



HAL
open science

First hominin from the Basal Member of the Hadar Formation, Dikika, Ethiopia

Zeresenay Alemseged, Jonathan Wynn, William Kimbel, Denné Reed, Denis Geraads, René Bobe

► **To cite this version:**

Zeresenay Alemseged, Jonathan Wynn, William Kimbel, Denné Reed, Denis Geraads, et al.. First hominin from the Basal Member of the Hadar Formation, Dikika, Ethiopia. *Journal of Human Evolution*, 2005, 49, pp.499-514. halshs-00009681

HAL Id: halshs-00009681

<https://shs.hal.science/halshs-00009681>

Submitted on 20 Mar 2006

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

First hominin from the Basal Member of the Hadar Formation, Dikika, Ethiopia

Zeresenay Alemseged

Department of Human Evolution,

Max Planck Institute for Evolutionary Anthropology,

Deutscher Platz 6, D-04103 Leipzig, Germany

E-mail - zeray@eva.mpg.de,

Tel.: 49 341 - 35 50 353

Fax: 49 341 - 35 50 399

Jonathan G. Wynn

Department of Geography and Geosciences,

Irvine Building, University of St. Andrews, St. Andrews, Fife,

Scotland, KY16 9AL, United Kingdom

E-mail - jonathan.wynn@st-andrews.ac.uk

William H. Kimbel

Institute of Human Origins & Dept. of Anthropology,

Arizona State University, P.O. Box 874101 ,

Tempe, AZ 85287-4101, USA

E-mail - wkimbel.iho@asu.edu

Denné Reed

Dept. of Paleobiology,

National Museum of Natural History Smithsonian Institution

10th and Constitution Ave. NW , Washington, DC 20560

E-mail - denne@umich.edu

Denis GERAADS

CNRS UPR 2147,

44 rue de l'Amiral Mouchez,

F-75014 PARIS, FRANCE

E-mail - dgeraads@ivry.cnrs.fr

René Bobe

Department of Anthropology,

State University of New York at Buffalo

380 MFAC Ellicott Complex, Buffalo NY 14261-0026

E-mail - renebobe@buffalo.edu

Running title: First hominin from the Basal Member of the Hadar...

Number of pages: 37

Number of Figures: 11

Number of Tables: 3

Key words: Pliocene, Hominin evolution, *Australopithecus afarensis*, Hadar Formation, Dikika, Ethiopia.

Abstract

In this paper new hominin remains are reported for the first time from the Basal Member of the Hadar Formation, at Dikika, in the Awash Valley of Ethiopia, dating to greater than 3.4 Ma. The new fossils are represented by a fragment of a left mandible and associated dentition. This mandible (DIK-2-1) was recovered by the Dikika Research Project (DRP) and is attributed to *Australopithecus afarensis* based on the suite of characters that it shares with this species. However, the new fossil possesses a few metric and morphological features that hitherto are not encountered in other specimens from the *A. afarensis* hypodigm, increasing the known degree of variation of the species.

Introduction

The Hadar Formation of Ethiopia is well known for its contributions to our knowledge of the species *Australopithecus afarensis* (e.g., Johanson et al., 1978, 1982; Kimbel et al., 1994, 2004). The vast majority of the species' hypodigm, including the partial skeleton known as "Lucy," comes from Hadar Formation sediments exposed at the Hadar site, which is located near the village of Eloaha in the Awash River valley. In addition to Hadar, remains of *A. afarensis* have been recovered from 1) the Laetolil Beds in Tanzania (where the type specimen, LH-4, was found); 2) undesignated strata near Fejej in southwestern Ethiopia (Asfaw et al., 1991; Kappelman et al., 1996); 3) the Tulu Bor Member of the Koobi Fora Formation, east of Lake Turkana, Kenya (Kimbel, 1988); 4) the Nachukui Formation, west of Lake Turkana, Kenya (Brown et al., 2001); and 5) undesignated strata of the Middle Awash valley of Ethiopia (White et al., 2000). The aggregate time span of the species is at least 0.7 myr (Kimbel et al., 2004).

