



Human Palaeontology and Prehistory

## The paleoanthropology of Hadar, Ethiopia

## Paléoanthropologie d'Hadar, Éthiopie

Donald Johanson

School of Human Evolution and Social Change, Institute of Human Origins, Arizona State University, PO Box 874101 Social Sciences Rm. 103, Tempe, AZ 85287-4101, USA



## ARTICLE INFO

## Article history:

Received 25 October 2016

Accepted after revision 26 October 2016

Available online 29 December 2016

Presented by Marcel Otte

## Keywords:

Hadar Formation

Afar depression

Ethiopia

*Australopithecus**Homo*

Palaeoanthropology

## ABSTRACT

Field research at the fossil-bearing deposits in the Afar Depression began in the 1970s. Prior to this, hominin fossils older than 3.0 Mya consisted of only a handful of fragments. During Phase I, the International Afar Research Expedition to Hadar, Ethiopia collected some 240 fossil hominins from Hadar over a time range of 3.0–3.4 Mya. Along with hominin fossils from Laetoli, they were deemed a new species, *Australopithecus afarensis*. This taxon was posited as the last common ancestor to robust *Australopithecus* and the *Homo* lineage in eastern Africa. Phase II research under the Hadar Research Project has added strength to the Phase I results, including the first association of a *Homo* fossil with stone tools at 2.4 Mya. This presentation is a cursory synopsis of the importance and implications of the hominin fossils recovered at Hadar during over the last 34 years.

© 2016 Published by Elsevier Masson SAS on behalf of Académie des sciences.

## R É S U M É

Les recherches de terrain sur les dépôts fossilifères de la dépression de l'Afar ont commencé dans les années 1970. Avant cela, les fossiles d'homininés vieux de plus de 3,0 Ma consistaient seulement en une poignée de fragments. Durant la phase I, l'*International Afar Research Expedition* à Hadar, en Éthiopie, a récolté quelque 240 homininés fossiles, sur un intervalle de temps de 3 à 3,4 Ma. Outre les fossiles d'homininés de Laetoli, une nouvelle espèce a été mise en évidence, *Australopithecus afarensis*. Ce taxon a été considéré comme le dernier ancêtre commun à la lignée d'*Australopithecus* et d'*Homo* en Afrique orientale. La phase II de recherche dans le cadre du projet de recherche Hadar a permis de renforcer les résultats de la phase I, en incluant la première association d'*Homo* fossile à des outils de pierre à 2,4 Ma. Cette présentation est un bref synopsis quant à l'importance et aux implications des fossiles d'homininés collectés à Hadar au cours des 34 dernières années.

© 2016 Publié par Elsevier Masson SAS au nom de Académie des sciences.

E-mail address: johanson.ih@ASU.edu

<http://dx.doi.org/10.1016/j.crpv.2016.10.005>

1631-0683/© 2016 Published by Elsevier Masson SAS on behalf of Académie des sciences.

## 1. Introduction

Following 34 years of paleoanthropological field research in South Africa inspired by the 1925 announcement of the Taung Baby, attention shifted to Africa's Great Rift Valley in 1959. This was the result of the July 17, 1959 recovery of the "Zinj" skull at Olduvai Gorge (now referred to as Oldupai Gorge) on the eastern edge of Tanzania's Serengeti Plain (Leakey, 1959).

The late Mary Leakey's Olduvai find led to discoveries of fossil hominin remains in the lower Omo Valley, Lake Rudolf (now Lake Turkana), Peninj, Kanapoi, and Lothagam, where all localities were closely associated with the Great Rift Valley. In contrast to the South African sites, such as Swartkrans, Sterkfontein, Kromdraai, and Taung, the Rift Valley sites offered an enhanced data set for understanding human origins.

The East African sites provided volcanic materials amenable to precise argon radiometric dating for fossil and archaeological finds. Additionally, the secure geological contexts from which these finds derived allowed associations of hominin and non-hominin faunal remains, stone artefacts, as well as precisising the depositional circumstances that preserved these finds.

During the 1960s, the transdisciplinary research strategy of paleoanthropology – knitting together expertise in the biological, geological and anthropological sciences – was articulated primarily by research teams in the circum-Turkana basin in Ethiopia and Kenya, as well as Olduvai Gorge, Tanzania.

With this successful and broad reaching approach to understanding human evolution, it was fortuitous that Maurice Taieb brought attention to unexplored and highly promising fossils fields in Ethiopia (Fig. 1). During the course of his late 1960s geological fieldwork in Ethiopia's Afar sedimentary basin (the Afar Region), the northeastern extension of the Great Rift Valley, Taieb encountered hitherto unknown Plio/Pleistocene sedimentary deposits

rich in well-preserved and diverse mammalian fossils. The Afar sedimentary basin, sometimes referred to as the Afar Triangle, comprises a vast area constrained to the west by the Western Ethiopian Escarpment, to the southeast by the Somali Escarpment and to the northeast by the Danikil Horst.

In early 1972, Taieb organized a small exploratory reconnaissance to the Afar Region to evaluate the potential of there for more extensive paleoanthropological field investigation. Following six weeks of survey, he formed the International Afar Research Expedition (IARE), a multinational, transdisciplinary team dedicated to exploring in greater depth these geological exposures with the goal of recovering fossil hominins (Taieb et al., 1972).

In 1973, field exploration focused on the site Hadar, (11°06' N, 40°35' E), where deep, fossil rich sedimentary exposures were situated just north of the Awash River (Fig. 2). A fossil knee joint estimated based on biostratigraphy to be in excess of three million years (now dated to 3.4 Mya) constituted the first fossil hominin to be found in the Afar Triangle (Fig. 3). The knee, and associated proximal femoral elements from Afar Localities 128 and 129 (A.L. 128 and A.L. 129), provided indisputable evidence for human bipedalism (Johanson and Coppens, 1976).

Subsequent IARE missions to Hadar were rewarded with a richness of fossil hominins. Particularly noteworthy was the 1974 discovery of partial skeleton, A.L. 288-1 (Fig. 4), and the 1975 recovery of over 200 hominin bones at A.L. 333. Dubbed the "First Family," they were undoubtedly the casualties of a catastrophic event. These two discoveries, dating to 3.2 Mya, proved invaluable for understanding anatomical and developmental variation in the Hadar hominins.

Beginning in 1981, a moratorium on field research was imposed by the Ethiopian Government due to the instabilities resulting from the *coup d'état* by the Marxist Derg and the overthrow of Emperor Haile-Selassie. This interruption of field research at Hadar lasted until 1990, as



Fig. 1. Overview of Hadar deposits looking south.

Fig. 1. Vue générale des dépôts d'Hadar, en regardant vers le sud.

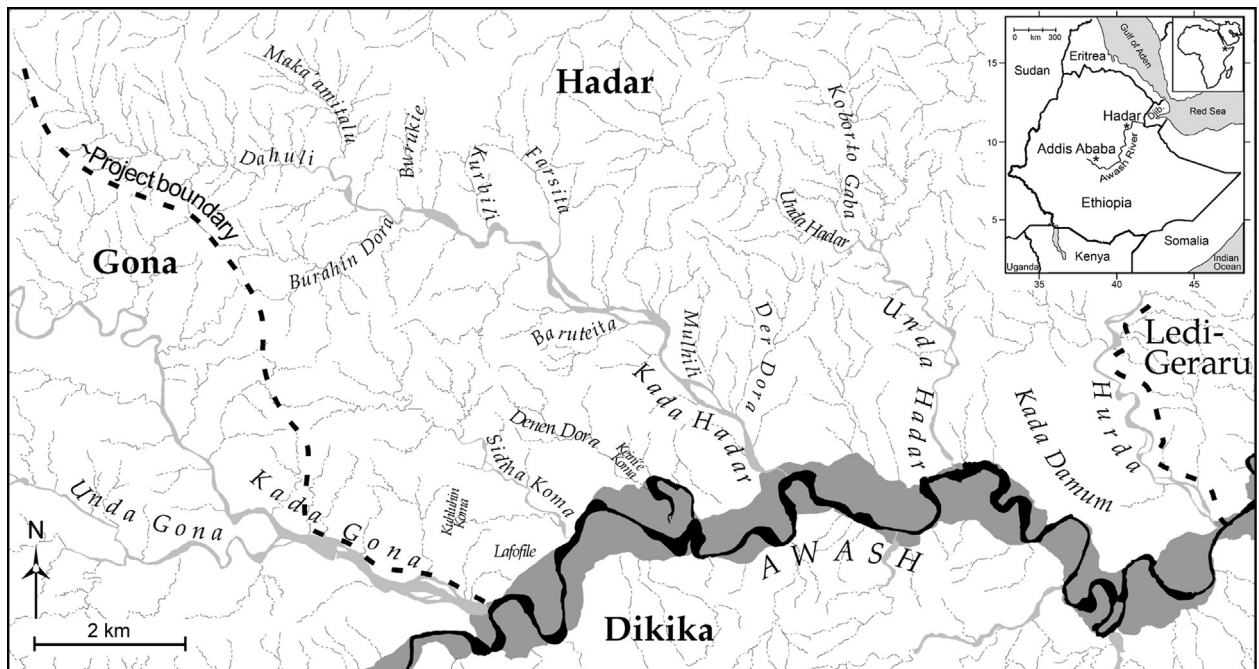


Fig. 2. Map of Hadar (Kimbel and Deleuzene, 2009).

