith PE. 1996. Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar member), Ethiopia. *J Hum Evol* 31:549–561.
- Kimbel WH, White TD. 1988a. A revised reconstruction of the adult skull of *Australopithecus afarensis*. *J Hum Evol* 17:545–550.
- Kimbel WH, White TD. 1988b. Variation, sexual dimorphism and the taxonomy of *Australopithecus*. In: Grine FE, editor. *Evolutionary history of the “Robust” Australopithecines*. New York: Aldine de Gruyter. p 175–192.

- Kimbel WH, White TD, Johanson DC. 1984. Cranial morphology of *Australopithecus afarensis*: a comparative study based on a composite reconstruction of the adult skull. *Am J Phys Anthropol* 64:337–388.
- Kimbel WH, White TD, Johanson DC. 1985. Craniodental morphology of the hominids from Hadar and Laetoli: evidence of “*Paranthropus*” and *Homo* in the Mid-Pliocene of eastern Africa. In: Delson E, editor. *Ancestors: the hard evidence*. New York: Liss. p 120–137.
- Kimbel WH, White TD, Johanson DC. 1988. Implications of KNM-WT 17000 for the evolution of the “Robust” *Australopithecus*. In: Grine FE, editor. *Evolutionary history of the “Robust” Australopithecines*. New York: Aldine de Gruyter. p 259–268.
- Kingston JD, Harrison T. 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: implications for early hominin paleoecology. *Palaeogeogr Palaeoclimatol Palaeoecol* 243:272–306.
- Kono RT. 2004. Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3-dimensional whole crown perspective. *Anthropol Sci* 112:121–146.
- Kupczik K, Spoor F, Pommert A, Dean C. 2005. Premolar root number variation in hominoids: genetic polymorphism vs. functional significance. In: Zadinska E, editor. *Current trends in dental morphology research*. Lodz: University of Lodz Press. p 257–268.
- Kyauka PS, Ndessokia P. 1990. A new hominid tooth from Laetoli, Tanzania. *J Hum Evol* 19:747–750.
- Lacruz RS, Bromage TG. 2006. Appositional enamel growth in molars of South African fossil hominids. *J Anat* 209:13–20.
- Lacruz RS, Dean CM, Ramirez-Rozzi F, Bromage TG. 2008. Megadontia, striae periodicity and patterns of enamel secretion in Plio-Pleistocene fossil hominins. *J Anat* 213:148–158.
- Lacruz RS, Ramirez-Rozzi F, Bromage TG. 2006. Variation in enamel development of South African fossil hominids. *J Hum Evol* 51:580–590.
- Lague MR. 2002. Another look at shape variation in the distal femur of *Australopithecus afarensis*: implications for taxonomic and functional diversity at Hadar. *J Hum Evol* 42:609–626.
- Lague MR, Jungers WL. 1996. Morphometric variation in Plio-Pleistocene hominid distal humeri. *Am J Phys Anthropol* 101:401–427.
- Larson SG. 1996. Estimating humeral torsion on incomplete fossil anthropoid humeri. *J Hum Evol* 31:239–257.
- Larson SG. 2007. Evolutionary transformation of the hominin shoulder. *Evol Anthropol* 16:172–187.
- Latimer B. 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Senut B, Coppens Y, editors. *Origine(s) de la bipédie chez les Hominidés*. Paris: CNRS. p 169–176.
- Latimer B, Lovejoy CO. 1989. The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *Am J Phys Anthropol* 78:369–386.
- Latimer B, Lovejoy CO. 1990a. Hallucal tarsometatarsal joint in *Australopithecus afarensis*. *Am J Phys Anthropol* 82:125–133.
- Latimer B, Lovejoy CO. 1990b. Metatarsophalangeal joints of *Australopithecus afarensis*. *Am J Phys Anthropol* 83:13–23.
- Latimer B, Ohman JC, Lovejoy CO. 1987. Talocalcral joint in African hominoids: implications for *Australopithecus afarensis*. *Am J Phys Anthropol* 74:155–175.
- Latimer B, Ward CV. 1993. The thoracic and lumbar vertebrae. In: Walker A, Leakey R, editors. *The Nariokotome Homo erectus skeleton*. Cambridge, Harvard University Press. p 266–293.
- Latimer BM, Lovejoy CO, Johanson DC, Coppens Y. 1982. Hominid tarsal, metatarsal and phalangeal bones recovered from the Hadar Formation: 1974–1977 collections. *Am J Phys Anthropol* 57:701–719.
- Leakey MD. 1979. 3.6 Million years old-footprints in the ashes of time. *Nat Geo* 155:446–457.
- Leakey MD. 1987. The hominid footprints: introduction. In: Leakey MD, Harris JM, editors. *Laetoli: a Pliocene site in Northern Tanzania*. Oxford: Oxford University Press. p 490–496.