Large hominin sample size and temporal continuity at Hadar have allowed researchers to assess variation in *A. afarensis* introduced by both sexual dimorphism (Kimbel & White, 1988; Kimbel et al., 1994, 2004) and time (Lockwood et al., 2000). However, data on *A. afarensis* and other early hominins are meager during the time period between that represented by Hadar and Laetoli (3.7-3.4 Ma), and between those and even older sites, such as Allia Bay and Kanapoi (3.9 – 4.1 Ma) that contain the remains of *A. anamensis*, the probable ancestor of *A. afarensis* (Leakey et al., 1995; Leakey et al., 1998; Kimbel et al., in prep.). While samples from Hadar and Laetoli are attributed to *A. afarensis*, there is perceptible morphological variation within the hypodigm of this species, mostly introduced by differences in geological age and

geographical location, with the older Laetoli sample resembling *A. anamensis* more closely than does the younger Hadar assemblage of *A. afarensis* (White, 1985; Lockwood et al., 2000; Kimbel et al., 2004, in prep.). Additional hominin fossils from this time interval are thus critically important as they could shed light on the nature of the differences between the Hadar and Laetoli samples and the relationship between *A. afarensis* and *A. anamensis*. Moreover, increasing the fossil sample from sediments older than 3.4 Ma could enable testing of hypotheses concerning the amount of lineage diversity during mid-Pliocene time (Brunet et al., 1996; Leakey et al., 2001).

In this paper, we describe DIK-2-1, a left mandibular fragment of a hominin from the Basal Member of the Hadar Formation, of Dikika, Ethiopia, and discuss its taxonomic affinities. This specimen is relevant to these issues because it is the first hominin recovered from the Basal member, which is the oldest of the formally recognized units of the Hadar Formation.

The Basal Member of the Hadar Formation, includes the strata below the Sidi Hakoma Tuff (SHT; older than 3.4 Ma [Walter and Aronson, 1993]), and is well exposed on the southeastern side of the Awash River adjacent to the Hadar and Gona research areas (Figure 1). Due to the slight dip of the sediments and regional faulting, the Basal Member is exposed in only small patches on the north banks of the Awash at Hadar. Positioned at approximately 11° 10' N 40° 60' E, Dikika is south of, and across the Awash River from, the Hadar research area (Figure 1). Part of the Dikika area was mapped as part of the RVRME (Rift Valley Research Mission in Ethiopia) during the 1970s, and its lithostratigraphy was defined as part of the Hadar Formation of the Awash Group by Kalb et al. (1982). Most stratigraphic descriptions of the Hadar Formation

made during the 1970's focused on the stratotype Hadar sections north of the Awash River. Some of this early work shows maps and sections of the Hadar Formation in the Dikika area south of the Awash River. The Dikika exposures were mapped as the Basal and Sidi Hakoma Members of the Hadar Formation (Taieb & Tiercelin, 1980; Kalb et al., 1982a; Tiercelin, 1986). Tiercelin (1986) provides several sections of the Basal Member at Ounda Leita, of which the thickest defines the stratotype. Stratigraphic columns of Kalb et al. (1982a) show generalized sections of the Hadar Formation near Gango Akidora, Andedo, and Mireh Kerone.

In 1974 and 1976, three hominin specimens subsequently attributed to *A. afarensis* were collected (A.L. 400-1; A.L. 277-1, A.L. 411-1; Johanson et al., 1982). Not since then, however, has paleontological and geological research been conducted in the area. The Dikika Research Project (referred as DRP hereafter), led by the senior author, has conducted four seasons (2000, 2002, and two in 2003) of field work at Dikika, under permit from the Authority for Research and Conservation of Cultural Heritage (ARCCCH) of the Ministry of Youth, Sports and Culture of Ethiopia.

Twenty faunal localities have been established at Dikika so far. Fossils of large mammals are very abundant on the surface of the deposits, including frequent occurrences of cranial fragments and long bones of elephants, hippopotamus, rhinoceros and other taxa. Two hominin fossils were also found during paleontological survey.

DIK-2-1 is a fragmentary mandible with partial dentition of an adult individual. It derives from a stratigraphic horizon ~ 20 m below the Sidi Hakoma Tuff and is the first hominin to be recovered from the Basal Member of the Hadar Formation. Another hominin (DIK-1-1) fossil is a spectacularly well-preserved partial skeleton of an

immature individual, stratigraphically from just above the Sidi Hakoma Tuff. The DIK-1-1 specimen consists of the entire skull, the scapulae, the ribs, the clavicles and some of the vertebral column and limb bones embedded in blocks of sandstone matrix. This specimen is, at the time of writing, undergoing cleaning and preparation, and will be the subject of forthcoming publications. In this paper, DIK-2-1, the adult mandible, is described and its significance for the evolution of early hominins is addressed.

Stratigraphic, Sedimentary and Paleoenvironmental Context of the DIK-2 Hominin Fossil

The DIK-2 locality lies at the base of a small ridge capped by a thin cross-bedded sandstone (at 6-7 meters in the section of Figure 2) in the headwaters of the Gango Akidora stream (Figure 1). The sedimentary unit producing the fossils falls stratigraphically below a very prominent channel exposure of redeposited vitric tephra and a co-occurring laterally extensive bentonite that we have identified as the Sidi Hakoma Tuff by chemical analysis of glass shards from the tuffaceous channel (Table 1). Using the date of 3.40 ± 0.03 Ma for the Sidi Hakoma Tuff (Brown, 1982; Brown and Cerling, 1982; Walter and Aronson, 1993), and extrapolating the sedimentation rate calculated from strata overlying the tuff, we estimate an age of slightly greater than 3.4 Ma for the hominin mandible.