Fig. 2. Carte d'Hadar (Kimbel et Deleuzene, 2009).

which time the Hadar Research Project (HRP) coordinated by the Institute of Human Origins re-initiated exploration that continues to this day.

## 2. Hadar chronology, geology and paleoenvironment

The Hadar Formation (Fig. 5), as defined by Taieb et al. (1972) consists primarily of fluvio-lacustrine related mudstones, siltstones, fine-grained sandstones and volcanic tuffs. The 150-meter thick formation is divided into four members: the Basal Member, the Sidi Hakoma Member, the Denan Dora Member and the Kada Hadar Member. Three tuffs, the Sidi Hakoma Tuff (SHT), the Triple Tuff (TT) and the Kada Hadar Tuff (KHT) separate the four members.

Reed (2008) identifies fluctuating paleoenvironments over the 400,000 years of time in the Hadar Formation. Habitat reconstructions were based on careful analysis of the faunal remains within the Hadar Formation. The Sidi Hakoma Member was characterized by a more closed habitat with high rainfall and low seasonality. The overlying Denan Dora Member was an edaphic grassland habitat. Finally, the Kada Hadar Member was even a more open and arid habitat as seen in the high abundance of antilopins; open area bovinds. *Australopithecus afarensis* was a eurytopic species found throughout the Hadar Formation, able to tolerate a wide range of habitats.

The Hadar Formation is separated from the overlying Busidima Formation just above the 2.95 Mya Bouroukie Tuff-2 (BKT-2) by a geological unconformity. Reed (2008) notes that above this datum, in significantly younger deposits, is a recognizable faunal turnover. She interprets this change as a response to a wooded grassland habitat

with floodplain environments. Notable is the absence of *A. afarensis* in the Busidima Formation, but a 2.4 Mya maxilla assigned to *Homo* (Kimbel et al., 1996, 1997) was found in the Makaamitalu Basin.

Fossil pollen recovered from the Hadar Formation (Bonnefille et al., 2004) confirmed a forested habitat in the Sidi Hakoma Member. Pollen from the Denan Dora Member reflects a drier habitat in contrast to the Kada Hadar Member, which was more wooded and humid.

Further evidence from studies of paleosols and carbon and oxygen isotopes of mollusks (Hailemichael, 2000; Hailemichael et al., 2002) agrees with the habitat reconstructions reported by Reed (2008). The fluctuations in paleo-habitats at Hadar do not support the notion that there was a trend toward more arid conditions as is the case for the Shungura Formation (Bobe and Eck, 2001). Confirmation of the paleoenvironmental picture for the Hadar Formation comes from detailed geological studies of depositional conditions (Campisano and Feibel, 2008a).

## 3. Phase I – International Afar research expedition

The recovery of more than 240 fossil hominin specimens by the end of the 1977 (Fig. 6) IARE field season offered an incredible storehouse clarifying the nature of pre-3 Mya hominins (for full descriptions see Johanson et al., 1982). In 1973 and 1974, when the first significant fossils were recovered, interpretation of anatomical and size variation pointed to the possibility of more than one taxon (Johanson and Taieb, 1976; Taieb et al., 1974, 1975). However, by late 1977, following extensive study of the fossil collection on temporary loan to the Cleveland Museum of Natural History (CMNH), a team decision concluded that



Fig. 3. A.L. 129-1a, b.  
Fig. 3. A.L. 129-1a, b.

only one hominin taxon was represented in the Hadar Formation. Currently all Hadar hominin fossils are curated in the National Museum of Ethiopia, Addis Ababa.

All of the fossil hominins recovered from the Hadar Formation, representing over 400,000 years of time were assigned to *A. afarensis*, as was announced at a Nobel Symposium in Karlskoga, Sweden, in May of 1978 (Johanson, 1978). The formal publication of *A. afarensis* appeared later that year in the CMNH's in-house journal, *Kirtlandia* (Johanson et al., 1978).

The type specimen, LH-4, from Laetoli, a 3.5-Mya mandible, was chosen because it was fully described and published (Fig. 7). Most importantly, it embodied a plethora of anatomical features found in abundance in the Hadar sample, indicating that the hominins found at these two sites were the same species. The Hadar and Laetoli specimens were placed in the genus *Australopithecus* not *Homo*,

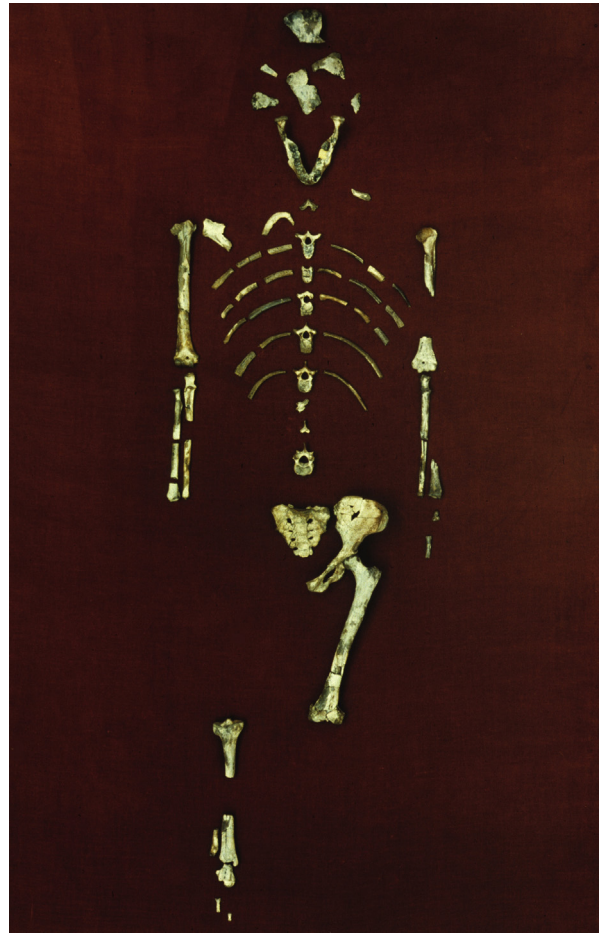


Fig. 4. A.L. 288-1. "Lucy".  
Fig. 4. A.L. 288-1. «Lucy».

largely because they lack facial reduction and cranial enlargement.

Several primitive cranial (Fig. 8) and postcranial features makes *A. afarensis* distinct from other species of *Australopithecus*: small cranial capacity, palate similar to African apes (parallel tooth rows, shallow, long from antero-posteriorly, narrow from side to side), primitive occipital and basal cranium anatomy, high frequency of unicuspid third premolars, prognathic face, and primitive mandibular anatomy. Postcranially, the pelvis, knee, ankle and foot indicate habitual, terrestrial bipedalism, but ape-like curved finger and foot bones are retained ancestral ape-like features. The high level of sexual dimorphism in *A. afarensis* (Fig. 9), with significantly larger males, is also characteristic of apes (except for the gibbon). For a detailed review of *A. afarensis* anatomy see Kimbel et al., 2004; Kimbel and Delezene, 2009.

There was initial opposition to the veracity of the newly named species, especially from the late Phillip Tobias (Tobias, 1980), who saw the Hadar and Laetoli hominins as two subspecies of *A. africanus*. Other scholars (Falk et al., 1995; Leakey and Walker, 1980; Olson, 1981; Senut, 1983; Tardieu, 1981) favored taxonomic diversity