- Leakey MD, Hay RL. 1979. Pliocene footprints in the Laetoli Beds at Laetoli, northern Tanzania. *Nature* 278:317–323.
- Leakey MD, Hay RL, Curtis GH, Drake RE, Jackes MK, White TD. 1976. Fossil hominids from the Laetoli Beds. *Nature* 262:460–466.
- 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 MG, Feibel CS, McDougall I, Ward C, Walker A. 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* 393:62–66.
- Leakey MG, Spoor F, Brown FH, Gathogo PN, Kiarie C, Leakey LN, McDougall I. 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410:433–440.
- Leakey REF. 1973. Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. *Nature* 242:447–450.
- Leakey REF. 1974. Further evidence of lower Pleistocene hominids from East Rudolf, North Kenya, 1973. *Nature* 248:653–656.
- Leakey REF, Walker AC. 1976. *Australopithecus, Homo erectus* and single species hypothesis. *Nature* 261:572–574.
- Leakey REF, Walker A. 1980. Status of *Australopithecus afarensis*. *Science* 207:1103–1103.
- Le Gros Clark WE. 1950. New paleontological evidence bearing on the evolution of Hominoidea. *Q J Geol Soc Lond* 105:225–264.
- Leonard WR, Hegmon M. 1987. Evolution of P₃ morphology in *Australopithecus afarensis*. *Am J Phys Anthropol* 73:41–63.
- Leutenegger W, Shell B. 1987. Variability and sexual dimorphism in canine size of *Australopithecus* and extant hominoids. *J Hum Evol* 16:359–367.
- Lewin R. 1987. *Bones of contention: controversies in the search for human origins*. Chicago: The University of Chicago Press.
- Lieberman DE. 1997. Making behavioral and phylogenetic inferences from hominid fossils: considering the developmental influence of mechanical forces. *Annu Rev Anthropol* 26:185–210.
- Lockwood CA, Kimbel WH, Johanson DC. 2000. Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*. *J Hum Evol* 39:23–55.
- Lockwood CA, Richmond BG, Jungers WL, Kimbel WH. 1996. Randomization procedures and sexual dimorphism in *Australopithecus afarensis*. *J Hum Evol* 31:537–548.
- Lockwood CA, Tobias PV. 1999. A large male hominin cranium from Sterkfontein, South Africa, and the status of *Australopithecus africanus*. *J Hum Evol* 36:637–685.
- Lovejoy CO. 1988. Evolution of human walking. *Sci Am* 256:118–125.
- Lovejoy CO. 2005a. The natural history of human gait and posture, Part 1: Spine and pelvis. *Gait Posture* 21:95–112.
- Lovejoy CO. 2005b. The natural history of human gait and posture, Part 2: Hip and thigh. *Gait Posture* 21:113–124.
- Lovejoy CO. 2007. The natural history of human gait and posture, Part 3: The knee. *Gait Posture* 25:325–341.
- Lovejoy CO, Heiple KG. 1972. Proximal femoral anatomy of *Australopithecus*. *Nature* 235:175–176.
- Lovejoy CO, Johanson DC, Coppens Y. 1982a. Elements of the axial skeleton recovered from the Hadar Formation: 1974–1977 collections. *Am J Phys Anthropol* 57:631–635.
- Lovejoy CO, Johanson DC, Coppens Y. 1982b. Hominid upper limb bones recovered from the Hadar Formation: 1974–1977 collections. *Am J Phys Anthropol* 57:637–649.
- Lovejoy CO, Johanson DC, Coppens Y. 1982c. Hominid lower limb bones recovered from the Hadar Formation: 1974–1977 collections. *Am J Phys Anthropol* 57:679–700.
- Lovejoy CO, Meindl RS, Ohman JC, Heiple KG, White TD. 2002. The Maka femur and its bearing on the antiquity of human walking: applying contemporary concepts of morphogenesis to the human fossil record. *Am J Phys Anthropol* 119:97–133.
- Lucas PW, Constantino PJ, Wood BA. 2008. Inferences regarding the diet of extinct hominins: structural and functional trends in dental and mandibular morphology within the hominin clade. *J Anat* 212:486–500.

- Macchiarelli R, Bondioli L, Debénath A, Mazurier A, Tourne-
piche J-F, Birch W, Dean C. 2006. How Neanderthal molar
teeth grew. *Nature* 444:748–751.
- McHenry HM. 1984. Relative cheek-tooth size in *Australopithe-
cus*. *Am J Phys Anthropol* 64:297–306.
- McHenry HM. 1986. The 1st bipeds—a comparison of the *A.
afarensis* and *A. africanus* postcranium and implications for
the evolution of bipedalism. *J Hum Evol* 15:177–191.