The entire section in the Gango Akidora and Ilanle areas exposes approximately 110 m of the Basal Member through lower Kada Hadar Members of the Hadar Formation, and contains a number of widespread stratigraphic markers identified in the Hadar Formation (stratigraphic terminology of Taieb et al., 1972). The SHT and its

associated bentonite can be traced throughout the area, as can a series of gastropod-bearing coquinas (SH-g), and regionally extensive ostracod-bearing clays (SH-o). The Triple Tuff-4 (TT-4) is clearly present within this clay deposit, and is recognized by its thin layer of feldspar crystals and altered glass shards (Walter, 1994). The Kada Hadar Tuff (KHT), which defines the base of the Kada Hadar Member, and a distinctive green, spheroidally weathering clay identified as the Confetti Clay (CC) cap the local section above DIK-2, occur near the top of the section.

Although there are intervals indicating lacustrine sedimentation, no part of the section indicates a large stable lake existing over extended periods of time. Rather, pedogenic modification of deltaic and shoreline deposits through most of the section indicates a rapidly fluctuating ephemeral lake within a delta or inland delta depositional system. Three periods of relatively stable lacustrine settings are indicated by a diatomite (overlying the SHT) and surrounding laminated clays (1-2 m thickness in most sections), the ostracod-bearing laminated clays in the upper Sidi Hakoma Member (up to 7 m), and the CC in the lower Kada Hadar Member (less than 1 m). Due to their regionally extensive depositional nature, these strata make good stratigraphic marker horizons, the first of which can be used as an approximation of the depositional surface of the SHT. The sedimentary character of the channel of SHT at DIK-2 indicates deposition in a large distributary channel. This extensive, tabular medium-scale cross bedded sand would have been deposited during a phase of high sediment transport when a delta channel lobe prograded across a low-gradient basin. Similar subaerial sedimentation in the delta plain and delta channel systems persists through the section below the SHT in Gango Akidora,

while the Basal Member elsewhere, such as at Ounda Leita, is entirely lacustrine (Tiercelin, 1986).

Average sediment accumulation through the Sidi Hakoma Member at Gango Akidora is 33 cm/ka, which is comparable to that calculated for the type section at Hadar (32 cm/ka), but lower than that calculated at Andedo and Simbildere to the east (43 cm/ky), and lower still than the 87 cm/ka calculated from the eastern Hadar area (Walter, 1994). The relatively low sediment accumulation of the Gango Akidora section is consistent with predominantly fluvial depositional environments, some distance from the local depocenter to the northeast.

Fauna and paleoenvironment

Faunal remains are not as common at DIK-2 as at other localities in the Dikika area. Nonetheless, the fauna does include aquatic taxa such as fishes, crocodiles, and hippopotamids. Land vertebrates from this locality include the tortoise *Geochelone*, a edentulous mandible fragment of a small carnivore, a tooth fragment of the impala *Aepyceros*, a mandible fragment of an alcelaphine bovid, and two teeth of the hipparionine equid *Eurygnathohippus* cf. *afarensis*. This faunal sample is insufficient for biostratigraphic conclusions. Ecologically, the faunal sample suggests rather open environments in the proximity of water. Previous analyses of the slightly younger Sidi Hakoma Member (3.4-3.22 Ma) at Hadar show results comparable to those presented here for DIK-2. The palynological work of Bonnefille (1995) stressed the abundance of aquatic pollen in that member, while recognizing that Gramineae was the dominant taxon. Harris (1991) regarded the Sidi Hakoma Member environment as an open grassland, but Reed (1997) described it as an open woodland. Edaphic grasslands, as

indicated by an abundance of reduncine bovids (e.g., waterbuck), were significantly less prevalent in the Sidi Hakoma Member times than in the later Denen Dora Member times (3.22-3.18 Ma). In sum, the vertebrate fauna collected thus far from DIK-2 indicates the presence of a woodland-grassland landscape, close to water and/or with frequent flooding.

Recovery of DIK-2-1

DIK-2-1 consists of a fragment of the left mandibular corpus and a portion of the symphyseal region, of which the P₃, M₁, M₃ and a fragment of the M₂ were also recovered (Table 2). The specimen was found on the 12th of December 2000 by ZA. The first piece to be recovered was the symphyseal fragment. This was followed by the recovery of two corpus pieces. Screening during the same field season led to the recovery of the P₃, which joins to the root in the mandible perfectly. More intensive screening in 2002 resulted in the recovery of a fragment that reunites the corpus and the symphyseal fragments. Except for the M₃ and M₂ fragment, all mandibular pieces and teeth join cleanly.