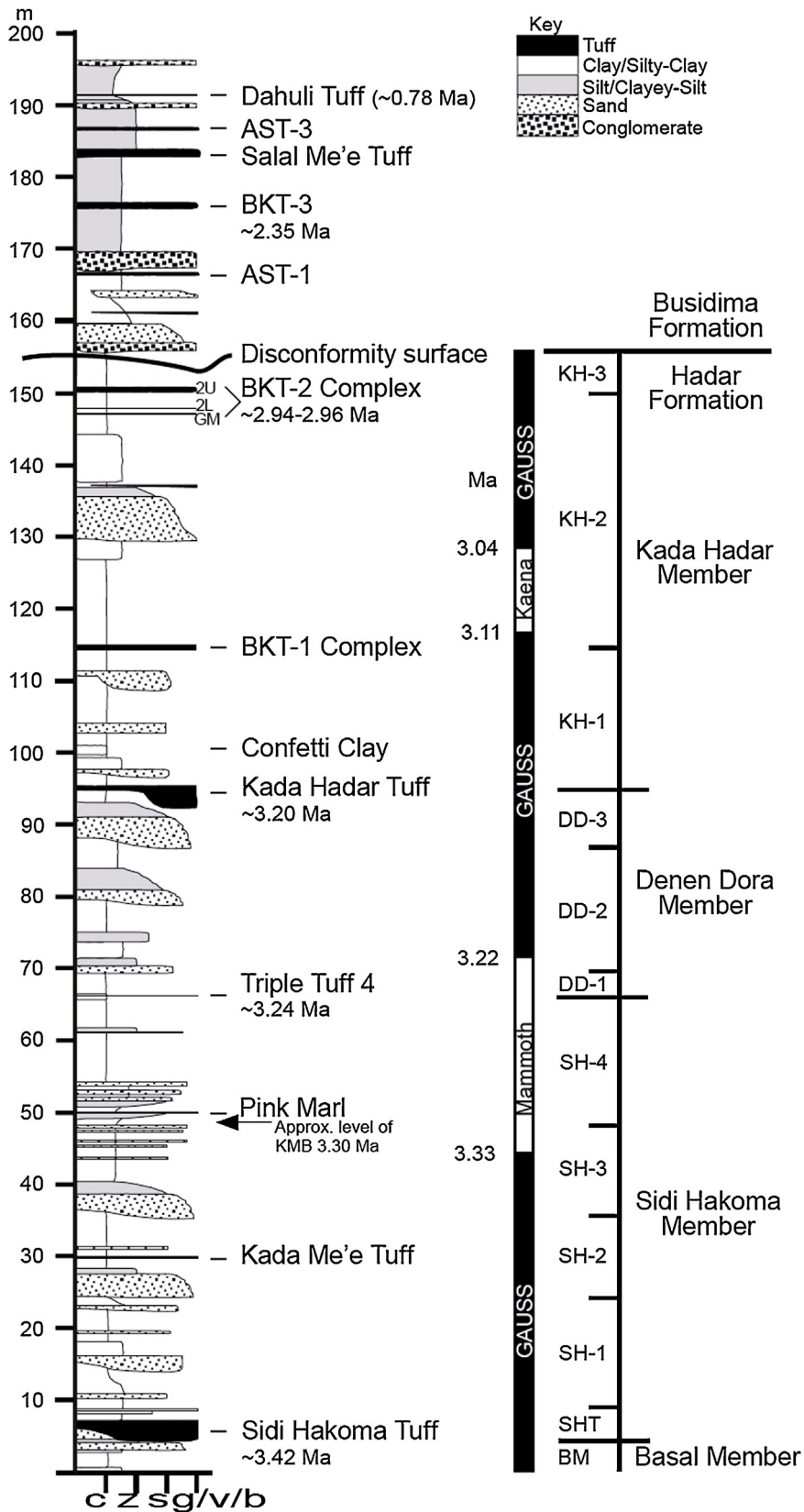
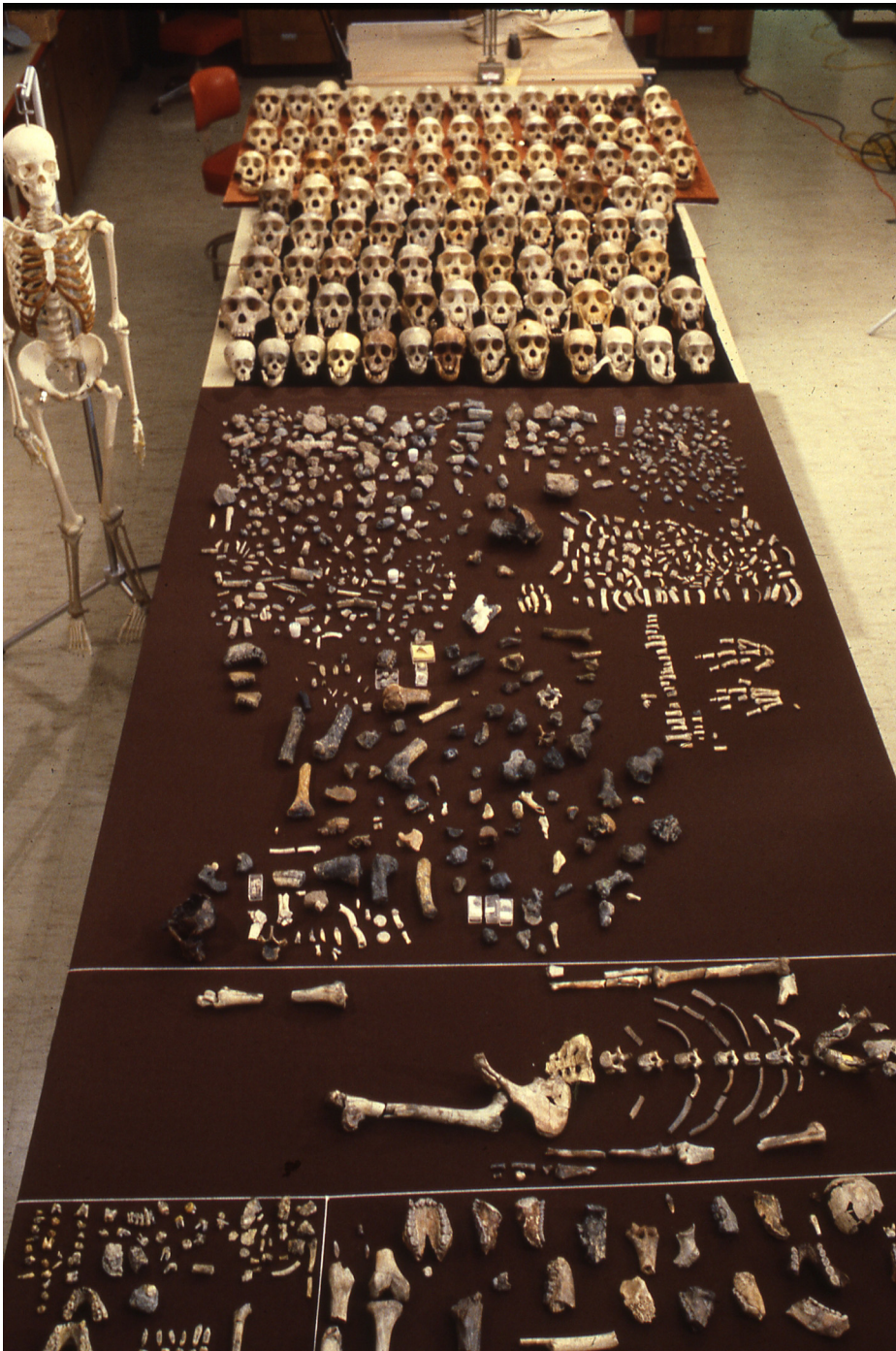


Fig. 5. Hadar stratigraphy (Campisano and Feibel, 2008a).

Fig. 5. Stratigraphie d'Hadard (Campisano et Feibel, 2008a).



**Fig. 6.** The 1970s Hadar Hominin collection; with casts of Laetoli in lower left corner.

**Fig. 6.** Récolte d'homininés d'Hadar des années 1970, avec des moulages de Laetoli dans le coin inférieur gauche.

within the Hadar collection, but were unable to separate convincingly the hominin material into distinctive morphs.

Extensive argument centered on the nature of bipedalism in *A. afarensis*. The rich collection of postcranial material, including a pelvis, a nearly complete foot and numerous lower limb bones, provided solid evidence that

*A. afarensis* was a fully-bipedal creature (Lovejoy, 1981, 1988). In contrast, others suggested that these creatures were highly arboreal, and that perhaps males and females walked differently (Stern and Susman, 1983; Susman et al., 1984). They further suggested that during terrestrial bipedal locomotion, *A. afarensis* was not capable of full extension at the hip and knee. However, the detailed



Fig. 7. LH-4, *A. afarensis* type mandible.  
Fig. 7. LH-4, mandibule type d'*A. afarensis*.

study of the biomechanics of the postcranial bones does not support this observation.

The excavation of a 3.6-Mya hominin footprint trail at Laetoli, Tanzania (Leakey and Harris, 1987) revealed that the prints impressed and preserved in a volcanic ash were identical to modern human footprints (Fig. 10). The presence of a large, adducted, great toe, used as a propulsive organ, the presence of longitudinal and transverse plantar arches and the alignment of lateral toes provide indisputable evidence for bipedalism in *A. afarensis* that is essentially equivalent to modern humans.

Following an extensive review of all Plio/Pleistocene hominin taxa (Johanson, 1978; Johanson and White, 1979; White et al., 1981), it was concluded that *A. afarensis* is characterized by a large number of primitive

(plesiomorphic) features in the face, cranial vault and dentition. Based on the generalized nature of the anatomy of *A. afarensis*, it was suggested that this species be entertained as the basal taxon to both the *Homo* lineage and the later *Australopithecus* (Fig. 11).

