The Skull of Australopithecus Afarensis

William H. Kimbel
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With a contribution on the brain endocast by

Ralph L. Holloway and Michael S. Yuan

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We dedicate this work to the memory of four dear friends:

Meles Kassa

Dato Ahmedu

Wubishet Fantu

Dato Adan

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W. H. K.
Tempe
Y. R.
Tel Aviv
D. C. J.
Tempe

Contents

The Skull of *Australopithecus afarensis*

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1

Background

Australopithecus afarensis is a fossil hominin species known from at least four East African Rift Valley sites ranging from northern Ethiopia in the north to northern Tanzania in the south and bridging the time period between approximately 3.6 and 3.0 million years ago (Ma) (see Figure 1.1).[1] First identified in the late 1970s as the bipedal but craniodentally apelike rootstock from which later *Australopithecus* and *Homo* evolved (Johanson et al., 1978; Johanson and White, 1979), *A. afarensis* constituted the first substantial record of unequivocal human ancestors older than 3.0 million years (Myr). An array of more recently made discoveries have placed *A. afarensis* in a pivotal position in early hominin phylogeny, bracketed in time between, on the one hand, two temporally successive species, *A. anamensis* and *Ardipithecus ramidus*, that jointly extend the hominin record back to 4.4 Ma (M. Leakey et al., 1995, 1998; White et al., 1994, 1995), and, on the other hand, the earliest strong (stratigraphic) evidence for hominin lineage diversification, with the first known records of *A. africanus* (ca. 2.7 Ma) in southern Africa, and of *A. aethiopicus* (ca. 2.7 Ma) and *A. garhi* (2.5 Ma) in eastern Africa (Walker et al., 1986; Asfaw et al., 1999).[2] The task of sorting out the relationships among all of these species hinges on the interpretation of *A. afarensis* itself, from its alpha taxonomy and phylogenetic role to its pattern of evolution over time. A prerequisite to achieving this goal is a more complete knowledge of the *A. afarensis* fossil record, narrowing gaps in our knowledge of anatomy and variation, as well as of distributions in space and time.

On sample size alone, *A. afarensis* is the best-known hominin species in the eastern African fossil record. The vast majority of fossils in the *A. afarensis* hypodigm, some 360 specimens, or approximately 90% of the total, have been recovered at the Hadar site, from the 200+ meter sequence of silts, sands, and clays that comprise the Hadar Formation, which is exposed along the drainages of the Awash River in the Afar Depression of northern Ethiopia (Johanson et al., 1982a; Kimbel et al., 1994) (Figure 1.2). The Hadar sample of *A. afarensis* spans 3.4 to 3.0 Ma and includes the iconic partial skeleton known as

Distribution of *Australopithecus afarensis*

Ma	Hadar	Middle Awash (Maka)	Koobi Fora	Laetoli
3.0	Kada Hadar			
3.2	Denen Dora			
			Tulu Bor	
3.4	Sidi Hakoma	Matabaietu		
3.6				Upper Laetolil
3.8				
4.0				

Figure 1.1. Temporal and geographic distribution in Africa of *Australopithecus afarensis*. Ma = millions of years ago. Geographic sites run from north to south across the top; the entries for temporal distribution are the *A. afarensis*-bearing stratigraphic units represented at each site.

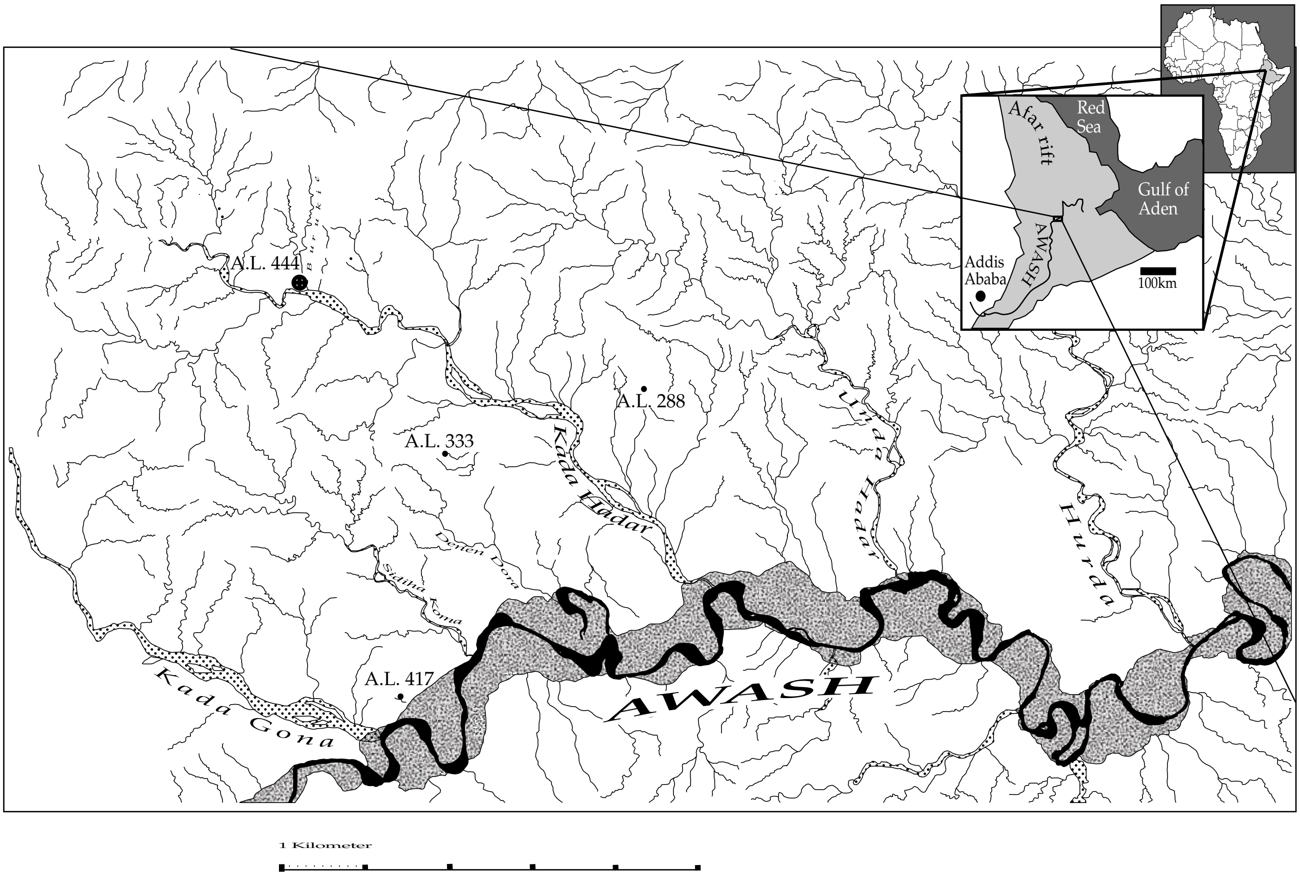


Figure 1.2. Map of the Hadar site showing geographic position of Afar Locality (A.L.) 444 and other key hominin-bearing localities. Base map courtesy of Dr. Gerald Eck.