- McHenry HM. 1988. New estimates of body weight in early
hominids and their significance to encephalization and mega-
dontia in ‘Robust’ *Australopithecus*. In: Grine FE, editor. *Evo-
lutionary history of the “Robust” Australopithecines*. New
York: Aldine de Gruyter. p 133–148.
- McHenry HM. 1991. Sexual dimorphism in *Australopithecus
afarensis*. *J Hum Evol* 20:21–32.
- McHenry HM. 1994. Tempo and mode in human evolution. *Proc
Natl Acad Sci USA* 91:6780–6786.
- McHenry HM, Berger LR. 1998. Body proportions in *Australopi-
thecus afarensis* and *A. africanus* and the origin of the genus
Homo. *J Hum Evol* 35:1–22.
- McHenry HM, Jones AL. 2006. Hallucial convergence in early
hominids. *J Hum Evol* 50:534–539.
- Millien V, Lyons SK, Olson L, Smith FA, Wilson AB, Yom-Tov Y.
2006. Ecotypic variation in the context of global climate
change: revisiting the rules. *Ecol Lett* 9:853–869.
- Moggi-Cecchi J, Grine FE, Tobias PV. 2005. Early hominid den-
tal remains from Members 4 and 5 of the Sterkfontein Forma-
tion (1966–1996 excavations): catalogue, individual associa-
tions, morphological descriptions and initial metrical analysis.
J Hum Evol 50:239–328.
- Moggi-Cecchi J, Tobias PV, Beynon AD. 1998. The mixed denti-
tion and associated skull fragments of a juvenile fossil homi-
nid from Sterkfontein, South Africa. *Am J Phys Anthropol*
106:425–465.
- Morwood MJ, Brown P, Jatmiko, Sutikna T, Saptomo EW, West-
away KE, Due RA, Roberts RG, Maeda T, Wasisto S, Djubian-
tono T. 2005. Further evidence for small-bodied hominins
from the Late Pleistocene of Flores, Indonesia. *Nature*
437:1012–1017.
- Ohman JC. 1986. The 1st rib of hominoids. *Am J Phys Anthropol*
70:209–229.
- Ohman JC, Krochta TJ, Lovejoy CO, Mensforth RP, Latimer B.
1997. Cortical bone distribution in the femoral neck of homi-
noids: implications for the locomotion of *Australopithecus
afarensis*. *Am J Phys Anthropol* 104:117–131.
- Olson TR. 1981. Basicranial morphology of the extant hominoids
and Pliocene hominids: the new material from the Hadar For-
mation, Ethiopia and its significance in early human evolu-
tion and taxonomy. In: Stringer CB, editor. *Aspects of human
evolution*. London: Taylor and Francis. p 99–128.
- Olson TR. 1985. Cranial morphology and systematics of the
Hadar Formation hominids and “*Australopithecus*” *africanus*.
In: Delson E, editor. *Ancestors: the hard evidence*. New York:
Liss. p 102–119.
- Organ JM, Ward CV. 2006. Contours of the hominoid lateral tib-
ial condyle with implications for *Australopithecus*. *J Hum
Evol* 51:113–127.
- Orr CM. 2005. Knuckle-walking anteater: a convergence test of
adaptation for purported knuckle-walking features of African
Hominidae. *Am J Phys Anthropol* 128:639–658.
- Partridge TC, Granger DE, Caffee MW, Clarke RJ. 2003. Lower
Pliocene hominid remains from Sterkfontein. *Science*
300:607–612.
- Pickford M, Senut B, Gommery D, Treil J. 2002. Bipedalism in
Ororin tugenensis revealed by its femora. *C R Palevol* 4:191–203.
- Pilbeam D. 1972. *The ascent of man*. New York: Macmillan.
- Pilbeam D. 1979. Recent finds and interpretations of Miocene
hominoids. *Annu Rev Anthropol* 8:333–352.
- Plavcan JM. 1993. Canine size and shape in male anthropoid
primates. *Am J Phys Anthropol* 92:201–216.
- Plavcan JM. 1998. Correlated response, competition, and female
canine size in primates. *Am J Phys Anthropol* 107:401–416.
- Plavcan JM. 2000. Inferring social behavior from sexual dimor-
phism in the fossil record. *J Hum Evol* 39:327–344.
- Plavcan JM. 2001. Sexual dimorphism in primate evolution.
Yrbk Phys Anthropol 44:25–53.
- Plavcan JM. 2003. Scaling relationships between craniofacial
sexual dimorphism and body mass dimorphism in primates:
implications for the fossil record. *Am J Phys Anthropol*
120:38–60.
- Plavcan JM, Lockwood CA, Kimbel WH, Lague MR, Harmon
EH. 2005. Sexual dimorphism in *Australopithecus afarensis*
revisited: how strong is the case for a human-like pattern of
dimorphism? *J Hum Evol* 48:313–320.