The cranio-dental anatomy of *A. africanus*, seen in the light of *A. afarensis*, is derived in the direction of robust *A. robustus*. In order for *A. africanus* to be an ancestor to *Homo*, a high number of evolutionary reversals would be necessary; an unlikely evolutionary event.

The novel phylogeny stimulated by *A. afarensis* implied that *A. africanus* evolved into *A. robustus* in South Africa, while a parallel set of evolutionary adaptations to a heavily masticated diet occurred in eastern Africa, culminating in *A. boisei*. With 1.2 million years separating the last occurrence of *A. afarensis* and the appearance of *A. boisei* and this scenario seemed unlikely to some investigators (Skelton et al., 1986).

This hypothesis was tested with the discovery of the Black Skull (Walker and Leakey, 1988; Walker et al., 1986). The cranium KNM-WT 17000, assigned to *A. aethiopicus*, was dated at 2.5 Mya (Fig. 12), chronologically intermediate between the disappearance of *A. afarensis* and the appearance of *A. boisei*.

Reflecting its ancestry, the Black Skull retained a number of features characteristic of *A. afarensis*, such as a highly prognathic face and cranial cresting. Yet other features of the skull, such as strong sagittal cresting, extremely enlarged cheek teeth, and so on, forecast the derived anatomy of the later *A. boisei*. The mosaic of ancient and derived features in *A. aethiopicus*, bridged the more than one million year gap between *A. afarensis* and *A. boisei*, and provided convincing evidence for an evolving lineage (Kimbel et al., 1988).

A possible interpretation here is that robust *Australopithecus* species evolved independently in eastern and South Africa. This suggests parallel evolution in these two geographical regions, most likely as adaptation to a heavily masticated diet. Furthermore, no species of

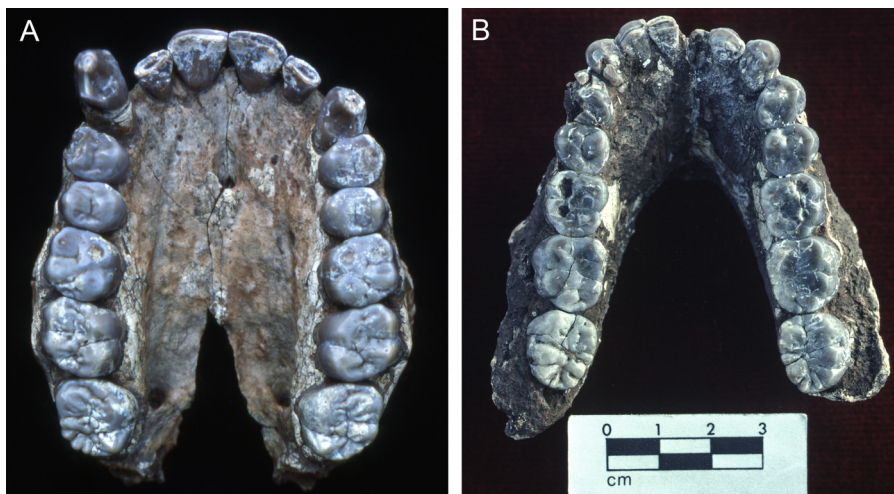


Fig. 8. Hadar jaws: left, A.L. 200-1 (right canine fossilized out of socket); right A.L. 400-1.  
Fig. 8. Mâchoires d'Hadar : à gauche, A.L. 200-1 (la canine droite est fossilisée en dehors de la cavité) ; à droite, A.L. 400-1.



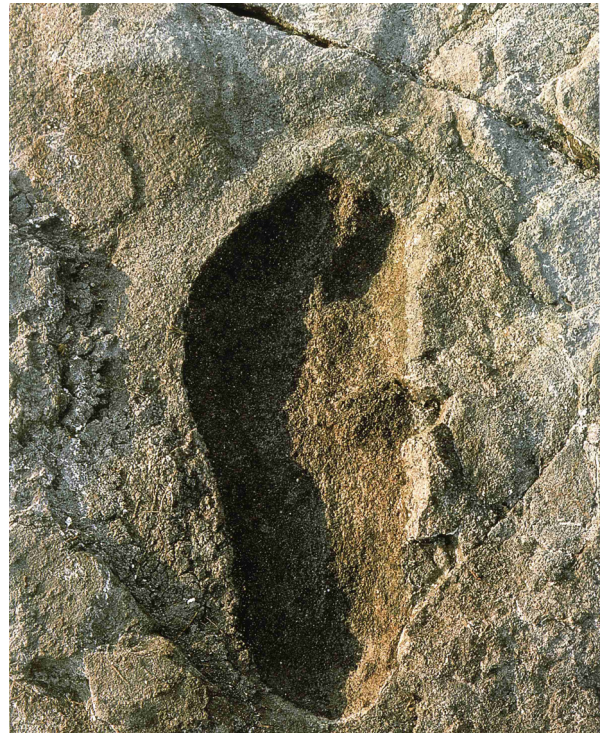
**Fig. 9.** Sexual dimorphism in *A. afarensis*. Left, A.L. 288-1; right A.L. 827-1.  
**Fig. 9.** Dimorphisme sexuel chez *A. afarensis*. À gauche, A.L. 288-1 ; à droite, A.L. 827-1.

*Australopithecus* is found in both regions, supporting the notion of independent evolutionary arenas.

#### 4. Phase II – Hadar research expedition (HRP)

Paleoanthropological field research at Hadar resumed in 1990. The HRP developed a strategic research program to address a number of outstanding but crucial questions concerning the geology, paleontology, and anthropology of the Hadar Formation.

There were multiple primary research goals. First, to resolve the geochronology of the Hadar Formation, with the objective of providing a precise chronological framework in



**Fig. 10.** An *A. afarensis* foot impression in the volcanic ash at Laetoli, Tanzania.

**Fig. 10.** Une empreinte de pied d'*A. afarensis* dans la cendre volcanique à Laetoli, Tanzanie.

which to assess faunal and geological evolution at the site. Second, to refine the paleoenvironmental settings in which the Hadar Formation accumulated, and the nature of the ecological settings in which vertebrates and hominids lived and interacted (see discussion above). Third, to assess the depositional history of the “First Family” locality and potential for further excavation. Fourth, to survey the upper Kada Hadar Member with the goal of extending the stratigraphic range of hominids at Hadar. Fifth, to test the hypotheses of *A. afarensis* systematics and paleobiology based on the recovery of additional (especially cranial) specimens.

In order to date more precisely the Hadar tuff horizons, both Single Crystal Laser Fusion  $^{40}\text{Ar}/^{39}\text{Ar}$  dating techniques (Walter, 1994; Walter and Aronson, 1993), and paleomagnetic dating (Renne et al., 1993) were employed.

These efforts led to one of the best-dated hominin-bearing geological formations in eastern Africa. The Sidi Hakoma Tuff was determined to be 3.42 Mya, and geochemically identical to the Tulu Bor tuff in the Koobi Fora Formation in Kenya, also dated to 3.42 Mya. The Triple Tuff was dated at 3.24 Mya, the Kada Damum Basalt at 3.30 Mya, the Kada Hadar Tuff at 3.20 Mya and the Bouroukie BKT Tuff-2, at 2.96 Mya and the BKT-3 at  $2.33 \pm 0.07$  (Fig. 5). See Campisano and Feibel (2008b) for more details of the tephrochronology.

The A.L. 333, or “First Family Site” presents an intriguing dilemma since we have no reasonable explanation for this catastrophic death assemblage. The vast majority of the more than 200 specimens collected at A.L. 333 during