"Lucy," as well as a collection of some 250 cranial, dental, and postcranial specimens—possibly representing a single biological population—from a hillside outcrop called Afar Locality (A.L.) 333. Yet despite (or perhaps because of) the unusual richness of the Hadar hominin sample, the taxonomy of *A. afarensis* has been debated ever since the species was first described.[3]

After comparative studies conducted in 1977–1978 first established the taxonomic hypothesis that the Hadar specimens were conspecific with diagnostic jaws and teeth from 3.5 to 3.7 Myr-old sediments at Laetoli, Tanzania (Johanson et al., 1978; Johanson and White, 1979), paleoanthropological reaction featured an alternative hypothesis that the *A. afarensis* hypodigm included more than one hominin species (R. Leakey and Walker, 1980; Olson, 1981, 1985; Coppens, 1983; Schmid, 1983; Senut, 1983; Tardieu, 1983; Zihlman, 1985; Shipman, 1986; McKee, 1989). Some critics focused on the high level of size or morphological variation (or both) in the Hadar sample, while others saw taxonomic differences between the temporally and geographically disjunct Hadar and Laetoli site samples. Still others decried the absence of a complete skull in the otherwise comprehensive hominin sample. Although the latter void was filled temporarily by a composite reconstruction that incorporated a dozen adult specimens from Hadar, mostly from the A.L. 333 sample (Kimbel et al., 1984; Kimbel and White, 1988a), large gaps in knowledge of *A. afarensis* adult skull morphology persisted (partly remedied by the 1981 discovery in the Middle Awash of the 3.8 Myr-old Belohdelie frontal fragment [Clark et al., 1984] attributed by Asfaw [1987] to *A.* aff. *afarensis*).

The 1980s witnessed intensive testing of the taxonomic hypothesis of Johanson and White (1979), which featured detailed investigations of quantitative and morphological variation in the *A. afarensis* hypodigm (Blumenberg and Lloyd, 1983; Blumenberg, 1985; White, 1985; McHenry, 1986, 1991; Cole and Smith, 1987; Kimbel and White, 1988b; Lovejoy et al., 1989). While all of these studies found *A. afarensis* to be characterized by moderate to very high levels of size variation, none of them found a strong statistical basis for dividing the sample taxonomically. Thus, out of this body of work developed the paleoanthropological consensus, which persists to the present day, that

Table 1.1 ***Australopithecus afarensis*** **Specimens from the 1990–1994 and 1999–2001 Hadar Field Seasons**

Locality/Specimen	Year	Discoverer	Identification	Stratigraphic Position
A.L. 58-22b	1993	Alemayehu Asfaw	Right maxilla frag. I^1–I^2 roots	Shu-DD-2
A.L. 125-11	1990	Alemayehu Asfaw	Left maxilla frag. P^3–M^1 frags.	SH, 2 m > SHT
A.L. 137-50	1990	Tim White	Right humerus	SH, 5 m > SHT
A.L. 152-2	1993	Alemayehu Asfaw	Right proximal femur	SH, 10 m < KMT
A.L. 176-35	1992	Abdu Mohamed	Left lower P4	DD-1
A.L. 198-22	1993	Dato Adan	Left mandible frag. M1–M2 f.	SH, 5.5 m < SH-2s
A.L. 207-17	1999	Mohamed Hussein	Right lower M3	SH, 1 m < TT-4
A.L. 224-9	1993	Alemayehu Asfaw	Occipital frag.	SH, 13 m < SH-2s
A.L. 225-8	1990	Dato Ahmedu	Left mandible frag. M1–M3	SH, 10 m > SHT
A.L. 228-2	1990	Mohamed Gofre	Left mandible frag. M1, isol. P4	SH-3s
A.L. 237-3	1993	Zelalem Assefa	Left mandible frag.	SH, 1.5 > SHT
A.L. 293-3	1992	Dato Adan	Upper central I	DD, 16 m > TT-5
A.L. 309-8	1993	Meles Kassa	Upper molar frag.	DD-3s
A.L. 315-22	1990	Alemayehu Asfaw	Right mandible frag., P3, M1	DD, 7.5 m < DD-3s
A.L. 330-5	1993	Alemayehu Asfaw	Mandible LC f., RP4–M3	SH, 4 m < TT-4
A.L. 330-6	1993	Alemayehu Asfaw	Right proximal tibia	DD-3s
A.L. 330-7	1999	Hamadu Meter	Right mandible frag. P4, M1	SH, 4 m < TT-4
A.L. 333-140	1993	Bill Kimbel	Subadult right distal femur	DD-2
A.L. 333-141	1993	Meles Kassa	Right metacarpal V	DD-2
A.L. 333-142	1994	Team	Subadult right proximal femur	DD-2
A.L. 333-144	1994	Team	Proximal frag. metacarpal III	DD-2
A.L. 333-145	1994	Team	Pedal proximal phalanx II	DD-2
A.L. 333-147	1994	Team	Right talus	DD-2
A.L. 333-148	1994	Team	Head intermed. hand phalanx	DD-2
A.L. 333-149	1994	Team	Intermed. hand phalanx	DD-2
A.L. 333-150	1994	Team	Intermed. hand phalanx	DD-2
A.L. 333-152	1994	Team	Thoracic vertebra	DD-2
A.L. 333-153	2000	Team	Proximal frag. left metacarpal III	DD-2
A.L. 333-154	2000	Team	Proximal foot phalanx	DD-2
A.L. 333-155	2000	Team	Rib fragment	DD-2
A.L. 333-156	2000	Team	Rib fragment	DD-2
A.L. 333-157	2000	Team	Proximal frag. left metatarsal III	DD-2
A.L. 333-158	2000	Team	Prox. frag. prox. foot phalanx I	DD-2
A.L. 333-159	2000	Team	Terminal phalanx	DD-2
A.L. 333-160	2000	Team	Left metatarsal IV	DD-2
A.L. 333-161	2000	Team	Rib fragment	DD-2
A.L. 333-162	1994	Team	Left proximal femur shaft	DD-2
A.L. 333-163	2001	Team	Proximal right MT II	DD-2
A.L. 333-164	2001	Team	Rib fragment	DD-2
A.L. 333-165	2001	Team	Tooth crown fragment	DD-2
A.L. 333-166	2001	Team	Tooth crown fragment	DD-2
A.L. 333n-1	1999	Edris Ahmed	Right juvenile mandible, dm2	DD-2
A.L. 333n-2	2000	Abrahim Nore	Distal frag. hand phalanx	DD-2
A.L. 413-1	1990	Alemayehu Asfaw	Right maxilla frag., C–M^3 roots	DD, 13 m > TT-5
A.L. 417-1a–d	1990–1993, 1999	Dato Adan, team	a: Left mandible frag. C–M3 b: Right mandible frag. M2–M3 c: Basioccipital, basisphenoid, right alisphenoid d: Maxilla, RI^2–M^3, LC–M^3	SH, 33 m > SHT
A.L. 418-1	1990	Dato Ahmedu	Left mandible frag. M2	SH, 31 m > SHT
A.L. 423-1	1990	Dato Adan	Right maxilla frag., P^4–M^1	SH, 4 m < KMT
A.L. 427-1a–c	1990	Ray Bernor, team	a: Maxilla LM^3 f. b: Occipital frag. c: Molar frag.	DD/KH, 0.5 m > DD-3s
A.L. 432-1	1990	Alemayehu Asfaw	Right mandible frag. M2–M3 ff.	DD-3s

(*continued*)

Table 1.1 (*continued*)