- Plavcan JM, van Schaik CP. 1997. Interpreting hominid behav-
ior on the basis of sexual dimorphism. *J Hum Evol* 32:345–
374.
- Plavcan JM, van Schaik CP, Kappeler PM. 1995. Competition,
coalitions and canine size in Primates. *J Hum Evol* 28:245–
276.
- Quade J, Levin N, Semaw S, Simpson S, Rogers M, Stout D.
2004. Paleoenvironments of the earliest toolmakers. *GSA Bull*
116:1529–1544.
- Raichlen D, Pontzer H, Sockol MD. 2008. The Laetoli footprints
and early hominin locomotor kinematics. *J Hum Evol* 54:112–
117.
- Rak Y. 1983. *The australopithecine face*. New York: Academic
Press.
- Rak Y. 1991. Lucy’s pelvic anatomy: its role in bipedal gait. *J
Hum Evol* 20:283–290.
- Rak Y, Ginzburg A, Geffen E. 2007. Gorilla-like anatomy on
Australopithecus afarensis mandibles suggests *Au. afarensis*
link to robust australopithecines. *Proc Natl Acad Sci USA*
104:6568–6572.
- Reed KE. 1997. Early hominid evolution and ecological change
through the African Plio-Pleistocene. *J Hum Evol* 32:289–322.
- Reed KE. 2008. Paleoeological patterns at the Hadar hominin
site, Afar Regional State, Ethiopia. *J Hum Evol* 54:743–768.
- Reid DJ, Dean MC. 2006. Variation in modern human enamel
formation times. *J Hum Evol* 50:329–346.
- Reid DJ, Schwartz GT, Dean C, Chandrasekera MS. 1998. A
histological reconstruction of dental development in the com-
mon chimpanzee, *Pan troglodytes*. *J Hum Evol* 35:427–448.
- Remane A. 1951. Die Zähne des *Meganthropus africanus*. *Z
Morphol Anthropol* 42:311–329.
- Remane A. 1954. Structure and relationships of *Meganthropus
africanus*. *Am J Phys Anthropol* 12:123–126.
- Renne P, Walter R, Verosub K, Sweitzer M, Aronson J. 1993.
New data from Hadar (Ethiopia) support orbitally tuned time
scale to 3.3 Ma. *Geophys Res Lett* 20:1067–1070.
- Renne PR, Swisher CC, Deino AL, Karner DB, Owens TL,
DePaolo DJ. 1998. Intercalibration of standards, absolute
ages and uncertainties in $^{40}\text{Ar}/^{39}\text{Ar}$ dating. *Chem Geol*
145:117–152.
- Reno RL, DeGusta D, Serrat MA, Meindl RS, White TD, Eck-
hardt RB, Kuperavage AJ, Galik K, Lovejoy CO. 2005a. Plio-
Pleistocene hominid limb proportions. *Curr Anthropol* 46:575–
588.
- Reno PL, Meindl RS, McCollum MA, Lovejoy CO. 2003. Sexual
dimorphism in *Australopithecus afarensis* was similar to that
of modern humans. *Proc Natl Acad Sci USA* 100:9404–9409.
- Reno PL, Meindl RS, McCollum MA, Lovejoy CO. 2005b. The
case is unchanged and remains robust: *Australopithecus afar-
ensis* exhibits only moderate skeletal dimorphism. A reply to
Plavcan et al. 2005. *J Hum Evol* 49:279–288.
- Richmond BG, Jungers WL. 1995. Size variation and sexual
dimorphism in *Australopithecus afarensis* and living homi-
noids. *J Hum Evol* 29:229–245.
- Richmond BG, Jungers WL. 2008. Orrorin tugenensis femoral
morphology and the evolution of hominin bipedalism. *Science*
319:1662–1665.
- Richmond BG, Strait DS. 2000. Evidence that humans evolved
from a knuckle-walking ancestor. *Nature* 404:382–385.
- Robbins LM. 1987. Hominid footprints from site G. In: Leakey
MD, Harris JM, editors. *Laetoli: a Pliocene site in Northern
Tanzania*. Oxford: Clarendon Press. p 497–502.
- Robinson JT. 1953. *Meganthropus, australopithecines and homi-
nids*. *Am J Phys Anthropol* 11:1–38.

- Robinson JT. 1954. Prehominid dentition and hominid evolution. *Evolution* 8:324–334.
- Robinson JT. 1956. The dentition of the Australopithecinae. *Transvaal Mus Mem* 9:1–179.
- Robinson JT. 1958. Cranial cresting patterns and their significance in the Hominoidea. *Am J Phys Anthropol* 16:397–428.
- Robinson JT. 1963. Adaptive radiation in the australopithecines and the origin of man. In: Howell FC, Bourliere F, editors. *African ecology and human evolution*. Chicago: Aldine. p 385–416.