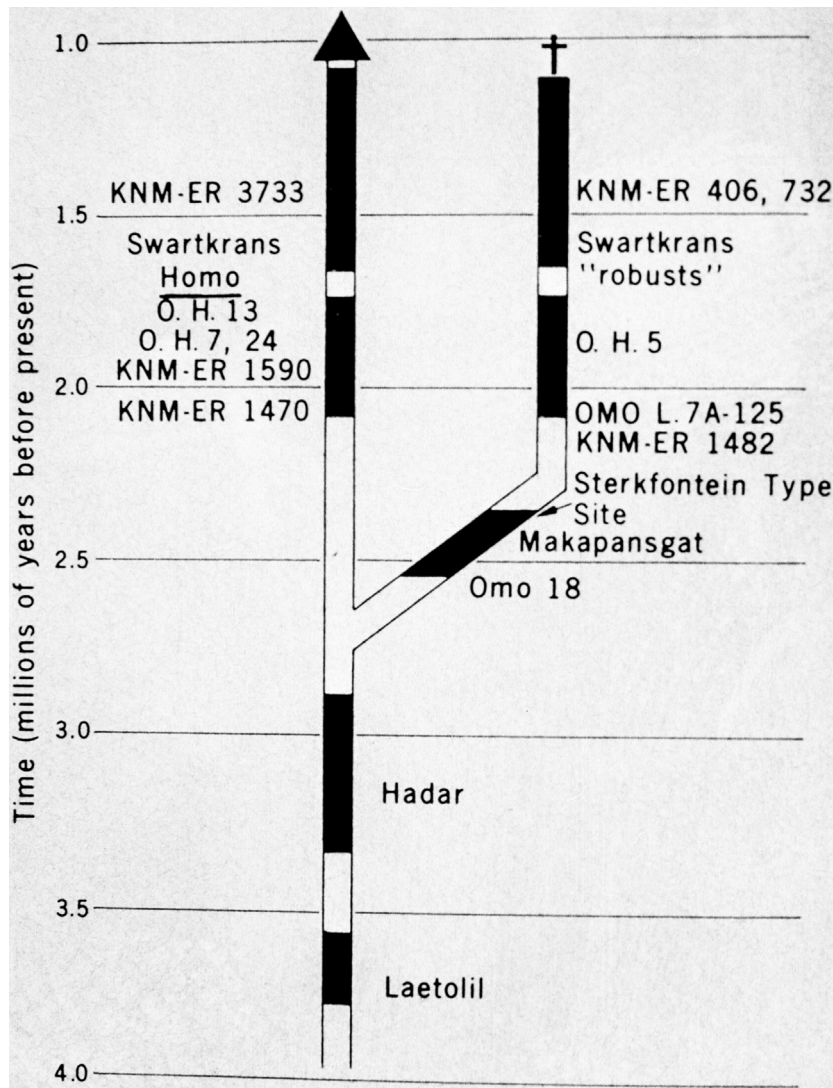


Fig. 11. Hypothetical Hominin Phylogeny (Johanson and White, 1979).  
 Fig. 11. Phylogénie hypothétique des hominés (Johanson et White, 1979).

Phase I were surface finds; however, 18 specimens were excavated *in situ* from an 80-cm thick horizon. The recovery of 39 additional postcranial and three mandibular and dental hominid specimens (1990–2012) has increased the estimate for the minimum number of individuals at A.L. 333 from 13 to at least 17 (nine adults, three adolescents and five juveniles).

Previous speculation proffered the notion that the A.L. 333 hominid assemblage was the result of a flash flood. However, detailed microstratigraphic study of the geological strata at the site indicated the hominins were interred in a shallow depression (swale) in the upper reaches of an abandoned channel, which originally flowed northwards (Behrensmeyer, 2008; Behrensmeyer et al., 2003).

Preservation of some fragile elements and still-articulated hand bones indicates little postmortem fluvial

transport. Lack of abrasion and extensive weathering suggest rapid burial perhaps within weeks of death. The underrepresentation of axial skeletal elements, as well as some postmortem carnivore damage, may reflect some level of feline predation.

Beginning in 1990, strategically focused field survey confirmed the relative paucity of fossils in the Kada Hadar Member. Yet recognition of a significant number of new hominid localities, many above the KHT, has doubled the temporal range for *A. afarensis* at Hadar from 200,000 to 400,000 years (Kimbel and Delezene, 2009; Kimbel et al., 1994). Noteworthy was the recovery of male (A.L. 444-2) and female (A.L. 822-1) skulls and a partial skeleton (A.L. 438-1) in the upper reaches of the Hadar Formation (Fig. 13). Between 1990 and 2012, a total of 187 additional fossil hominin specimens were collected bringing the total to 427.



**Fig. 12.** The “Black Skull” KNM-WT 17000. Note large sagittal crest and prognathic face.

**Fig. 12.** Le « Crâne noir » KNM-WT 17000. À noter la grande crête sagittale et la face prognathe.



**Fig. 14.** 2.4 Mya *Homo* sp. maxilla A.L. 666-1 dated back to 2.4 Mya, from the Busidima Formation.

**Fig. 14.** Maxillaire A.L. 666-1 d'*Homo* sp. datant de 2,4 Ma, en provenance de la formation Busidima.

## 5. The genus *Homo* at Hadar

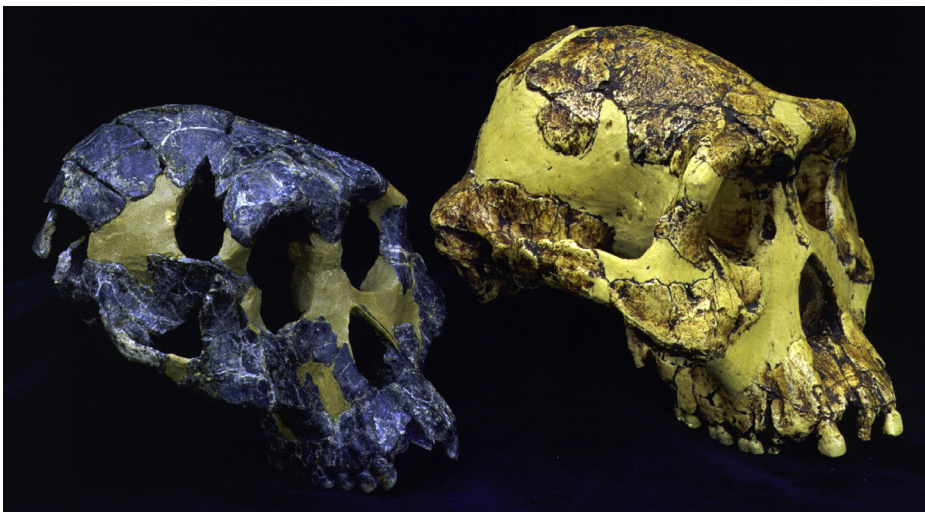
In November 1994, a *Homo* maxilla (Fig. 14) was discovered at A.L. 666 (Kimbel et al., 1996) in the Makaamitalu Basin in “upper” Kada Hadar Member. The maxilla and associated stone tools scattered on the hillside eroded from a siltstone horizon 80 cm below the BKT-3, thus providing a minimum age of  $2.33 \pm 0.07$  Mya for this locality. A.L. 666 preserves the oldest known co-occurrence of *Homo* and Oldowan stone tools.

The presumably male (large canine) maxilla lacks *Australopithecus* morphology, and presents classic *Homo* anatomy, such as a deep, short antero-posteriorly, and broad, deep palate with a parabolic dental arcade. Other

*Homo* features include mild subnasal prognathism, a broad, flat subnasal plane angled relative to the floor of the nasal cavity, and square anterior maxillary profile.

Many of the morphological features resemble later *Homo* and are probably apomorphic within the *Homo* clade, making it difficult to assign A.L. 666-1 to a later species of *Homo*. Bearing this in mind, the narrowing of the M<sup>1</sup> and the “rhomboidal” shape of the M<sup>3</sup> suggest similarities to *H. habilis* (Kimbel et al., 1997).

Excavations at A.L. 894, penecontemporaneous with A.L. 666 in the Makaamitalu Basin, uncovered *in situ* bone and lithic artifacts. The excavated lithics consist of small flakes



**Fig. 13.** Hadar Skulls: left female, A.L. 822-1; right, male, A.L. 444-1.

**Fig. 13.** Crânes d'Hadar : à gauche, femelle, A.L. 822-1 ; à droite, mâle, A.L., 444-1.

and flake fragments as well as some larger flakes and a core. That these artifacts were produced “on the spot” as is confirmed by the refitting of an angular flakes onto cores (Hovers, 2009).

*A. afarensis* fossil remains are now known from other sites in Ethiopia: Maka (White, 1993; White et al., 2000), Dikika (Alemseged et al., 2006), Galili (Macchiarelli et al., 2004), Belohdelie (Asfaw, 1987), Lake Turkana (Kimbel, 1988), Woranso-Mille (Haile-Selassie et al., 2010), and Omo (Suwa, 1990). The Bahr-el-Ghazal mandible from Chad (Brunet et al., 1996) is assigned here to *A. afarensis*.

*A. afarensis* is, therefore, the most geographically widely ranging and the longest temporally enduring species – 800,000 years – of *Australopithecus*. The Hadar sample, now consisting of more 400 specimens, represents more than 90% of the *A. afarensis* hypodigm.

One crucial missing element in understanding *A. afarensis* anatomy was a complete skull. An adult male skull reconstruction of an *A. afarensis* skull was based on 13 specimens from the Hadar Formation (Kimbel and White, 1988; Kimbel et al., 1984). This composite served as a guide to skull architecture, but an associated cranium and mandible was needed to better understand details of the cranio-facial architecture.

The recovery in 1990 of a 3.0 Mya male skull from A.L. 444 fulfilled a vital gap in our knowledge (Kimbel et al., 1994) of *A. afarensis* cranio-facial anatomy (Fig. 13). The A.L. 444 skull from an elderly individual based on heavy dental wear constitutes the largest *Australopithecus* skull thus far discovered.