Locality/Specimen	Year	Discoverer	Identification	Stratigraphic Position
A.L. 433-1a–c	1990	Dato Adan, A. Asfaw	a: Right mandible frag. P4 f.	DD/KH, 1 m > DD-3s
			b: Left mandible frag.	
			c: Molar root frag.	
A.L. 436-1	1990	Dato Ahmedu	Right mandible frag., M2–M3 roots	SH, SH-2s
A.L. 437-1	1992	Dato Ahmedu	Left mandible frag., P4–M3	KH, 17 m < BKT-2
A.L. 437-2a–c	1992	Zelalem Assefa	a: Mandible, LI1–C frags., RI1–I2 frags., RM2–3 frags.	KH, 17 m < BKT-2
			b, c: Isol. LP3, M2 frags.	
A.L. 438-1a–v	1992	Don Johanson, team	a: Left ulna	KH, 10–12 m < BKT-2
			b: Frontal frag.	
			c: Right proximal humerus shaft	
			d: Left metacarpal III	
			e: Left metacarpal II	
			f: Right metacarpal II	
			g: Right mandible w/ramus	
			h: Right lower M1	
			i: Right lower M3	
			j: Right lower I1	
			k: Right P^4 frag.	
			l: Proximal right radius frag.	
			m: Shaft frag. right ulna	
			n: Humeral shaft frag.	
			o: Humeral shaft frag.	
			q: Upper molar root frag.	
			s: Maxilla frag.	
			u: Left lower molar root	
			v: Clavicle frag.	
A.L. 438-2	1992	Team	Right lower P3	
A.L. 438-3	1992	Team	Left lower P3 frag.	
A.L. 438-4	1992	Team	Proximal hand phalanx	
A.L. 439-1	1992	Zelalem Assefa	Occipital	KH, 17.5 m < BKT-2
A.L. 440-1	1992	Dato Ahmedu, team	Right mandible frag. C, P3; isol. LI1, C, P4–M2	KH, 7.5 m < BKT-2
A.L. 441-1	1992	Abdu Mohamed	Molar frag.	DD, 5 m > TT-5
A.L. 442-1	1992	Dato Ahmedu	Right maxilla, M2	DD, 5 m > TT-5
A.L. 443-1	1993	Hamadu Meter	Left mandible frag., P4, M2	SH lower
A.L. 444-1a, b	1992	Yoel Rak	a: Right occipital frag.	KH, 12 m < BKT-2
			b: Left occipital frag.	
A.L. 444-2a–h	1992	Yoel Rak, team	a: Maxilla, RI^1, C, P^4–M^3 LI^1, C–M^3	KH, 10.5 m < BKT-2
			b: Mandible, I ff., RC, P4–M1	
			c: Right zygomatic	
			d: Frontal w/right parietal frag.	
			e: Left parietal	
			f: Occipital + right and left temporals	
			g: Right parietal fragment	
			h: Nasal bones	
A.L. 444-3	1992	Team	Right lunate	
A.L. 444-4	1992	Team	Manual proximal phalanx	
A.L. 444-5	1992	Team	Phalanx frag.	
A.L. 444-6	1992	Team	Right lower dm2 frag.	
A.L. 444-7	1992	Team	Last lumbar vertebra body	
A.L. 444-8	1992	Team	Thoracic vertebra spine	

(*continued*)

Table 1.1 (*continued*)

Locality/Specimen	Year	Discoverer	Identification	Stratigraphic Position
A.L. 444-9	1992	Team	Cervical vertebra frag.	
A.L. 444-10	1992	Team	Thoracic vertebra frag.	
A.L. 444-11	1992	Team	Thoracic vertebra frag.	
A.L. 444-12	1992	Team	Thoracic or cervical vertebra frag.	
A.L. 444-13	1992	Team	Left humerus shaft frag.	
A.L. 444-14	1992	Team	Left humeral epiphysis frag.	
A.L. 444-15	1992	Team	Right distal humerus shaft frag.	
A.L. 444-16	2000	Elizabeth Harmon	Frag. $LM_{1/2}$	
A.L. 444-29	1992	Team	Lower deciduous central incisor	
A.L. 444-30	1992	Team	Lower molar frag.	
A.L. 452-18	1999	Zeresenay Alemseged	Molar frag.	KH, 9 m < BKT-2
A.L. 457-2	1994	Abdu Mohamed	Right parietal fragment	KH, 17 m < BKT-2
A.L. 462-7	1999	Hamadu Mohamed	Left lower M3	KH, 16.1 M < BKT-2
A.L. 465-5	1993	Hamadu Meter	Lower molar frag.	SH, 1.5 m > SHT
A.L. 466-1	1993	Hamadu Meter	Maxillary M^2–M^3 ff.	SH, 5 m < SH-3s
A.L. 486-1	1993	Meles Kassa	Left maxilla, I^1–I^2, P^3–M^3	DD-3s
A.L. 487-1a–g	1993	Abrahim Nore, team	a: Right mandible frag., M3 f. b: Two left mandible frags., P3–M3 roots c: Left maxilla frag., C d: Right maxilla frag., P^3–P^4 ff. e: Left palate frag. f: Lower LC g: Lower RC	DD, 2.4 m < KHT
A.L. 545-3	1993	Don Johanson	Right distal tibia	DD, 12.5 m < DD-3s
A.L. 557-1	1993	Dato Adan	Maxillary molar	KH “upper”
A.L. 582-1	1993	Meles Kassa	Mandible frag., I1, LP4–M1, RP3–M1 ff.	DD, 4.6 m < CC
A.L. 604-1	1993	Zelalem Assefa	Left mandible ramus frag.	Shu–DD-2
A.L. 620-1	1994	Abrahim Nore	Left mandible, M3	DD-2
A.L. 651-1	1990	Dato Ahmedu	Left maxillary frag., P^3–M^3	SH, 4 m < SH-2s
A.L. 655-1	1994	Million H/Michael	Left lower P3 w/roots	SH, 5.4 m < TT-4
A.L. 660-1	1994	Ali Samla	Lower LM2 frag.	SH-1
A.L. 697-1	1994	Dato Adan	Molar fragment	SH-1
A.L. 699-1	1994	Abrahim Nore	Right lower P4 frag.	DD-3s
A.L. 701-1	1994	Dato Adan	Left frontoparietal frag.	DD-3u/KH-1
A.L. 724-1	1999	Hamadu Meter	Proximal phalanx	KH, 16.7 m < BKT-2
A.L. 724-3	1999	Hamadu Meter	Proximal phalanx	KH, ~ 15 m < BKT-2
A.L. 729-1	1999	Charles Lockwood	Mandible	KH, 6.2 m < BKT-2
A.L. 762-1	1999	Maumin Alahandu	Right lower M3 frag.	DD, 2.75 m > TT-4
A.L. 763-1	1999	Hamadu Meter	Left upper canine with root	DD, 4.75 m < KHT
A.L. 766-1	1999	Abrahim Nore	Mandible symphysis frag.	DD, 4 m < KHT
A.L. 769-1	1999	Dato Adan	Right distal humerus frag.	SH, 5.7 m < SH-2s
A.L. 770-1a, b	1999	Nore Ali, Mohamed Ahamedin	a: Left maxilla frag. b: Right maxilla frag.	SH, 0.75–2 m > SHT
A.L. 772-1	1999	Charles Lockwood	Right lower dm2 frag.	DD, 1.5 m < KHT
A.L. 777-1	1999	Hamadu Meter	Right lower dm1 frag.	SH, 10.25 m < SH-2s
A.L. 822-1	2000	Dato Adan	Partial skull	KH, 5 m < BKT-1
A.L. 827-1	2000	Dato Adan	Femur	KH, 2 m > BKT-1
A.L. 922-1	2000	Dato Adan	Maxilla, frag. LI^1–M^1, M^2–M^3; frag. RI^1–M^3	KH, ~11m > BKT-1
A.L. 996-1	2001	Hamadu Meter	Left mandible frag., P4–M1	KH, ~11m > BKT-1
A.L. 1017-1	2001	Team	Premolar fragments	KH, ~11m > BKT-1

SH, Sidi Hakoma member; DD, Denen Dora member; KH, Kada Hadar member; >, above; <, below.