Preservation

The mandible is preserved irregularly up to about the distal level of the M₁ posteriorly (Figure 3D). Laterally the corpus surface is abraded and pitted, with cortex lost in some areas (Figure 3A). The roots of the canine, the two premolars, and the first molar are preserved. The mesiobuccal face of the canine root is exposed (Figure 3A). The isolated crowns of the P₃ and the M₁ join the exposed roots perfectly. Only part of the anterior aspect of the symphyseal region was recovered. Posteriorly, a portion of the incisive planum is preserved (Figure 3C). The region around the genioglossal fossa is

intact, but the most inferior part of the symphyseal region is considerably abraded.

Medially, bone is missing from the alveolar region below P₄ (Figure 3B). The corpus is complete to the basal margin level below M₁, but this margin is missing below C-P₄ (Figure 3B). The alveolar bone is appreciably abraded.

Sex and Age

An enlarged canine root combined with a large P₃ indicate that DIK-2-1 is a male. The canine root measures ~ 14 mm mesiodistally. This suggests that the crown was very large. Also, corpus depth below M₁ puts DIK-2-1 among the large mandibles of *A. afarensis*. The degree of occlusal wear on the teeth demonstrates that this individual was fully adult at death. Description and comparisons¹

Mandible

Lateral Aspect (Figure 3A)

There is no hint of the lateral prominence below M₁ as there is in most *A. afarensis* specimens; instead this surface is flat and vertical to the basal margin of the corpus, at least in the preserved part. The lateral corpus hollow in DIK-2-1 is vertically oriented and is anteroposteriorly very narrow. Thus, the hollow does not display the typical *A. afarensis* morphology, in which the hollow is anterosuperiorly elongate and

¹ In this study comparison are made with fossil material that are roughly contemporaneous with the specimen described here, namely that of *A. afarensis* and *A. anamensis*. It is worthwhile mentioning however that *Kenyanthropus platyops* and *Australopithecus bahrelghazali*, proposed early hominin taxa come from time periods roughly contemporaneous with that from which DIK-2-1 derives. No mandible can be attributed to *K. platyops* with certainty. However, Leakey et al. (2001) pointed out that even if KNM-WT 8556 were attributed to *A. afarensis* (as suggested by Brown et al., 2001), affiliation of this mandible with the *K. platyops* type is not contradicted by its molarized P₄. But the same authors recognized that the size of the molars is not consistent with this interpretation. On the other hand, Brown et al. (2001) showed that this specimen could be accommodated in *A. afarensis*. Thus, at this stage DIK-2 can't be compared with *K. platyops*. The holotype of *A. bahrelghazali*, KT 12/H1, is mandible fragment that comes from the Koro Toro site of Chad, and is thought to be 3.0 to 3.5 myr old on biochronological grounds (Brunet et al., 1996). However, there is little information as to the distinctiveness of this species. The features that are suggested to characterize this species, such as the morphology of the planum alveolare and the size of the transverse tori and a few others, are variably observed in *A. afarensis*.

bordered by the root of the ramus, the anterosuperiorly sweeping basal marginal torus, and the swollen alveolar region. We infer that the root of the ramus would have been more posteriorly located than in other *A. afarensis* specimens. In the Dikika mandible the mental foramen is set below mid-corpus at the level of the P₄ talonid, 25 mm inferior to the alveolar margin. It opens antero-superiorly as is common in *A. afarensis*.

Anterior Aspect

Anteriorly, the symphyseal region is flat and mildly inclined posteroinferiorly. The substantial posteroinferior inclination and marked convexity of this region in *A. anamensis* from Kanapoi, and *A. afarensis* from Laetoli (LH-4) is not observed in the Dikika specimen. The inclination of the symphyseal cross section is highly variable in *A. afarensis*, from nearly vertical (as in A.L. 288-1, 417-1, 620-1 and 444-2) to moderately inclined posteriorly (as in A.L. 277-1, 333w-60, and 400-1). The anterior surface of symphyseal region is also variable in *A. afarensis*, ranging from narrow and “pointed” to some extent, as in A.L. 288-1 and MAK-VP-1/12, to rounded and bulbous in A.L. 266-1 and 438-1. DIK-2-1 approximates the morphology of A.L. 400-1a in having rather flat anterior external corpus, but is similar to A.L. 417-1 in a more vertical orientation of the symphyseal contour.