Overall, the male skull confirms earlier observations made on the composite skull, but provides further anatomical detail of regions missing in that reconstruction. A small sagittal crest is present posteriorly, rather than commencing on the frontal squama, as in *A. boisei*. Like other *A. afarensis* occipitals, this skull has an ape-like compound temporal/nuchal crest. In facial view, the orbits are squared off laterally and the face is very tall. While little can be said of endocranial gyri and sulci patterns, the endocranial volume is estimated to be  $550 \pm 10 \text{ cm}^3$ ; larger in comparison to estimates for A.L. 162 (female) of  $400 \text{ cm}^3$ , and for A.L. 333-45 (male) of  $485 \text{ cc}$ . (see Kimbel et al., 2004, for a monographic treatment of the anatomy of A.L. 444-1).

A slightly older, 3.1 Mya, but nearly complete second skull (Fig. 13) was found in 2002 at A.L. 822 (Johanson and Edgar, 1996). The anatomy of this small, presumably female, skull demonstrates classic *A. afarensis* cranial anatomy with expected minor anatomical variations.

While small in size, the A.L. 822-1 is larger than A.L. 288-1, confirming that “Lucy” is one of the smallest examples of her species. The A.L. 822 mandible is intermediate in size between the smaller A.L. 288 and the much larger A.L. 444 mandibles.

While the majority of Hadar hominid specimens recovered since 1990 are dental and cranial remains, a partial, very large, skeleton from A.L. 438 (Kimbel et al., 1994) offers some insight into both locomotion and size variation of *A. afarensis*. This specimen dated to 3.0 Mya preserves the right half an edentulous mandible, a fragment of frontal bone, a complete left ulna, two second metacarpals, one

third metacarpal and portions of a humerus, radius, right ulna and fragment of clavicle.

Although the slightly curved A.L. 438 ulna is nearly twice the size of the “Lucy” ulna, the two ulnae are otherwise anatomically identical, further confirming a high level of sexual dimorphism in *A. afarensis*. Drapeau et al. (2005) concluded that the anatomy of the metacarpal and ulna are shared with humans. Rather than interpreting the marked muscularity in the ulna as indicating significant arboreal activity, she posits that it may reflect activities associated with food gathering.

## 6. Phylogenetic considerations

Examples of anagenesis in early hominin evolution have been notoriously challenging to identify. This has been due to a number of factors, most notably the paucity of well-dated and complete fossils, but with enlarged data sets we can begin to extend a number of reasonable hypotheses by assessing ancestor-descendant anatomies. A case in point is the proposed *A. afarensis*, *A. aethiopicus*, *A. boisei* lineage outlined above.

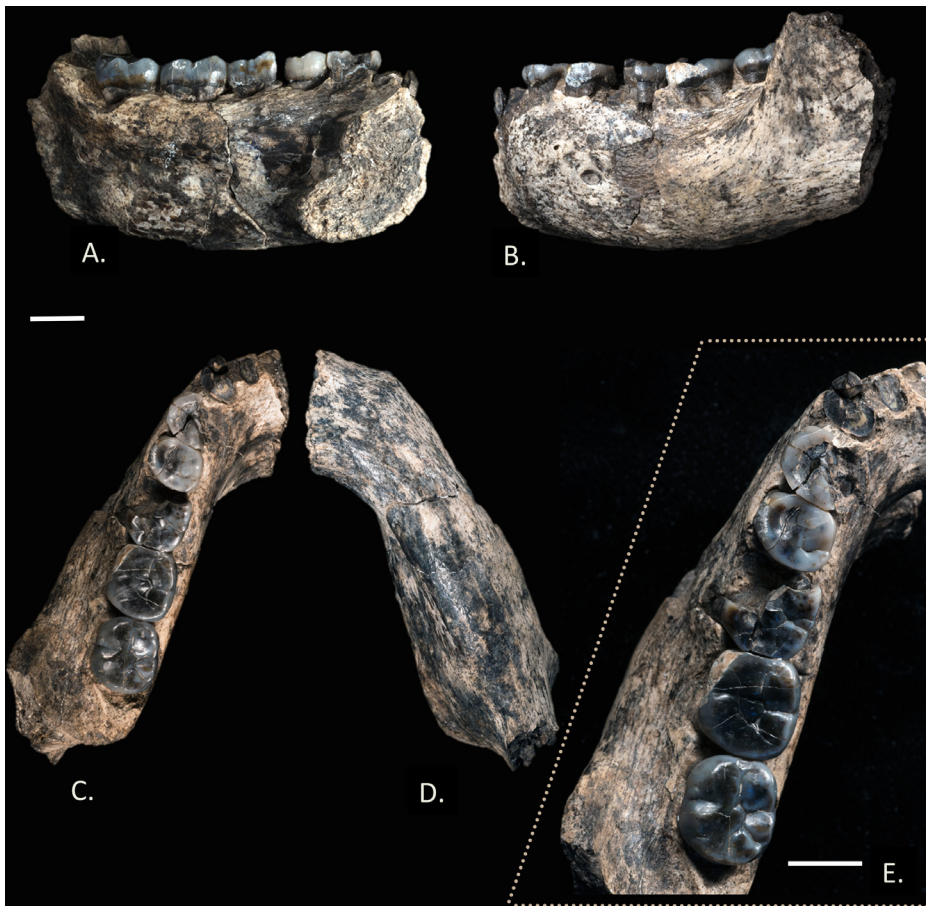
*A. anamensis*, first identified in the Lake Turkana region at two sites, Kanapoi (Fig. 15) and Allia Bay (Leakey et al., 1995, 1998; Ward et al., 2001) is dated to between 4.2 and 3.9 Mya. This is chronologically just prior to the appearance of *A. afarensis*, hence it was logical to undertake a detailed comparison of the 80 *A. anamensis* specimens with the more than 400 *A. afarensis* fossils.

Following exhaustive comparative investigation of some 20 characters found in the mandible, maxilla and dentition, we conducted a phylogenetic analysis employing McClade 4.07 to generate trees based on the collected character-state data. It was concluded that the most parsimonious explanation, consistent with both chronology and



Fig. 15. *A. anamensis* mandible from Kanapoi, Kenya.

Fig. 15. Mandibule d'*A. anamensis* de Kanapoi, Kenya.



**Fig. 16.** Ledi-Geraru, Ethiopia 2.8 Mya *Homo* mandible, LD350-1. Views: A. Medial. B. Lateral. C. Occlusal. D. Basal. E. Close up of teeth. (Courtesy W. H. Kimbel).

**Fig. 16.** Mandibule LD350-1 d'*Homo* datant de 2,8 Ma de Ledi-Geraru, Éthiopie. Vues : A. Médiale. B. Latérale. C. Occlusale. D. Basale. E. Obturation des dents (avec l'aimable autorisation de W.H. Kimbel).

character-state was anagensis, meaning that *A. anamensis* was the ancestor to *A. afarensis* (Kimbel et al., 2006).

Attempts to understand the ancient roots of the *Homo* lineage have been hampered by the dearth of *Homo* fossils dating in excess of 2.0 Mya. By roughly 2.0 Mya we see some diversity in *Homo* species: *H. habilis*, *H. rudolfensis*, *H. ergaster* and perhaps *H. georgicus* (Gabounia et al., 2002) hinting at a pre-2.0 Mya origin of the genus. From a paleontological point of view, it is worth observing we know much more about the genus *Australopithecus* than we do about our own genus.

Recovery of the A.L. 666-1 *Homo* mandible dated to 3.4 Mya bridged part of the temporal gap between 1.8-2.0 Mya. However, this still leaves a 600,000 gap between the last occurrence of *A. afarensis* and *Homo* at 2.4 Mya in the Makaamitalu Basin.

The recent fortuitous discovery of a 2.8 Mya partial mandible with teeth from the Ledi-Geraru research area in the Afar Triangle attributed to *Homo* allows further testing of the hypothesis that *A. afarensis* was ancestral to later *Homo* (Villmoare et al., 2015). Analysis of the anatomy of LD 350-1 (Fig. 16) revealed symmetrical premolars and narrow, mesiodistally elongated molars as well as