Table 1.2. Distribution of 1990–2001 Hadar Hominins by Skeletal Part (n = 112)

	Postcranial							
Skeleton[a]	Upper	Lower	Indet.	Axial	Skull	Cranium	Mandible	Teeth[b]
438-1	137-50	152-2	333-148	333-152	417-1	58-22b	198-22	176-35
	333-141	330-6	333-159	333-155	444-2	125-11	225-8	207-17
	333-144	333-140	444-5	333-156	487-1	224-9	228-2	293-3
	333-149	333-142	724-1	333-161	822-1	413-1	237-3	309-8
	333-150	333-145	724-3	333-164		423-1	315-22	333-165
	333-153	333-147		444-7		427-1	330-5	333-166
	333n-2	333-154		444-8		439-1	330-7	438-2
	438-4	333-157		444-9		442-1	333n-1	438-3
	444-3	333-158		444-10		444-1	418-1	441-1
	444-4	333-160		444-11		457-2	432-1	444-6
	444-13	333-162		444-12		486-1	433-1	444-16
	444-14	333-163				651-1	436-1	444-29
	444-15	545-3				701-1	437-1	444-30
		827-1				770-1	437-2	452-18
						922-1	440-1	462-7
							443-1	465-5
							582-1	466-1
							604-1	557-1
							620-1	655-1
							729-1	660-1
							766-1	697-1
							996-1	699-1
								762-1
								763-1
								772-1
								777-1
								1017-1
Totals:								
1	13	14	5	11	4	15	22	27

[a]Includes associated postcranial, mandible, and cranial elements.

[b]Specimens listed comprise isolated teeth only. Specimens listed under Cranium and Mandible may also include teeth.

A. afarensis is, indeed, both biologically and statistically speaking, a "good" species.

At the same time, the first round of numerical cladistic analyses in paleoanthropology produced ambiguous results about the relationships of *A. afarensis* to subsequent hominin species (Skelton et al., 1986; Wood and Chamberlain, 1986, 1987; Chamberlain and Wood, 1987). Johanson and White (1979) had proposed that the southern African species *A. africanus* was phylogenetically linked exclusively to *A. robustus* and *A. boisei* by a series of shared-derived craniodental characters related to heavy mastication (see also White et al., 1981; Rak, 1983; Kimbel et al., 1984). While almost all of these early numerical cladistic analyses supported the basal position of *A. afarensis* relative to *A. africanus*, opinion divided on several mutually exclusive phylogenetic hypotheses:

1. *A. africanus* is the plesiomorphic sister taxon to an *A. robustus* + *A. boisei* clade (indicated chiefly by the teeth, jaws and face—this is the Johanson and White [1979] hypothesis; see Chamberlain and Wood, 1987).
2. *A. afarensis* is the plesiomorphic sister taxon to an *A. robustus* + *A. boisei* clade, with a separate *A. africanus* + *Homo* clade (as suggested by some aspects of calvarial morphology and cranial venous outflow systems; originally proposed by Olson, 1981, 1985, and Falk and Conroy, 1983; see Wood and Chamberlain, 1986).
3. *A. africanus* is the plesiomorphic sister taxon to a clade comprising *A. robustus* + *A. boisei* and *Homo habilis* (based on derived character states shared by these taxa, such as fixation of the large P_3 metaconid, but for which *A. afarensis* retained the primitive state [see list in Kimbel et al., 1984: 375]; Skelton et al., 1986).

Combining plesiomorphic characters shared with *A. afarensis* but *not* with *A. africanus*, and derived characters shared uniquely with *A. robustus* and *A. boisei*, the 2.5

Myr-old KNM-WT 17000 cranium of *A. aethiopicus*, described by Walker et al. in 1986, showed that neither the Johanson and White (1979) hypothesis nor the Skelton et al. (1986) hypothesis was likely to be true (e.g., Kimbel et al., 1988). This specimen also underscored the likelihood that the early evolution of the hominin skull was characterized by significant homoplasy, the nature and degree of which depended on the phylogenetic role accorded *A. africanus* (which, in turn, was affected by growing doubts concerning its taxonomic unity; see, e.g., Clarke, 1988; Kimbel and White, 1988b) and on whether southern and eastern "robust" *Australopithecus* species constituted a monophyletic or polyphyletic assemblage (see contributions in Grine, 1988; Skelton and McHenry, 1992). Thus, at the close of the 1980s, the state of early hominin taxonomy and phylogeny was unsettled.

Beginning in 1990, renewed fieldwork in Ethiopia, both at Hadar and in the Middle Awash, sought to address these unresolved issues with new fossil data recovered in refined chronostratigraphic and paleoenvironmental contexts (White et al., 1993; Kimbel et al., 1994). A major goal of Hadar fieldwork was to augment the *A. afarensis* sample, in part by following its record up-section through scrutiny of large tracts of previously unsurveyed outcrops sampling the upper strata of the Kada Hadar Member, the youngest of the four currently recognized members of the Hadar Formation (Figure 1.3). These strata are now dated to <3.18 Ma, the $^{40}Ar/^{39}Ar$ age obtained for the Kada Hadar Tuff (KHT) that marks the base of the Kada Hadar Member (Walter, 1994). The goal of exploring these particular sediments was closing the chronological gap between *A. afarensis* and the earliest species of the post-3.0-Myr lineage diversification, *A. africanus* and *A. aethiopicus*, which would potentially clarify the abovementioned uncertainties about hominin phylogeny.

The upper sediments of the Kada Hadar Member were essentially a blank at the cessation of fieldwork in 1976–1977, but they postdated the youngest of the *A. afarensis* specimens then known ("Lucy"—A.L. 288-1; see Figure 1.3). Before 1992, when systematic paleontological surveying of these young sediments began, only 2 of 28 (ca. 7%) hominin localities were known from sediments stratigraphically above KHT; in contrast, 16 of 47 (ca. 34%) new hominin-bearing localities logged during the 1990s lie within the Kada Hadar Member. Discoveries made during a 10-day period in 1992 at five localities in the upper reaches of the main Kada Hadar tributary (A.L. 437, 438, 439, 440, and 444) nearly doubled the temporal range of *A. afarensis* in the Hadar Formation from ca. 0.2 to ca. 0.4 Myr by extending the species' last known appearance datum to approximately 3.0 Ma. All of the hominin fossils from this geographically concentrated cluster of localities lie between 7.5 and 17 m stratigraphically below the BKT-2 tephra, which has an $^{40}Ar/^{39}Ar$ age of 2.94 Myr (Kimbel et al., 1994; Semaw et al., 1997). This important series of discoveries includes the first, much anticipated, fairly complete adult skull of *A. afarensis* (A.L. 444-2), as well as other jaws, teeth, and cranial fragments and a partial upper limb skeleton associated with cranial and mandibular elements (Kimbel et al., 1994; Drapeau, 2001).