- Robinson JT. 1972. Early hominid posture and locomotion. Chicago: The University of Chicago Press.
- Robson SL, Wood B. 2008. Hominin life history: reconstruction and evolution. *J Anat* 212:394–425.
- Ruff CB. 2009. Relative limb strength and locomotion in *Homo habilis*. *Am J Phys Anthropol* 138:90–100.
- Ryan AS, Johanson DC. 1989. Anterior dental microwear in *Australopithecus afarensis*: comparisons with human and non-human primates. *J Hum Evol* 18:235–268.
- Sanders WJ. 1998. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. *J Hum Evol* 34:249–302.
- Sarich VM. 1974. Just how old is the hominid line? *Yrbk Phys Anthropol* 17:98–113.
- Sarna-Wojcicki AM, Meyer CE, Roth PH, Brown FH. 1985. Ages of tuff beds at East African early hominid sites and sediments in the Gulf of Aden. *Nature* 313:306–308.
- Schultz AH. 1955. The position of the occipital condyles and of the face relative to the skull base in primates. *Am J Phys Anthropol* 13:97–120.
- Schwartz GT. 2000. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. *Am J Phys Anthropol* 111:221–244.
- Schwartz GT, Reid DJ, Dean MC. 2001. Developmental aspects of sexual dimorphism in hominoid canines. *Int J Primatol* 22:837–860.
- Scott JE, Stroik LK. 2006. Bootstrap tests of significance and the case for humanlike skeletal-size dimorphism in *Australopithecus afarensis*. *J Hum Evol* 51:422–428.
- Scott RS, Ungar PS, Bergstrom TS, Brown CA, Grine FE, Teaford MF, Walker A. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436:693–695.
- Semaw S, Renne R, Harris JWK, Feibel CS, Bernor RL, Fessaha N, Mowbray K. 1997. 2.5-Million-year-old stone tools from Gona, Ethiopia. *Nature* 385:333–335.
- Semaw S, Simpson SW, Quade J, Renne PR, Butler RF, McIntosh WC, Levin N, Dominguez-Rodrigo M, Rogers MJ. 2005. Early Pliocene hominids from Gona, Ethiopia. *Nature* 433:301–305.
- Senut B. 1983. Les hominides Plio-Pleistocènes: essai taxinomique et phylogénétique a partir de certains os longs. *Bull Mém Soc d'Anth Paris* 10:325–334.
- Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). *C R Acad Sci IIa* 332:137–144.
- Senut B, Tardieu C. 1985. Functional aspects of Plio-Pleistocene hominid limb bones: implications for taxonomy and phylogeny. In: Delson E, editor. *Ancestors: the hard evidence*. New York: Liss. p 193–201.
- Senyürek M. 1955. A note on the teeth of *Meganthropus africanus* (Weinert) from Tanganyika Territory. *Bulleten* 73:1–55.
- Sheffellbine SJ, Tardieu C, Carter DR. 2002. Development of the femoral bicondylar angle in hominid bipedalism. *Bone* 30:765–770.
- Silverman N, Richmond B, Wood BA. 2001. Testing the taxonomic integrity of *Australopithecus boisei sensu stricto*. *Am J Phys Anthropol* 115:167–178.
- Simons EL. 1976. Nature of transition in dental mechanism from pongids to hominids. *J Hum Evol* 5:511–528.
- Simpson SW, Quade J, Levin NE, Butler R, Dupont-Nivet G, Everett M, Semaw S. 2008. A female *Homo erectus* pelvis from Gona, Ethiopia. *Science* 322:1089–1092.
- Skelton RR, McHenry HM, Drawhorn GM. 1986. Phylogenetic analysis of early hominids. *Curr Anthropol* 27:21–43.
- Smith BH. 1986. Dental development in *Australopithecus* and early *Homo*. *Nature* 323:327–330.
- Smith BH. 1987. Reply to Maturational patterns in early hominids. *Nature* 328:674–675.
- Smith BH. 1989. Dental development as a measure of life history in Primates. *Evolution* 43:683–688.
- Smith BH. 1994. Patterns of dental development in *Homo*, *Australopithecus*, *Pan*, and *Gorilla*. *Am J Phys Anthropol* 94:307–325.
- Smith BH, Tompkins RL. 1995. Toward a life history of the Hominidae. *Annu Rev Anthropol* 24:257–279.
- Smith RJ, Gannon PJ, Smith BH. 1995. Ontogeny of australopithecines and early *Homo*: evidence from cranial capacity and dental eruption. *J Hum Evol* 29:155–168.
- Smith TM. 2006. Experimental determination of the periodicity of incremental features in enamel. *J Anat* 208:99–113.