**Fig. 17.** *A. garhi* cranium from Bouri, Ethiopia (Courtesy David Brill).

**Fig. 17.** Crâne d'*A. garhi*, en provenance de Bouri, Éthiopie) (avec l'aimable autorisation de David Brill).

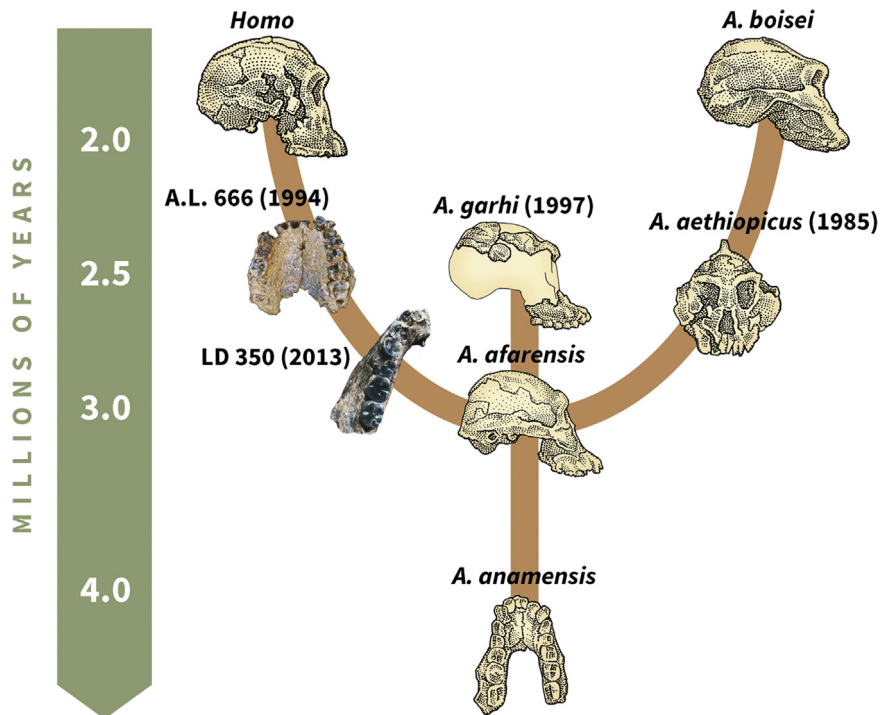


Fig. 18. Current status of early hominin phylogeny.

Fig. 18. État actuel de la phylogénie des premiers hominins.

an evenly- proportioned mandible, from front to back; features all shared with later mandibles of *Homo*.

On the other hand, the mandible preserves *A. afarensis*-like anatomy in the anterior portion of the jaw. The primitive anterior corpus, inclined symphyseal cross section, bulbous anterior symphyseal face and the projecting inferior transverse torus are typical of *A. afarensis*.

The discovery of a 2.5 Mya cranium from Bouri, Middle Awash, Ethiopia (Asfaw et al., 2004) also appears to be a lineal descendant of *A. afarensis* (Fig. 17). The cranium (BOU-VP-112/130) with a small cranial capacity of 450 cc, exhibits a number of features that link it to *A. afarensis* particularly in the marked subnasal prognathism, posteriorly placed sagittal crest, large canine and U-shaped dental arcade.

What distinguishes this specimen, assigned to *A. garhi*, is the megadont postcanine dentition, shared with robust *Australopithecus*. In *A. boisei*, the large postcanine dentition is linked to an orthognathic, dish-shaped face, but in *A. garhi* it is linked to a very prognathic face, like in *A. afarensis*. It therefore appears that *A. garhi* may also be an evolutionary descendant of *A. afarensis*; one that apparently left no descendants.

It thus appears that *A. afarensis* gave rise to at least three descendant lineages: *Homo*, *A. garhi*, and *A. aethiopicus* to *A. boisei*. Furthermore, *A. anamensis* is the mostly likely ancestor to *A. afarensis*. There is no doubt that additional hominin discoveries may alter this hypothesis, but for the moment it is consistent with the anatomical and chronological data (Fig. 18).

## 7. Conclusion

From this brief overview it is clear that *A. afarensis* continues to play a pivotal role in our ever-expanding knowledge of early hominin evolution. The large data set for this species, and numerous specimens that have not yet been described, make *A. afarensis*, the most comprehensively represented ancient hominin species, over time and geography.

The discovery and naming of *A. afarensis* during the 1970s stimulated four decades of novel research approaches to early hominin paleoanthropology. This species serves as a critical resource for interpreting other Pliocene fossil hominin discoveries.

The disappearance of *A. afarensis* around the 3.0 Mya data and the subsequent diversification into at least three lineages is provocative. There is much debate about climate change and resulting speciation among hominins, but *A. afarensis* currently presents an ape-like species that sits at a pivotal place on the human family tree between more primitive species and more derived species.

While *A. afarensis* is clearly not the most ancient or most ape-like hominin species, it is by far the foremost fossil record for major transitions in the locomotor, cranial and masticatory systems. And, as a result of the intense focus by the IARE and the HRP at Hadar and the surrounding area, other teams are finding crucial fossils, further fleshing out our comprehension of the genus *Australopithecus*, but also the origins of the human genus, *Homo*.

## Acknowledgments

I wish to express my gratitude to the organizer, Marcel Otte, for his invitation to present a paper at the colloquium on *L'évolution humaine : des gènes à la culture*, sponsored by the Académie des sciences, Institut de France. I also thank him for his patience in waiting for my contribution.

My special appreciation to the Ethiopian Ministry of Culture and Tourism, the Authority for Research and Conservation of Cultural Heritage, and the National Museum of Ethiopia for all their generous assistance during our research in Ethiopia. The Afar Regional State Government and the residents of Eloaha village deserve much appreciation for their friendship and participation during our field expeditions at Hadar.

There have been 100s of colleagues, students, friends, who deserve my sincerest gratitude for the work I have done in Ethiopia over the last 46 years.

The scientific results presented in this article are the result of the dedication of a host of colleagues and students who have chosen to explore one of the most engaging questions humans ask themselves – Where did we come from?

Finally, I wish to dedicate this paper to my dear friend, Maurice Taieb. Maurice is one of the most generous scholars I have ever met, and if we know more about human origins, we thank Maurice, since he was the intrepid explorer who led us all to the Afar Triangle – “Merci”, Maurice. . .