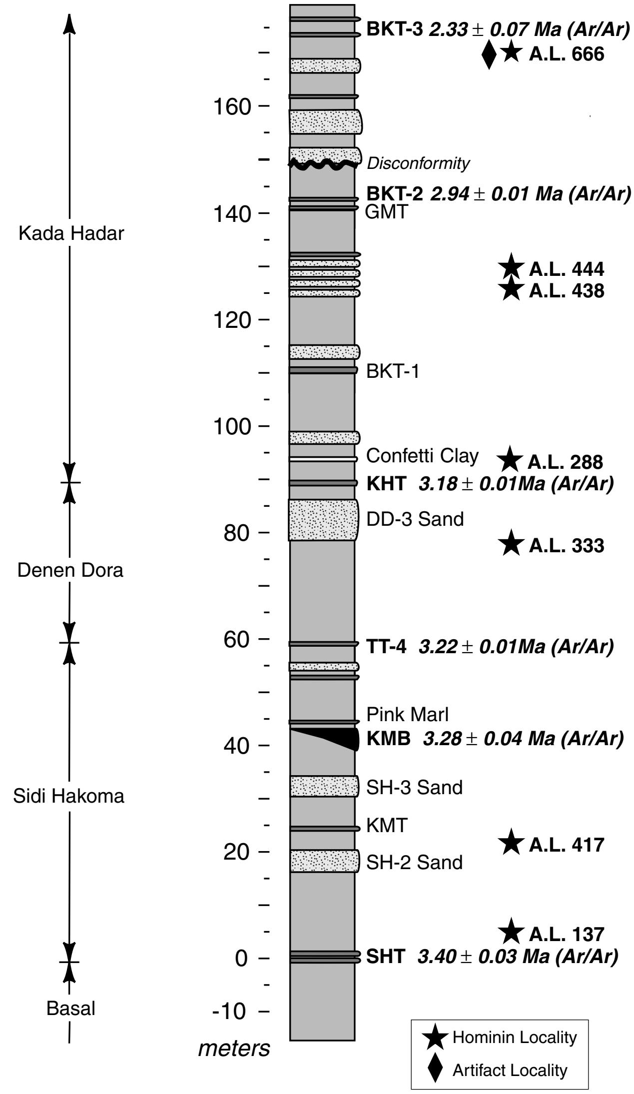


Figure 1.3. Composite stratigraphic section of the Hadar Formation showing position of A.L. 444 and other key hominin-bearing localities. Tephra dated by $^{40}Ar/^{39}Ar$ are indicated (see Renne et al., 1993; Walter and Aronson, 1993; Walter, 1994; Kimbel et al., 1996; Semaw et al., 1997).

The A.L. 444-2 skull is the center of the work presented in this volume. It is important for three reasons, beyond the mere fact of its relative completeness:

1. It includes cranial regions that were previously poorly represented in adult *A. afarensis* from Hadar, such as the frontal bone (only a small

supraorbital fragment and a posterior segment of the squama remain of the "Lucy" frontal bone).

2. It is the first *A. afarensis* adult specimen to preserve the upper face and mandible of a single individual; this combination was repeated with the discovery of the A.L. 417-1 maxilla and mandible during fieldwork at Hadar in the 1990s (Kimbel et al., 1994).
3. It is among the geologically youngest known specimens of *A. afarensis*, which, as noted, ranges in time at Hadar from 3.4 to 3.0 Ma, about double the temporal extent of the species based on the stratigraphic spread of the 1970s sample.

Thus, A.L. 444-2 presents an unprecedentedly full portrait of the *A. afarensis* skull at one end of the species' temporal range. At the other end there remain open questions (see Lockwood et al., 2000a). The Laetoli sample of *A. afarensis*, centered in time around 3.6 Ma, includes no adult cranial remains except for the original Garusi I maxillary fragment of 1939, while the partial frontal bone from the Middle Awash site of Belohdelie, isolated at 3.9 Ma, may represent the oldest fossil attributable to the species (Asfaw, 1987; Kimbel et al., 1994).

This volume presents the results of our comparative morphological study of A.L. 444-2. The monograph is organized in chapters, as follows:

Chapter 2: Recovery and Reconstruction of A.L. 444-2. The skull was recovered in a fragmentary and partially damaged state. After summarizing the recovery procedure in the field, in this chapter we describe the process of restoring the specimen to its final state, which featured the use of three-dimensional computerized tomography and stereolithography (Zollikofer et al., 1995).

Chapter 3: A.L. 444-2: The Skull as a Whole. In this chapter we describe and compare A.L. 444-2 from the perspective of observations that transcend the morphology of the individual skull bones, focusing on the size and shape relationships among the different anatomical regions of the skull. Here the specimen is examined in standard anatomical views, which is followed by a brief comparison of the skull with the 1984/1988 White-Kimbel skull reconstruction, and then by analyses of the cranial cresting pattern and the endocranial venous drainage pattern.

Chapter 4: Endocranial Morphology of A.L. 444-2. In this chapter Ralph Holloway and Michael Yuan join us to detail the results of their efforts to estimate the endocranial volume of the new skull and to record their observations on the form of the endocast.

Chapter 5: A.L. 444-2: Elements of the Disarticulated Skull. In this chapter we describe in detail the anatomy of the individual cranial bones, the mandible, and the dentition, following Sherlock Holmes's axiom that "the little things are infinitely the most important." Each element is first described and then submitted to comparative analysis. One objective of this chapter is the assessment of the effect of A.L. 444-2 and other new additions to the Hadar sample on previous characterizations of *A. afarensis* skull and dental variation.

Chapter 6: Implications for the Taxonomic and Phylogenetic Status of *Australopithecus afarensis*. After summarizing the main conclusions of the preceding chapters, we focus discussion on their implications for the taxonomy of *A. afarensis* and its role in hominin phylogeny. The ≥30% increase in the size of the Hadar hominin sample over the 1970s collection affords a fresh look at old arguments about the "acceptable" degree of size variation for a single hominin species. Finally, we reexamine the phylogenetic position of *A. afarensis* vis-à-vis other *Australopithecus* species, especially in light of the recently described *A. anamensis* from the early Pliocene of eastern Africa.

Our method is classical comparative anatomy. Although we are currently engaged in analytical projects that apply recently developed quantitative methods to the description and comparison of cranial form (e.g., Lockwood et al., 2002), here our primary concern is to create a document of record, including description, measurement, and comparison of the first complete adult *A. afarensis* skull.

2

Recovery and Reconstruction of A.L. 444-2

Recovery

The A.L. 444-2 skull was found on 26 February 1992, during a strategic paleontological survey of Kada Hadar Member sediments that are stratigraphically situated between BKT-1 and BKT-2 tephras, on the eastern edge of the Awash River's Kada Hadar tributary (Figures 1.2, 2.1, and 2.2). Yoel Rak discovered two fragments of hominin occipital bone (A.L. 444-1) at the base of a steep hill composed of Kada Hadar Member silts and clays capped by a weathered sandstone remnant (Figure 2.2). Subsequent examination of the upslope surface revealed additional hominin skull fragments (the temporal bones and maxillae) clustered together and partially exposed in a narrow gully that dissected the face of the hill. During the next seven days, probing and dry sieving of the gully infill and hillside colluvium over a 77 m^2 area led to the recovery of fragments representing about 75%–80% of a single hominin skull. It was immediately apparent that the upslope finds duplicated the anatomical parts represented by the two A.L. 444-1 occipital fragments and therefore constituted a second hominin individual, cataloged as A.L. 444-2. In addition, the lambdoidal suture of the A.L. 444-1 occipital is completely unfused, suggest-

Figure 2.1 View to the north of the A.L. 444 hill showing the location of the probable in situ horizon (arrow) relative to the 2.94 Myr-old BKT-2 tephra, which lies stratigraphically ca. 10.5 meters above it. The fossil-bearing sediments at A.L. 444 are estimated to be 3.0±0.02 Myr old.

Figure 2.2 View to the southeast of A.L. 444, on whose surface the remains of skull A.L. 444–2 were discovered by Yoel Rak on 26 February 1992. The dry Kada Hadar tributary of the Awash River is in the background.

ing subadult status, whereas fused cranial sutures and extreme dental occlusal wear indicate an advanced ontogenetic age for A.L. 444-2.

Stratigraphic Provenance and Geological Age

In February–March 1993 the A.L. 444 hillside was excavated in an effort to locate missing parts of the A.L. 444-2 skull and to determine its precise stratigraphic provenance (Figure 2.2). No further remains of the hominin skull were encountered in situ, but a complete viverrid cranium and indeterminate fragments of large mammal bone with preservation and patina (mottled dark gray, white, and yellowish gray) identical to those of the hominin were excavated in an unstratified, cemented carbonate silt that exactly matches the matrix adhering to A.L. 444-2. We are confident that the hominin skull is from this sedimentary horizon. It is approximately 10.5 m stratigraphically below the BKT-2 tephra, which outcrops in the immediate vicinity of A.L. 444 (Figure 2.1).