- Smith TM. 2008. Incremental dental development: methods and applications in hominoid evolutionary studies. *J Hum Evol* 54:205–224.
- Smith TM, Olejniczak AJ, Reh S, Reid DJ, Hublin J-J. 2008. Brief communication: enamel thickness trends in the dental arcade of humans and chimpanzees. *Am J Phys Anthropol* 136:237–241.
- Smith TM, Reid DJ, Dean MC, Olejniczak AJ, Martin LB. 2007. Molar development in common chimpanzees (*Pan troglodytes*). *J Hum Evol* 52:201–216.
- Stern JT. 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis*. *Evol Anthropol* 9:113–133.
- Stern JT, Jungers WL. 1990. The capitular joint of the 1st rib in primates—a reevaluation of the proposed link to locomotion. *Am J Phys Anthropol* 82:431–439.
- Stern JT, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. *Am J Phys Anthropol* 60:279–317.
- Stern JT, Susman RL. 1991. “Total morphological pattern” versus the “magic trait”: conflicting approaches to the study of early hominid bipedalism. In: Senut B, Coppens Y, editors. *Origine(s) de la bipédie chez les Hominidés*. Paris: CNRS. p 99–111.
- Strait DS, Grine FE. 2004. Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. *J Hum Evol* 47:399–452.
- Strait DS, Weber GW, Neubauer S, Chalk J, Richmond BG, Lucas PW, Spencer MA, Schrein C, Dechow PC, Ross CF, Grosse IR, Wright BW, Constantino P, Wood BA, Lawn B, Hylander WL, Wang Q, Byron C, Slice DE, Smith AL. 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proc Natl Acad Sci USA* 106:2124–2129.
- Su DF, Harrison T. 2007. The paleoecology of the Upper Laetoli Beds at Laetoli; a reconsideration of the large mammal evidence. In: Bobe R, Alemseged Z, Behrensmeyer AK, editors. *Hominin environments in the East African Pliocene: an assessment of the faunal evidence*. Dordrecht: Springer. p 279–313.
- Su DF, Harrison T. 2008. Ecological implications of the relative rarity of fossil hominins at Laetoli. *J Hum Evol* 55:672–681.
- Susman RL. 1994. Fossil evidence for early hominid tool use. *Science* 265:1570–1573.
- Susman RL, Stern JT, Jungers WL. 1984. Arboreality and bipedality in the Hadar hominids. *Folia Primatol* 43:113–156.
- Susman RL, Stern JT, Jungers WL. 1985. Locomotor adaptations in the Hadar hominids. In: Delson E, editor. *Ancestors: the hard evidence*. New York: Liss. p 184–192.
- Suwa G. 1990. A comparative analysis of hominid dental remains from the Shungura and Usno Formations, Omo valley, Ethiopia. Ph.D. Dissertation, University of California, Berkeley.
- Suwa G, Asfaw B, Beyene Y, White TD, Katoh S, Nagaoka S, Nakaya H, Uzawa K, Renne P, WoldeGabriel G. 1997. The first skull of *Australopithecus boisei*. *Nature* 389:489–492.
- 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.

- Suwa G, Wood BA, White TD. 1994. Further analysis of mandibular molar crown and cusp areas in Pliocene and early Pleistocene hominids. *Am J Phys Anthropol* 93:407–426.
- Tague RG, Lovejoy CO. 1986. The obstetric pelvis of A.L. 288–1 (Lucy). *J Hum Evol* 15:237–255.
- Taieb M, Coppens Y, Johanson DC, Kalb J. 1972. Dépôts sédimentaires et faunes du Plio-Pléistocène de la basse vallée de l’Awash (Afar central, Éthiopie). *C R Acad Sci D* 275:819–822.
- Taieb M, Johanson DC, Coppens Y. 1975. Expédition internationale de l’Afar, Éthiopie (3^{ème} campagne 1974) découverte d’Hominidés Plio-Pléistocènes à Hadar. *C R Acad Sci* 281:1297–1300.
- Taieb M, Johanson DC, Coppens Y, Aronson JL. 1976. Geological and palaeontological background of Hadar hominid site, Afar, Ethiopia. *Nature* 260:289–293.
- Taieb M, Johanson DC, Coppens Y, Bonnefille R, Kalb JE. 1974. Découverte d’Hominidés dans les séries Plio-pléistocènes d’Hadar (Bassin de l’Awash; Afar, Éthiopie). *C R Acad Sci D* 279:735–738.
- Taieb M, Tiercelin J-J. 1979. Sédimentation Pliocène et paléoenvironnements de rift: exemple de la formation à Hominidés d’Hadar (Afar, Éthiopie). *Bull Soc Geol Fr* 21:243–253.