## References

- Alemseged, Z., Spoor, F., Kimbel, W.H., Bobe, R., Geraads, D., Reed, D., Wynn, J.G., 2006. A juvenile early hominin skeleton from Dikika, Ethiopia, and its geological context. *Nature* 443 (21), 296–301.
- Asfaw, B., 1987. The Belohdelie frontal: new evidence of early hominid cranial morphology from the Afar of Ethiopia. *J. Hum. Evol.* 16 (7), 611–624.
- Behrensmeyer, A.K., 2008. Paleoenvironmental context of the Pliocene AL 333 ‘first family’ hominin locality, Hadar Formation, Ethiopia. *Geol. Soc. Amer. Spec. Pap.* 446, 203–214.
- Behrensmeyer, K., Harmon, E.H., Kimbel, W.H., 2003. Environmental context and taphonomy of the First Family hominid locality, Hadar, Ethiopia. *J. Vert. Paleontol.* 23 (Suppl. 3), 33A.
- Bobe, R., Eck, G.G., 2001. Responses of African bovids to Pliocene climatic change. *Paleobiology* 27 (Suppl. 2), 1–48.
- 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. U.S.A.* 101 (33), 12125–12129.
- Brunet, M., Beauvilain, A., Coppens, Y., Heintz, E., Moutaye, A.H.E., Pilbeam, D., 1996. *Australopithecus bahrelghazali*, une nouvelle espèce d’Hominidé ancien de la région de Koro Toro (Tchad). *C. R. Acad. Sci. Paris, Ser. II* 322, 907–913.
- Campisano, C.J., Feibel, C.S., 2008a. Depositional environments and stratigraphic summary of the Pliocene Hadar formation at Hadar, Afar depression, Ethiopia. *Geol. Soc. America Special Papers* 446, 179–201.
- Campisano, C.J., Feibel, C.S., 2008b. Tephrostratigraphy of the Hadar and Busidima Formations at Hadar, Afar Depression, Ethiopia. *Geol. Soc. Amer. Spec. Pap.* 446, 135–162.
- Drapeau, M.S.M., Ward, C.V., Kimbel, W.H., Johanson, D.C., Rak, Y., 2005. Associated cranial and forelimb remains attributed to *Australopithecus afarensis* from Hadar, Ethiopia. *J. Hum. Evol.* 48 (6), 593–642.
- Falk, D., Gage, T.B., Dudek, B., Olson, T.R., 1995. Did more than one species of hominid coexist before 3.0 ma? Evidence from blood and teeth. *J. Hum. Evol.* 29 (6), 591–600.
- Gabounia, L., de Lumley, M.A., Vekua, A., Lordkipanidze, D., de Lumley, H., 2002. Découverte d’un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie). *C. R. Palevol* 1, 243–253.
- Hailemichael, M., (Ph.D. Dissertation) 2000. The Pliocene environment of Hadar, Ethiopia: a comparative isotopic study of paleosol carbonates and lacustrine mollusk shells of the Hadar Formation and of modern analogs. Case Western Reserve University.
- Hailemichael, M., Aronson, J.L., Savin, S., Tevesz, M.J.S., Carter, J., 2002.  $\delta^{18}\text{O}$  mollusk shells from Pliocene Lake Hadar and modern Ethiopian lakes: implications for history of the Ethiopian monsoon. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 186, 81–99.
- Haile-Selassie, Y., Bruce, M., Latimer, B.M., Mulugeta Alene, M., Deino, A.L., Gibert, L., Melillo, S.M., Saylor, B.Z., Scott, G.R., Lovejoy, C.O., 2010. An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia. *Proc. Natl. Acad. Sci. USA.* 107 (27), 12121–12126.
- Hovers, E., 2009. Learning from mistakes: flaking accidents and knapping skills in the assemblage of AL 894 (Hadar, Ethiopia). *The Cutting Edge: New Approaches to the Archaeology of Human Origins*, 3. Stone Age Institute Press Publications, Series, pp. 137–148.
- Johanson, D.C., 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, D.C., et al. (Eds.), 1982. Pliocene Hominid Fossils from Hadar, Ethiopia. *Am. J. Phys. Anthropol.* 57, 373–719.
- Johanson, D.C., Taieb, M., 1976. Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. *Nature* 260, 293–297.
- Johanson, D.C., White, T.D., Coppens, Y., 1978. A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa. *Kirtlandia* 28, 1–11.
- Johanson, D.C., 1978. Early African hominid phylogenesis: a re-evaluation. In: Königsson, L.-K. (Ed.), Current argument on early man. Proc. of a Nobel symposium organized by the Royal Swedish Academy of Sciences and held at Björkborns Herrgård, Karlskoga, Sweden, 21–27 May, 1978, Pergamon (1980), pp. 31–69.
- Johanson, D.C., Edgar, B., 1996. From Lucy to Language. Simon and Schuster, pp. 272 p.
- Johanson, D.C., White, T.D., 1979. A systematic assessment of early African hominids. *Science* 203 (4378), 321–330.
- Kimbel, W.H., 1988. Identification of a partial cranium of *Australopithecus afarensis* from the Koobi Fora Formation, Kenya. *J. Hum. Evol.* 17 (7), 647–656.
- Kimbel, W.H., White, T.D., 1988. A revised reconstruction of the adult skull of *Australopithecus afarensis*. *J. Hum. Evol.* 17, 45–50.
- Kimbel, W.H., Deleuzene, L.K., 2009. Lucy redux: A review of research on *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 140 (S49), 2–48.
- Kimbel, W.H., White, T.D., Johanson, D.C., 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, W.H., White, T.D., Johanson, D.C., 1988. Implications of KNM-WT 17000 for the Evolution of the ‘Robust’ *Australopithecus*. In: Grine, F.E. (Ed.), Evolutionary History of the ‘Robust’ Australopithecines. pp. 259–268.
- Kimbel, W.H., Johanson, D.C., Rak, Y., 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature* 368 (6470), 449–451.
- Kimbel, W.H., Walter, R.C., Johanson, D.C., Reed, K.E., Aronson, J.L., Assefa, Z., Marean, C.W., Eck, G.G., Bobe, R., Hovers, E., Rak, Y., 1996. Late Pliocene *Homo* and Oldowan Tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *J. Hum. Evol.* 31 (6), 549–561.
- Kimbel, W.H., Johanson, D.C., Rak, Y., 1997. Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. *Am. J. Phys. Anthropol.* 103, 235–262.
- Kimbel, W.H., Rak, Y., Johanson, D.C., 2004. The skull of *Australopithecus afarensis*. Oxford University Press.
- Kimbel, W.H., Lockwood, C.A., Ward, C.V., Leakey, M.G., Rak, Y., Johanson, D.C., 2006. Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record. *J. Hum. Evol.* 51 (2), 134–152.
- Leakey, L.S.B., 1959. A new fossil skull from Olduvai. *Nature* 184 (4685), 491–493.
- Leakey, M.D., Harris, J.M., 1987. Laetoli, a Pliocene site in northern Tanzania. Clarendon Press, Oxford University Press.
- Leakey, R.E., Walker, F.A.C., 1980. On the status of *Australopithecus afarensis*. *Science* 207, 1103.
- Leakey, M.G., Feibel, C., McDougall, I., Walker, A., 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376 (6541), 565–571.
- Leakey, M.G., Feibel, C., McDougall, I., Ward, C., Walker, A., 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* 393 (6680), 62–66.
- Lovejoy, C.O., 1988. Evolution of human walking. *Sci. Am.* 259 (5), 118–125.
- Lovejoy, C.O., 1981. The origin of man. *Science* 211 (4480), 341–350.

- Macchiarelli, R., Bondioli, L., Falk, D., Faupl, P., Illerhaus, B., Kullmer, O., Richter, W., Said, H., Sandrock, O., Schäfer, K., Urbanek, C., 2004. Early Pliocene hominid tooth from Galili, Somali region, Ethiopia. *Coll. Antropol.* 28 (2), 65–76.
- Olson, T.R., 1981. Basicranial morphology of the extant hominoids and Pliocene hominids: the new material from the Hadar Formation, Ethiopia and its significance in early human evolution and taxonomy. In: Stringer, C.B. (Ed.), *Aspects of Human Evolution*. Taylor and Francis, London, pp. 99–128.
- Reed, K.E., 2008. Paleocological Patterns at the Hadar Hominin Site, Afar Regional State, Ethiopia. *J. Hum. Evol.* 54, 743–768.
- 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 (11), 1067–1070.
- Senut, B., 1983. Les hominidés plio-pléistocènes : essai taxinomique et phylogenetique à partir de certains os longs. *Bull. Mem. Soc. Anthropol.* 10 (3), 325–334.
- Skelton, R.R., McHenry, H.M., Drawhorn, G.M., Bilsborough, A., Chamberlain, A.T., Wood, B.A., Vančata, V., 1986. Phylogenetic analysis of early Hominids (and comments and reply). *Curr. Anthropol.* 1986, 21–43.
- Stern Jr., J.T., Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60 (3), 279–317.
- Susman, R.L., Jack, T., Stern Jr., J.T., Jungers, W.L., 1984. Arboreality and bipedality in the Hadar hominids. *Folia Primatol.* 43 (2–3), 113–156.
- Suwa, G., 1990. A comparative analysis of Hominid Dental remains from the Shungura and Usno formation, Omo Valley, Ethiopia, Vol. 1. University of California, Berkeley.
- Taieb, M., Coppens, Y., Johanson, D.C., Kalb, J., 1972. Dépôts sédimentaires et faunes du plio-pléistocène de la basse vallée de l'Awash (Afar central, Éthiopie). *C. R. Acad. Sci. Paris Ser. D* 275, 819–882.
- Taieb, M., Johanson, D.C., Coppens, Y., Bonnefille, R., Kalb, J.E., 1974. Découverte d'Hominidés dans les séries plio-pléistocènes d'Hadar (bassin de l'Awash; Afar, Éthiopie). *C. R. Acad. Sci. Paris Ser. D* 279, 735–738.
- Taieb, M., Johanson, D.C., Coppens, Y., 1975. Expédition internationale de l'Afar, Éthiopie (3<sup>e</sup> campagne 1974), découverte d'Hominidés plio-pléistocènes à Hadar. *C. R. Acad. Sci. Paris, Ser. D* 281, 1297–1300.
- Tardieu, C., 1981. Morpho-functional analysis of the articular surfaces of the knee-joint in primates. In: *Primate evolutionary biology*. Springer Berlin Heidelberg, pp. 68–80.
- Tobias, P.V., 1980. *Australopithecus afarensis* and *A. africanus*: critique and an alternative hypothesis. *Palaeont. Afr.* 23, 1–17.
- Villmoare, B., Kimbel, W.H., Seyoum, C., Campisano, C.J., DiMaggio, E.N., Rowan, J., Braun, D.R., Arrowsmith, J.R., Reed, K.E., 2015. Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science* 347 (6228), 1352–1355.
- Walker, A., Leakey, R.E., 1988. The evolution of *Australopithecus boisei*. Evolutionary history of the 'Robust' Australopithecines. Aldine de Gruyter Hawthorne, New York, pp. 247–258.
- Walker, A., Leakey, R.E., Harris, J.M., Brown, F.H., 1986. 2.5-myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature* 322, 517–522.
- Walter, R.C., 1994. Age of Lucy and the first family: single-crystal <sup>40</sup>Ar/<sup>39</sup>Ar dating of the Denen Dora and lower Kada Hadar members of the Hadar Formation, Ethiopia. *Geology* 22 (1), 6–10.
- Walter, R.C., Aronson, J.L., 1993. Age and source of the Sidi Hakoma tuff, Hadar formation, Ethiopia. *J. Hum. Evol.* 25 (3), 229–240.
- Ward, C.V., Leakey, M.G., Walker, A., 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *J. Hum. Evol.* 41 (4), 255–368.
- White, T.D., Suwa, G., Simpson, S., Asfaw, B., 2000. Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *Am. J. Phys. Anthropol.* 111 (1), 45–68.
- White, T.D., Johanson, D.C., Kimbel, W.H., 1981. *Australopithecus africanus*: its phyletic position reconsidered. *S. Afr. J. Sci.* 77, 445–470.
- White, T.D., 1993. New discoveries of *Australopithecus* at Maka in Ethiopia. *Nature* 366 (6452), 261–265.