Posterior Aspect (Figure 3C)

What remains of the post-incisive planum is biconcave, as in most *A. afarensis* mandibles. The planum is much shorter and more vertically disposed than in *A. anamensis* mandible (KNM-KP 29281). DIK-2-1 has well developed superior and mildly developed inferior transverse tori, similar to that of A.L. 400-1a and MAK-VP-1/12. The genioglossal fossa is well defined and circular.

Medial Aspect (Figure 3B)

A prominent superior transverse torus dominates the medial aspect, which is separated from the weak inferior transverse torus by a shallow subalveolar fossa. As in *A. afarensis*, but unlike in *A. anamensis*, there is no smooth transition from the subalveolar fossa to the genioglossal fossa. In medial view, the corpus becomes thinner superiorly and inferiorly from the most prominent part of the superior transverse torus, which lies above mid-corpus. The alveolar margin is damaged considerably on this side.

Basal Aspect

The narrowness of the corpus base below M₁ is remarkable, but can be matched in Hadar specimen A.L. 266-1. In contrast, MAK-VP 1/12 has a relatively thick, swollen base as in A.L. 288-1i. The preserved part of the Dikika mandible corpus base demonstrates moderate lateral eversion, as is commonly encountered in Hadar mandibles of *A. afarensis*.

Occlusal Aspect (Figure 3C)

Occlusally, the dental row from P₃ to M₁ is straight. The long axis of the tooth row runs slightly posteromedially, forming a small angle with the alveolar process, which passes posterolaterally. The nature of the transition from the lateral to anterior corpus is difficult to assess, as bone is missing in this region. But it is clear that the P₃ jugum does not mark the curved transition of the lateral corpus to the anterior aspect of the corpus, as it does in most *A. afarensis* mandibles. However, in the Dikika mandible the canine root, despite its impressive size, lies almost entirely medial to the anteroposterior axis of the postcanine tooth row (Fig. 3C), as in *A. afarensis*, and in contrast to the condition in *A. anamensis*, in which the canine is transected by this axis (Ward et al., 2001). For what is

preserved, the lateral alveolar margin is straight. The alveolar margin in this view is oriented anterolaterally, as in most *A. afarensis* but unlike *A. anamensis*, where this region is straight and aligned with the dental row.

Mandibular corpus cross section

The mandibular corpus cross section at M₁ shows that DIK-2-1 has a very flat lateral surface and a pronounced superior transverse torus (Figure 4). This combination gives the Dikika mandible an overall profile most similar to that encountered in Hadar mandible A.L. 198-1. However the latter specimen, most likely a female, exhibits more pronounced lateral hollowing and a less prominent medial superior transverse torus compared to DIK-2-1. Even though there is no trace of lateral prominence below M₁, the minimum corpus breadth of DIK-2-1 exceeds the mean in *A. afarensis*. However, because the corpus is quite tall, it has a relatively low breadth/height ratio (54.4%). The mean value for *A. afarensis* is 57.5 % with a range of 48.4% to 68.9%. Overall the Dikika mandible is comparable in size to the larger mandibles from Hadar (Figure 5).

Dentition

P₃ – The crown of the DIK-2 P₃ is complete. It is quite large, measuring 11.2 mesiodistally and 13.8 buccolingually (see below for discussion). The Dikika tooth is heavily worn, but there is evidence of a strong mesially placed transverse crest connecting the protoconid and metaconid. Occlusal wear has flattened the protoconid with an apical rounded dentine pit is exposed atop it. The protoconid is considerably larger than the metaconid and is buccally placed, as in *A. afarensis* and not as in *A. anamensis*, in which the protoconid occupies a more central post on the crown. Compared to the overall size of the tooth, the anterior fovea is small (however, this

reduction is enhanced to some degree by flattening of the mesial face from interproximal wear) and the edges of the ridges surrounding this fovea are not as sharp as in *A. anamensis*. The anterior fovea opens anteriorly and slightly lingually as in most *A. afarensis* P₃s. In *A. anamensis* this fovea opens predominantly lingually with a slight anterior component, and descends down to the level of the cervix (Ward et al., 2001; Kimbel et al., in prep). In most *A. afarensis* P₃s the prominence of the metaconid results in a bulging lingual face that partly overhangs the alveolar margin. This aspect of the P₃ crown is even more pronounced in DIK-2-1. This feature separates DIK-2-1 and most *A. afarensis* P₃s, on one hand, and those of *A. anamensis*, on the other, in which the lingual face is much less prominent due to the very small metaconid. In some *A. afarensis* mandibles, such as the Maka specimen, MAK-VP 1/12, the lingual face of the P₃ is rather flat. In DIK 2-1 the buccal face of the tooth slopes towards the apex only slightly, as in *A. afarensis*. The *A. anamensis* P₃s have much more sloping buccal faces due to the centrally positioned protoconid (Ward et al. 2001). Distally an interproximal facet of 8.5 mm flattens the distal aspect of this tooth.