- Tardieu C. 1981. Morpho-functional analysis of the articular surfaces of the knee-joint in primates. In: Chiarelli AB, Corruccini, editors. *Primate evolutionary biology*. Berlin: Springer Verlag. p 68–80.
- Tardieu C. 1983. L’articulation du genou des primates catarhiens et hominidés fossiles: implications phylogénétique et taxinomique. *Bull Mem Soc Anthropol Paris* 10:355–372.
- Tardieu C, Damsin JP. 1997. Evolution of the angle of obliquity of the femoral diaphysis during growth—correlations. *Surg Radiol Anat* 19:91–97.
- Tardieu C, Glard Y, Garron E, Boulay C, Louve J-L, Dutour O, Boetsch G, Bollini G. 2006. Relationship between formation of the femoral bicondylar angle and trochlear shape: independence of diaphyseal and epiphyseal growth. *Am J Phys Anthropol* 130:491–500.
- Tattersall I, Eldredge N. 1977. Fact, theory, and fantasy in human paleontology. *Am Sci* 65:204–211.
- Teaford MF, Ungar PS. 2000. Diet and the evolution of the earliest human ancestors. *PNAS* 97:13506–13511.
- Terhune C, Kimbel W, Lockwood C. 2007. Variation and diversity in *Homo erectus*: a 3D geometric morphometric analysis of the temporal bone. *J Hum Evol* 53:41–60.
- Tiercelin J-J. 1986. The Pliocene Hadar Formation, Afar depression of Ethiopia. In: Frostick LE, Renaut RW, Reid I, Tiercelin J-J, editors. *Sedimentation in the African rifts*. Oxford: Blackwell Scientific Publications. p 221–240.
- Tobias PV. 1967. The cranium and maxillary dentition of *Australopithecus (Zinjanthropus) boisei*. Olduvai Gorge, Vol. 2. London: Cambridge University Press.
- Tobias PV. 1973. New developments in hominid paleontology in South and East Africa. *Annu Rev Anthropol* 2:311–334.
- Tobias PV. 1976. African hominids: dating and phylogeny. In: Isaac G, McCown, ER, editors. *Human origins: Louis Leakey and the East African evidence*. Menlo Park, CA: W.A. Benjamin. p 377–422.
- Tobias PV. 1978. The South African australopithecines in time and hominid phylogeny, with special reference to the dating and affinities of the Taung skull. In: Jolly CJ, editor. *Early Hominids of Africa*. London: Duckworth. p 45–84.
- Tobias PV. 1980b. “*Australopithecus afarensis*” and *A. africanus*: critique and an alternative hypothesis. *Palaeont Afr* 23:1–17.
- Tobias PV, Falk D. 1988. Evidence for a dual pattern of cranial venous sinuses on the endocranial cast of Taung (*Australopithecus africanus*). *Am J Phys Anthropol* 76:309–312.
- Tocheri MW, Orr CM, Jacofsky MC, Marzke MW. 2008. The evolutionary history of the hominin hand since the last common ancestor of *Pan* and *Homo*. *J Anat* 212:544–562.
- Tocheri MW, Orr CM, Larson SG, Sutikna T, Jatmiko, Saptomo EW, Due RA, Djubiantono T, Morwood MJ, Jungers WL. 2007. The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science* 317:1743–1745.
- Tuttle RH. 1967. Knuckle-walking and the evolution of hominoid hands. *Am J Phys Anthropol* 26:171–206.
- Tuttle RH. 1981. Evolution of hominid bipedalism with prehensile capabilities. *Philos Trans R Soc Lond B Biol Sci* 292:89–94.
- Tuttle RH. 1987. Kinesiological inferences and evolutionary implications from laetoli bipedal trails G-1, G-2/3, and A. In: Leakey MD, Harris JM, editors. *Laetoli: a Pliocene site in Northern Tanzania*. Oxford: Oxford University Press. p 503–523.
- Tuttle RH, Webb DM, Baksh M. 1991. Laetoli toes and *Australopithecus afarensis*. *Hum Evol* 6:193–200.
- Ungar P. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. *J Hum Evol* 46:605–622.
- Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS One* 3:1–6.
- Vrba ES. 1975. Some evidence of chronology and paleoecology of Sterkfontein, Swartkrans and Kromdraai from fossil Bovidae. *Nature* 254:301–304.
- Walker A, Leakey RE. 1988. The evolution of *Australopithecus boisei*. In: Grine FE, editor. *Evolutionary history of the “Robust” Australopithecines*. New York: Aldine de Gruyter. p 247–258.
- Walker A, Leakey RE, Harris JM, Brown FH. 1986. 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature* 322:517–522.
- Walter RC. 1994. Age of Lucy and the first family: single-crystal ⁴⁰Ar/³⁹Ar dating of the Denen Dora and lower Kada Hadar members of the Hadar Formation, Ethiopia. *Geology* 22:6–10.