Single-crystal laser fusion (SCLF) $^{40}Ar/^{39}Ar$ ages for BKT-2 and Kada Hadar Tuff (KHT) bracket the geological age of A.L. 444-2 between 2.94 and 3.18 Myr (Kimbel et al., 1994; Walter, 1994; Semaw et al., 1997) (see Figure 1.3). Further refinement of the age of the skull can be achieved based on the stratigraphic position of the top of the Kaena paleomagnetic subchron, dated to 3.04 Myr (Cande and Kent, 1995), ca. 22.5 m below BKT-2 (J. L. Aronson, personal communication). Assuming constant sedimentation, interpolation yields an age estimate of 2.99 Myr for the inferred in situ horizon. Using the stratigraphic position of KHT (62.5 m below BKT-2) as the reference point for the calculation yields an age estimate for the skull horizon of 2.98 Myr. We consider 3.0 ± 0.02 Myr to be the best estimate of the geological age of A.L. 444-2, making it approximately 160 kiloyears (Kyr) younger than "Lucy," 180 Kyr younger than the A.L. 333 hominin accumulation, and 380 Kyr younger than the oldest hominin fossils from the Hadar Formation (Walter and Aronson, 1993; Walter, 1994) (Figure 1.3).

The 444 locality is situated in a dense cluster of faunal localities that sample a fluviatile depositional cycle of the Kada Hadar Member between BKT-1 and BKT-2 volcanic marker beds. The BKT-2 tephra, dated to 2.94 myr (Kimbel et al., 1994; Semaw et al. 1997), is widely exposed in this area, and the fossil-bearing units lie stratigraphically between 7.5 and 17 m below it. Outcropping in this region are fossiliferous sands and silts related to a major stream channel and its overbank and floodplain. At A.L. 444 the fossil hominin skull derives from a floodplain silt proximal to the stream channel (possibly its levee), denoted by a sand/pebble conglomerate unit that outcrops at equivalent stratigraphic position some 50 m to the west of the locality (Christopher Campisano, personal communication).

Hominin fossils were found at eight localities in this region (A.L. 437, A.L. 438, A.L. 439, A.L. 440, A.L. 444, A.L. 452, A.L. 457, A.L. 462) spanning a maximum linear distance of ca. 0.9 km. From three of these (A.L. 437, A.L. 438, A.L. 444) the remains of more than one hominin individual were recovered. In addition to the adult skull, the sample from A.L. 444 contains at least one, and perhaps as many as three subadult individuals (A.L. 444-1, occipital fragments; A.L. 444-6 and A.L. 444-29, deciduous teeth).

Besides hominins, the faunal sample from these deposits includes a wide variety of micro- and macromammalian taxa. Both cercopithecines and colobines have been recovered, including the partial skeleton of a juvenile individual at A.L. 437. Bovid taxa include the tribes Alcelaphini, Antilopini, Reduncini, Bovini and Tragelaphini. Suids, giraffids, equids, deinotherids, murid rodents, and viverrids were also recovered. Although these localities are associated with stream channel sedimentation—as suggested by the lithology as well as fossils indicative of riverine forest habitats (monkeys, *Tragelaphus* cf. *T. pricei*, and frequently encountered fossil wood)—the relatively high abundance of antilopine and alcelphine bovids argue for an overall drier habitat with fewer trees than in deposits stratigraphically beneath the BKT-1 marker bed (Reed, in prep).

The local ecological setting around A.L. 444 evidently was attractive, but potentially risky for hominins, as testified to by the frequency with which their remains are found here. At least one specimen bears clear carnivore puncture marks (A.L. 437-1, an adult mandible corpus). However, lengthy postmortem exposure on the surface does not appear to have been typical. Most of the hominin as well as nonhominin bones in the area appear relatively fresh, retain good to excellent surface detail and sharp edges where broken, and lack obvious signs of prolonged surface weathering or significant transport in water. In one or two cases, hominin individuals were probably interred as partial carcasses, which implies minimal transport after death. At A.L. 438 parts of both arms and hands were associated on the surface and in situ with an adult's mandible, partial frontal bone, and maxillary fragments (A.L. 438-1), while at A.L. 444 a large adult's vertebral, humeral, wrist, and hand elements were recovered from the surface deposits with the A.L. 444-2 adult skull (although there is no direct way to associate these A.L. 444 specimens with one another).

Taphonomic Aspects and Reconstruction of the Skull

The A.L. 444-2 skull was recovered in approximately 50 fragments, not including isolated teeth, tooth crown and root fragments, and indeterminate bone scraps. These fragments have been joined to form eight major parts (Figure 2.3 a–c):

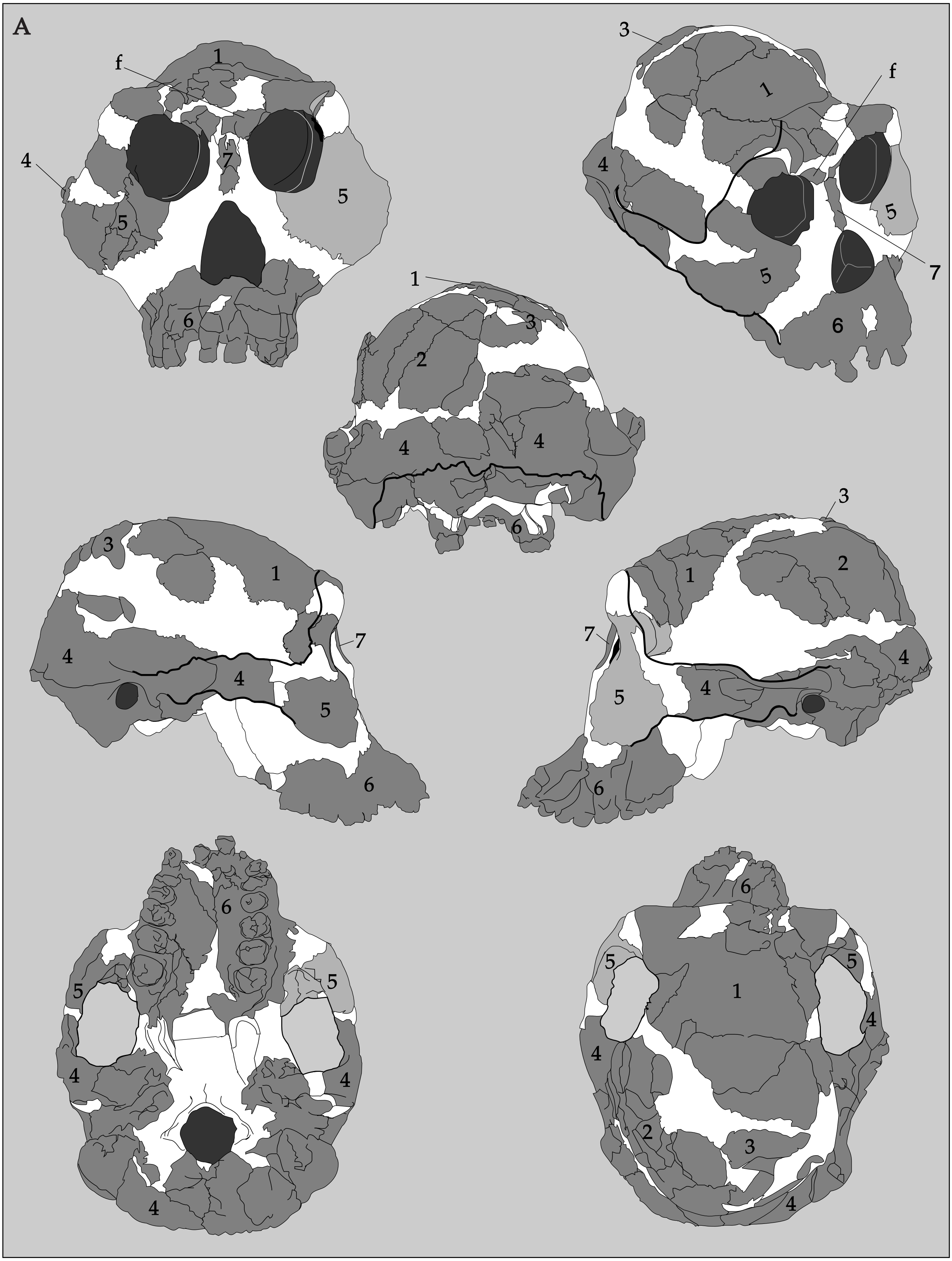
1. Frontal bone with attached anterosuperior fragment of right parietal
2. Left parietal with adhering superior fragment of squamous temporal
3. Small posterior fragment of right parietal, located approximately midway along bregma–lambda arc and in contact with the left parietal along the sagittal suture
4. Posterior calvaria, composed of the occipital squama and both temporal bones
5. Right zygomatic bone
6. Maxilla, with RI^1, R^C, RP^4–M^3, LI^1, L^C, and LP^3–M^3
7. Partial nasal bones
8. Right mandible corpus and symphyseal region, with left and right incisors, partial R_C, damaged RP_4–M_1