In sum, the DIK-2-1 P₃ is morphologically similar to most *A. afarensis* P₃s. It differs from *A. anamensis* in the buccally placed protoconid, and a small anterior fovea that is confined to the occlusal half of the crown's mesial aspect.

M₁

The DIK-2 M₁ measures 14.7 mesiodistally and 14.0 buccolingually. The protoconid and hypoconid are heavily worn and connected by a hour-glass shaped dentine exposure measuring 9.5 mm mesiodistally and (maximally) 4.2 mm buccolingually. One mm diameter dentine pits are exposed atop the metaconid and hypoconulid; the entoconid

shows just a dot of dentine exposure. Overall, the morphology and wear pattern is similar to that of MAK-VP-1/12, but the DIK-2-1 tooth is more square (quadrate), whereas the Maka M₁ occlusal profile narrows slightly posteriorly. This means that the distal aspect displays a buccolingually expanding profile in DIK-2-1, as in A.L. 400-1a. Among the Hadar specimens of *A. afarensis*, the DIK 1-2 occlusal morphology is most similar to that of A.L. 333w-60 (Johanson et al., 1982).

M₂

This tooth preserves only a fragment of the mesial part with the metaconid and part of a heavily worn protoconid. For the preserved part, the wear pattern is as in the M₁. The enamel is thickest at the exposed distal part of the metaconid, measuring here ~ 2.2 mm.

M₃ (Figure 3E)

The DIK-2 M₃ is heavily worn and measures 18.1 mesiodistally and 14.7 buccolingually. The protoconid and hypoconid are connected by a deep dentine exposure which is 10.2 mm long and 5.5 mm wide (maximally). The metaconid, entoconid, and hypoconulid are worn flat but without dentine exposure. The occlusal morphology is similar to that observed in most *A. afarensis* M₃s, but without the considerable tapering posteriorly of the occlusal profile. The most similar specimen in this regard is A.L. 188-1. As in MAK-VP-1/12 and other *A. afarensis* specimens, there is strong wear gradient combined with retained cusp saliency. The M₃ in DIK-2 has occlusally projecting metaconid and entoconid rims but less so than in the Maka M₃.

Dental metrics

As noted already, the DIK-2 P₃ crown is very large. Its mesiodistal length lies within the *A. afarensis* range (n=23) and the value is greater than the maximum for *A.*

anamensis (n=5) (figure 6; Table 3). The buccolingual dimension surpasses that of all P₃s of *A. anamensis* (n=5) and *A. afarensis* (Hadar +Laetoli, n=23), exceeding the broadest *A. afarensis* specimen (A.L. 333w- 60) by 1 mm and the mean value for the species by about 3 mm (Figure 7; Table 3). This creates a relatively low crown shape index [(.82, compared to Hadar mean of .89 (n=21)] — i.e., a buccolingually expanded crown — but one which is similar to Hadar specimens such as A.L. 417-1a (.82), A.L. 440-1 (.83) and A.L. 288-1 (.84), and to MAK-VP- 1/12 (.84). On the other hand, the Dikika crown shape index is much lower than that calculated for the Laetoli sample (100.3, n=5), though it comes closest to LH-24 (.87).

The mesiodistal dimension of the Dikika M₁ (14.7) lies at the high end of *A. afarensis* distribution, where it falls between A.L. 241-1 and A.L. 444-2 (14.6) and A.L. 440-1 (A.L. 14.8) (Figure 8). In buccolingual breadth, DIK-2 falls 0.1 mm above maximum dimension for the pooled sample (LH-2) and 0.5 mm above the two broadest Hadar teeth (A.L. 333-74, 241-1) (Figure 9). For M₃, the mesiodistal length of DIK-2 falls above the range for *A. afarensis* teeth (by 0.9 mm; A.L. 487-1), but is within the range for buccolingual breadth, exceeded only by A.L. 188-1 and A.L. 620-1 (Figure 10 & 11). For M₁ and M₃, DIK-2-1 surpasses all *A. anamensis* specimens in both mesiodistal and buccolingual dimensions (Figures 8-11).