- Walter RC, Aronson JA. 1982. Revisions of K/Ar ages for the Hadar hominid site, Ethiopia. *Nature* 296:122–127.
- Walter RC, Aronson JA. 1993. Age and source of the Sidi Hakoma Tuff, Hadar Formation, Ethiopia. *J Hum Evol* 25:229–240.
- Ward CV. 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? *Yrbk Phys Anthropol* 45:185–215.
- Ward CV, Leakey MG, Brown B, Brown F, Harris J, Walker A. 1999a. South Turkwel: a new Pliocene hominid site in Kenya. *J Hum Evol* 36:69–95.
- Ward CV, Leakey MG, Walker A. 1999b. The new hominid species *Australopithecus anamensis*. *Evol Anthropol* 7:197–205.
- Ward CV, Leakey MG, Walker A. 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *J Hum Evol* 41:255–368.
- Ward SC, Hill A. 1987. Pliocene partial hominid mandible from Tabarin, Baringo, Kenya. *Am J Phys Anthropol* 72:21–37.
- Ward SC, Johanson DC, Coppens Y. 1982. Subocclusal morphology and alveolar process relationships of hominid gnathic elements from the Hadar Formation: 1974–1977 collections. *Am J Phys Anthropol* 57:605–630.
- Weidenreich F. 1943. The skull of *Sinanthropus pekinensis*. *Palaeontol Sin New Ser D* 10:1–484.
- Weinert H. 1950. Über die neuen Vor- und Frühmenschenfunde aus Afrika, Java, Cina und Frankreich. *Z Morphol Anthropol* 42:113–148.
- White TD. 1977a. The anterior mandibular corpus of early African Hominidae: functional significance of shape and size. Ph.D. Dissertation, University of Michigan, Ann Arbor.
- White TD. 1977b. New fossil hominids from Laetoli, Tanzania. *Am J Phys Anthropol* 46:197–230.
- White TD. 1980a. Evolutionary implications of Pliocene hominid footprints. *Science* 208:175–176.
- White TD. 1980b. Additional fossil hominids from Laetoli, Tanzania: 1976–1979 specimens. *Am J Phys Anthropol* 53:487–504.
- White TD. 1981. Primitive hominid canine from Tanzania. *Science* 213:348–349.
- White TD. 1985. The hominids of Hadar and Laetoli: an element-by-element comparison of the dental samples. In: Delson E, editor. *Ancestors: the hard evidence*. New York: 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. 1987. Hominid footprints at Laetoli: facts and interpretations. *Am J Phys Anthropol* 72:485–514.
- White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371:306–312.
- 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, Simpson S, Asfaw B. 2000. Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *Am J Phys Anthropol* 111:45–68.
- White TD, WoldeGabriel G, Asfaw B, Ambrose S, Beyene Y, Bernor RL, Boisserie JR, Currie B, Gilbert H, Haile-Selassie Y, Hart WK, Hlusko LJ, Howell FC, Kono RT, Lehmann T, Louchart A, Lovejoy CO, Renne PR, Saegusa H, Vrba E, Wesselman H, Suwa G. 2006. Asa Issie, Aramis and the origin of *Australopithecus*. *Nature* 440:883–889.
- Wolpoff MH. 1983. Australopithecines: the unwanted ancestors. In: Reichs K, editor. *Hominid origins: inquiries past and present*. Lanham, MD: University Press of the Americas, p 109–126.
- Wood B. 1993. Early *Homo*: how many species? In: Kimbel WH, Martin LB, editors. *Species, species concepts, and primate evolution*. New York: Plenum Press. p 485–522.
- Wood BA. 1976. Remains attributable to *Homo* in the East Rudolf succession. In: Coppens Y, Howell FC, Isaac GL, Leakey REF, editors. *Earliest man and environments in the Lake Rudolf Basin*. Chicago: University of Chicago Press. p 490–506.
- Wood BA. 1988. Are ‘robust’ australopithecines a monophyletic group? In: Grine FE, editor. *Evolutionary history of the “Robust” Australopithecines*. New York: Aldine de Gruyter. p 269–284.
- Wood BA, Abbott SA. 1983. Mandibular molars, crown area measurements and morphological traits. *J Anat* 136:197–219.
- Wood BA, Abbott SA, Uytterschaut H. 1988. Analysis of the dental morphology of Plio-Pleistocene hominids 4: mandibular post-canine root morphology. *J Anat* 156:107–139.
- Wood BA, Chamberlain AT. 1986. *Australopithecus*: grade or clade? In: Wood B, Martin L, Andrews P, editors. *Major topics in primate and human evolution*. Cambridge: Cambridge University Press. p 220–248.
- Yemane T. 1997. Stratigraphy and sedimentology of the Hadar Formation. PhD. dissertation, Iowa State University.