Details of Preservation

1. The frontal bone, composed of eight fragments, is missing the ends of both zygomatic processes, the glabellar mass and adjacent medial orbital walls, small patches of the squama in the supraglabellar region, the inferior part of the right temporal surface (pterionic region), and, internally, almost all of the floor of the anterior cranial fossa. The anterosuperior piece of the right parietal bone, consisting of four fragments, is attached to the frontal along the coronal suture, running from bregma laterally for about 65 mm.

The left side of the frontoparietal fragment is mostly intact and minimally deformed. Plastic deformation has affected the right side of the specimen through moderate superomedial rotation of the supraorbital region and adjacent temporal surface, artificially accentuating the arch of the supraorbital torus and elevating the squama on this side. The line along which this deformation occurs is clearly visible as a crack through the internal and external surfaces; it begins anteriorly at the supraorbital torus about 16 mm to the right of the midline, passes posteriorly to the temporal line, and then drops posteroinferiorly on the medial wall of the temporal fossa. The attached parietal is also flattened and plastically deformed upward just posterior to the (completely fused) coronal suture, and much of its endocranial surface is destroyed. Significant damage occurs in the glabellar region, which is lost except for three very thin fragments of the supraglabellar platform (recovered from a crushed block), consisting of the fragile walls of the frontal sinus and superior midfacial bones (including the nasals), which had been pushed down onto the left maxilla. These fragments were inserted into the supraglabellar region. Cortical bone has been abraided from most surfaces, both internally and externally, reducing thickness by 0.5–1.0 mm in some areas and obliterating some anatomical detail.

2. The left parietal consists of five pieces that articulate perfectly to form most of the central portion of the bone. A superior fragment of the temporal squama is pushed up and away from its articulation along the squamosal suture; because it is very delicate, it has been left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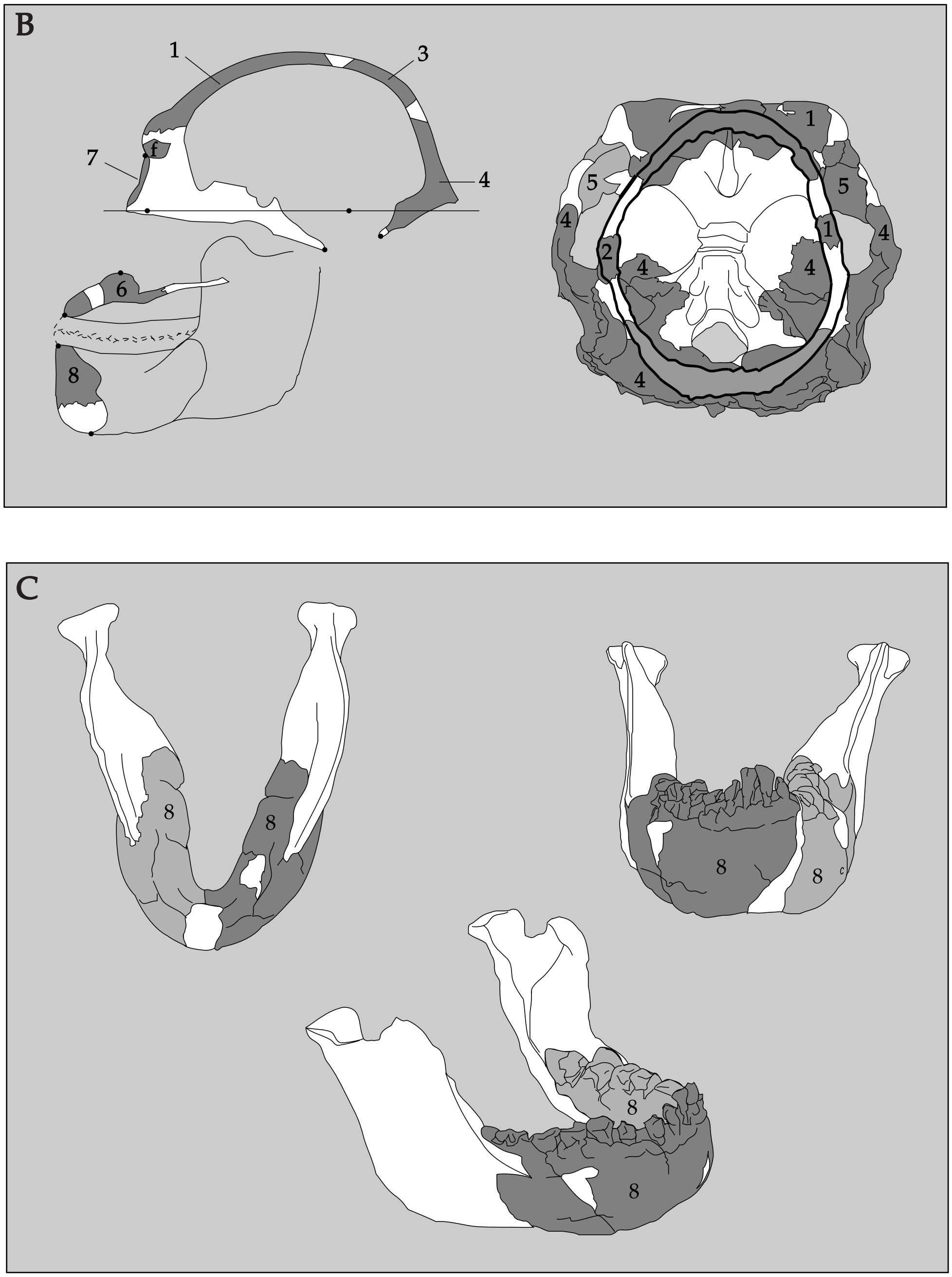

Figure 2.3 Schematic views of the reconstructed A.L. 444-2 skull. Dark gray areas represent original bone, light gray areas represent stereolithographic reconstructions, and the white areas represent wax reconstructions of missing bone. The skull is preserved in eight major segments, not including the teeth (see numbered segments in figure, which correspond to numbered fragments in the description in the text). The letter "f" refers to parts of the frontal bone based on specimen A.L. 438–1b (see text). (A) Seven views of the cranium. (B) *Left*, median cross section of the skull; *right*, endocranial aspect of the cranial base. (C) Three views of the mandible.

in this incorrect anatomical position. The coronal margin and most of the temporal margin are missing. The posterior half of the sagittal margin is intact, as is the medial part of the lambdoidal margin, to which is fused a small section of the occipital squama. The mastoid and sphenoid angles are broken. Endocranial surface and diploë have been lost along the sagittal and broken coronal edges. The preserved detail is fair to good on most surfaces.