Discussion

DIK-2-1 possesses some of the suite of traits that have been suggested to diagnose *A. afarensis* (e.g., Johanson et al., 1978; 1982; Johanson, 1985). These include a corpus bearing a lateral hollow above the mental foramen, which lies below mid-corpus height

and opens anterosuperiorly; a rounded midsagittal profile of the anterior corpus earlier you say it is flat; and a posteriorly strong superior transverse torus and a rounded, basally set inferior transverse torus. The DIK-2-1 P₃ is also morphologically similar to that of most *A. afarensis* specimens, and differs from *A. anamensis*, in the buccally placed protoconid, a relatively prominent mesially placed metaconid, and an anterolingually directed anterior fovea that opens only part way down to the cervix (Ward et al., 2001; Kimbel et al., in prep). In addition, DIK-2-1 has a more vertically oriented symphyseal region than in *A. anamensis*. Based on these features, we attribute DIK-2-1 to *Australopithecus afarensis*. However, the Dikika specimen differs from most *A. afarensis* mandibles in the placement of the lateral corpus hollow superior but not posterior to the mental foramen; the absence of strong bulge below P₃ demarcating the hollow anteriorly; and the absence of any hint of the root of the ramus and lateral prominence below M₁. Also, the Dikika specimen's P₃ is extremely expanded, mesiodistally but especially buccolingually, and its M₃ is more rectangular rather than narrowing posteriorly.

There is a broad consensus concerning the assignment of hominins from Hadar and Laetoli to *Australopithecus afarensis* (see Kimbel et al., 2004 for a recent summary). However, many questions related to the tempo and mode of evolution of this species are not yet fully understood, although some progress along these lines has been made (Leonard & Hegmon, 1987; Lockwood et al., 2000; Ward, et al., 2003; Kimbel et al., in prep.). There remains a time gap between the two site-samples. While it has been suggested that the species exhibits stasis throughout its temporal range (Johanson & White 1979; White et al., 1993; Kimbel et al., 1994), temporal trends in dental and mandibular dimensions have also been documented (Leonard & Hegmon, 1987;

Lockwood et al., 2000). DIK-2-1 is relevant to the conclusions presented by Lockwood et al. (2000) regarding the decrease in P₃ mesiodistal length between Laetoli and Hadar, and the increase in mandible size in the upper part of the *A. afarensis*-bearing sequence at Hadar. The Dikika P₃ is the largest in the *A. afarensis* sample, with a crown area of 152.3 mm², which exceeds the means for both Laetoli (115.2, s.d. = 12.8) and Hadar (96.4, s.d. = 10.8) samples. The large mesiodistal dimension in DIK-2 is more similar to those from Laetoli than to specimens from Hadar, which are smaller in this regard. However, in the Laetoli sample, the large P₃ mesiodistal dimension is associated with a relatively narrow buccolingual dimension, whereas in the Dikika jaw the large mesiodistal dimension is accompanied by tremendous buccolingual expansion, rendering the MD/BL ratio close to what is observed in Hadar specimens. This results in a crown shape index for DIK 2-1 of 82%, within the range of the Hadar sample, for which the mean value is 88%, and outside of the range for the Laetoli specimens, for which the mean is 100 %.

Corpus dimensions place DIK 2-1 among the larger *A. afarensis* mandibles from Hadar. The geometric mean of corpus breadth and height measured at M₁ is 28.4 mm, which is close to that of A.L. 333w-60 (30.1), 444-2 (30.7), 438-1 (31.9), 437-1 (28.3), and 437-2 (29.2). The latter four of these specimens constitute the sample of geologically young mandibles on which basis Lockwood et al. (2000) inferred a statistically significant temporal trend toward large corpus size in the “upper” Kada Hadar member at Hadar (<3.18 Ma). But, DIK-2-1, the oldest Hadar Formation hominin, does not follow the trend. Yet, the DIK-2 mandible is also very similar in size to the A.L. 333w-60 mandible, which derives from sediments in the middle of the Hadar sequence (Denen Dora Member). Additional teeth and mandibles from the Dikika time period are required

to test whether the trends identified by Lockwood et al. (2000) can be applied to the whole Laetoli-Hadar temporal interval in which *A. afarensis* is encountered.

Recent discoveries from different parts of Africa show that the Laetoli–Hadar time period was characterized by an increased diversity of hominin species (Brunet et al., 1996; Leakey et al., 2001). More recently, White (2003) challenged this presumed diversity, pointing to the importance of increased sample size in order to better understand variation in early hominins before such conclusions can be drawn. DIK-2-1, dated to slightly older than 3.4 Ma, is relevant to this discussion. While DIK-2-1 is attributable to *A. afarensis*, it shows unique quantitative and qualitative features not observed in other specimens of the species, implying that variability of *A. afarensis* might be even greater than what is known today, once the actual temporal and geographical ranges of the species are more completely documented. The extensive size variation in the *A. afarensis* mandible sample suggested earlier on the basis of the Hadar and Laetoli fossils (White et al., 1981; Johanson, 1985; Kimbel et al., 1994; Lockwood et al., 2000) has been supported more recently by the recovery of large and small specimens from a single sedimentary horizon at Maka (White et al., 2000). Additional hominins from Dikika and other sites pre-dating Hadar are needed to understand whether the suggested patterns qualitative and quantitative variations hold true for the pre-3.4 myr time period in the Afar basin and elsewhere, and to help address important questions concerning temporal patterns of early hominin diversity. The DRP aims at recovering more hominin remains relevant to these issues.