3. The small, roughly triangular portion of the posterior right parietal bone, consisting of four fragments, has been flattened somewhat by plastic deformation. It bears a short section of sagittal suture and temporal line, and it contacts the left parietal approximately midway along bregma–lambda arc.

4. The posterior calvaria originally consisted of three major pieces: the occipital squama with an attached fragment of the posterior right parietal bone and the two temporal bones. The right temporal was separated at the occipitomastoid suture, whereas the left temporal had broken just medial to the suture; both temporals articulate with the occipital. The occipital bone preserves most of the squamous part and the right pars lateralis. A short segment of the foramen magnum margin just anterior to opisthion is present bilaterally (6.0 mm long on the left and 10.5 mm on the right), but opisthion itself is missing.

The two halves of the occipital were originally compressed toward the midline, resulting in the slight overlapping of the nuchal plane along a sagittally oriented "fault" that approximates the midline. This break was cleaned, and the two halves were separated and reattached along the break in their proper position. At present, the left and right halves of the nuchal plane are offset vertically by 2 to 3 mm; this separation increases posteriorly toward the external occipital protuberance, which is crushed. The right posterior cranial fossa is "folded" along a crack that runs diagonally from the occipitomastoid suture, across the cerebellar fossa, to the superior limb of the cruciate eminence. The transition across the endocranial bone table from the cerebellar fossa to the cerebral fossa on this side is artificially sharp along the fold.

An undistorted posterior section of right parietal bone is intact along the (externally fused) lambdoidal suture between lambda and asterion. This segment includes a narrow strip, built from three separate fragments, that runs anteriorly above the supramastoid region to form the posterior part of the vault's lateral contour.

Both temporal bones are fairly complete and well preserved. The right temporal is in better condition than the left, which has survived moderate plastic deformation and bone plate displacement. Bone loss due to breakage on both sides chiefly affects the squamosal portions of the calvarial walls. On the left side this part of the squama is completely destroyed down to the level of the temporal shelf, whereas on the right it is preserved for about 25–35 mm above the shelf. Both zygomatic processes, broken at their roots, were recovered separately and have been reattached. The left zygomatic process, although intact, is plastically deformed and rotated laterally such that its medial surface faces superomedially. Although it is much less deformed than the left, the anterior half of the right process is artificially flared laterally and pushed inferiorly to about 5 mm below its correct articulation with the posterior half.

The left petrous pyramid sits in a more superior position than the right, with the left porion approximately 8 mm lower than the right porion. This discrepancy can be explained by noting that, relative to the undeformed right temporal, the left has been artificially rotated inferolaterally on the sagittal plane and pivoted about the midline break through the nuchal plane of the occipital, lowering porion while elevating the petrous.

Basal anatomy is fairly complete and very well preserved, especially on the right side, where only a small triangular section in the center of the mandibular fossa's roof and the apical half of the petrous pyramid are missing. The entire left petrous is present but is badly crushed anterior to the carotid foramen. Also lost on the left side is the preglenoid plane, the tip of the entoglenoid process, the middle third of the articular eminence, part of the roof of the mandibular fossa, and the medial two-thirds of the postglenoid process. Internally the right temporal is in good condition, except for the aforementioned loss of the petrous apex and moderate loss of surface bone from the petrous's anterior surface. The left petrous is in poor condition; its anterior and posterior surfaces are mostly broken medial to the internal auditory meatus. The matrix that secures crushed and displaced pieces of the petrous has not been disturbed.

5. The right zygomatic bone was recovered in two pieces: the frontal process and the body of the bone. Both frontal and temporal processes are missing their tips. The frontal process, although separated along its base from the body, is in perfect contact with the body at the inferior margin of the orbit. The body of the zygomatic suffers from deformation at three sites: (1) along the inferior margin of the orbit, where the maxillary process has been displaced about 5 mm laterally; (2) along the posterior wall of the maxillary sinus, which has been bent posterolaterally to form a right angle with the rest of the temporal surface; and (3) along the zygomaticomaxillary suture, where there has been modest superficial bone displacement.

6. Excluding teeth and dental fragments (see Chapter 5 for details of tooth preservation), the maxilla was recovered in three primary pieces: the entire right half, the left half anterior to the M^2 position, and the alveolar

bone and maxillary sinus walls above left M^2 and M^3, which were part of a separate block that also contained the supraglabellar plates and upper midfacial bones, which had been crushed downward into the maxillary sinus. On both sides the lateral ends of the horizontal plates of the palatine bones are in place; on the right the inferior tip of the pterygoid process of the palatine is also present. Most of the zygomatic and frontal processes are broken; on the left they are preserved to a more superior level than on the right. Although the left maxilla is somewhat more complete, it is less well preserved than the right. It is both plastically deformed and broken along a major crack that runs inferiorly from the root of the zygomatic process to the alveolar margin at P^3/P^4; along this crack there is a considerable overlapping of the bone table. Another significant crack runs from the alveolar margin at right I^1 into the nasal cavity at the corner of the nasal aperture, where it separates the lateral margin of the aperture from its inferior margin. The relatively undeformed right maxilla joins perfectly with the left along a break that approximates the midline. Missing bone leaves gaps between the two sides on the nasoalveolar clivus and the posterior half of the palatal roof. It is at the latter point that there is a discrepancy in the elevation of the two sides of the palatal roof along an artificial step in the midline, the left side being higher than the right. This discrepancy gradually decreases anteriorly and is negligible anterior to the P^3 level. When all the pieces are assembled, it is evident that plastic deformation compressed the maxilla along the midline step and skewed it backward and to the left of the midsagittal plane, rendering it asymmetric.

7. The nasal bridge fragment, composed of the fused left and right nasal bones, was recovered from within the block of upper midfacial fragments that was crushed down onto the left maxilla. Superior, inferior, and lateral margins are broken. The preserved fragment is 28 mm tall and 10 mm wide.

8. The right side and anterior corpus of the mandible were recovered in three pieces, not including teeth and dental fragments. The left side is represented by alveolar bone below the I_1 and I_2 positions. The corpus is broken along a line running from the left I_2/C interdental septum diagonally to the base below the right canine. The posterior part of the right corpus (containing M_2–M_3 and the root of the ascending ramus) is displaced laterally, disrupting the natural path of the postcanine tooth row and creating a gap and slight step on the lateral surface that measures 3.5 mm wide just below the alveolar margin at the M_1/M_2 level and running anteroinferiorly to the base below P_4/M_1, where it narrows to about 1 mm. The medial surface of the corpus is crushed inward slightly between P_4 and M_2 just below midcorpus level.

Reconstructing the Skull

Initial joining of skull fragments that showed fresh, clean breaks occurred in the field during the 1992 season. This was followed by three months of preparation, reconstruction, molding, and study at the National Museum of Ethiopia, Addis Ababa, in 1993–1995.

Almost all of the skull fragments were coated to one degree or another with a hard, calcareous silt matrix. Large-scale reduction of this matrix, which was sometimes loosened through the parsimonious application of acetic acid, was achieved through the use of electric scribes mounted with sharpened carbide points. Removal of the matrix close to the bone surface was accomplished under a binocular microscope with a sharpened steel sewing needle mounted in a pin vise.

The nature and pattern of bone breakage and displacement in the original state of discovery reveal the trajectory of the geological forces that deformed the cranium while it was still intact. It is clear that the force was directed diagonally downward from above the right orbit toward the left posterior region of the cranial base (see Figures 2.4, 2.5, 2.6).

The major portions of the skull were assembled in the following stages:

1. The left parietal bears the sagittal suture with both sets of temporal lines, establishing both the

Figure 2.4 The effect of postmortem deformation on A.L. 444-2. The arrow represents the direction of the postmortem geological pressure on the skull.