Acknowledgments

Thanks go to the Authority for Research and Conservation of Cultural Heritage (ARCCH), the National Museum of the Ethiopia, Ministry of Youth, Sports and Culture, and the Afar regional government for permits; to Emma Mbua and Meave Leakey for access to *A. anamensis* material; to Asamirew Dessie, Tilahun Gebreselassie, Getu Assefa, Amabachew Kebede, Mesfin Mekonnen, Haimanot Defar, Assaye Zerihun, Achamyeleh Takele, and the people of the Dikika area for field assistance; to Alemu Admassu for lab assistance; to Matt Trocheri for scanning; to the Institute of Human Origins at Arizona State University and the National Geographic Society for financial and logistical support. ZA thanks Donald Johanson for his support.

REFERENCES

- Asfaw, B., Beyene, Y., Semaw, S., Suwa, G., White, T. & WoldeGabriel, G. (1991). Fejej: A new paleontological research area in Ethiopia. *J. Hum. Evol.* 21, 137-143.
- Bonnefille, R. (1995). A reassessment of the Plio-Pleistocene pollen record of East Africa. In (E.S. Vrba, G.H. Denton, T.C. Partridge & L.H. Burkle, Eds) *Paleoclimate and Evolution*, pp. 299-310. New Haven: Yale University Press.
- Brown, B., Brown, F.H. & Walker, A. (2001). New Hominids from the Lake Turkana Basin, Kenya. *J. Hum. Evol.* 41, 29-44.
- Brown, F.H. (1982). Tulu Bor Tuff at Koobi Fora correlated with the Sidi Hakoma Tuff at Hadar. *Nature* 300, 631-635.
- Brown, F.H. & Cerling, T.E. 1982. Stratigraphic significance fothe Tulu Bor Tuff. *Nature* 299, 212-215.
- 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.* 322, 907-913.
- Harris, J.M. (1991). Koobi Fora Research Project, Vol. 3. The fossil ungulates: geology, fossil artiodactyls, and paleoenvironments. Clarendon. Oxford.
- Johanson, D.C., White T.D. & Coppens Y. (1978). A new species of the genus *Australopithecus* (Primate: Hominidae) from the Pliocene of eastern Africa. *Kirtlandia* 28, 1-14.
- Johanson, D.C. & White T.D. (1979). A systematic assessment of early African hominids. *Science* 203, 321-330.

- Johanson, D.C., White, T.D. & Coppens, Y. (1982). Dental remains from the Hadar Formation, Ethiopia: 1974-1977 collections. *Am. J. Phys. Anthrop.* 57, 545-603.
- Johanson, D.C. (1985). The most primitive *Australopithecus*. In (P.V. Tobias, Ed) *Hominid Evolution: Past, Present and Future*. pp. 203-212. New York: Alan R. Liss.
- Kalb, J.E., Oswald, E.B., Mebrate, A., Tebedge, S. & Jolly, C. (1982). Stratigraphy of the Awash Group, Middle Awash Valley, Afar, Ethiopia. *Newsletters on Stratigraphy* 11 3, 95-127.
- Kappelman, J., Swisher, C.C., Fleagle, J.G., Yirga, S., Bown, T.M. & Feseha, M. (1996). Age of *Australopithecus afarensis* from Fejej, Ethiopia. *J. Hum. Evol.* 30, 139-146.
- Kimbel, W.H. & White, T.D. (1988). Variation, Sexual Dimorphism and the Taxonomy of *Australopithecus*. In (F. Grine, Ed) *Evolutionary history of the robust australopithecine*. pp. 175-198. New York: De Gruyter.
- Kimbel, H.W., Rak, Y. & Johanson, D. (1994). The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature* 386, 449-451.
- Kimbel, W.H., Rak, Y. and Johanson, D.C. (2004). *The Skull of Australopithecus afarensis*. New York: Oxford University Press.
- Leakey M.G., M.G., Feibel, C.S., McDougall, I, Ward, C.V. & Walker, A. (1998). New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* 393, 62 – 66.
- Leakey, M.G., Feibel, C.S., McDougall, I & Walker, A. (1995). New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376, 565-571.

- Leakey, M.G., Spoor, F., Brown, F.H., Gathogo, P.N., Kiarie, C., Leakey, L.N. & McDougall, I. (2001). New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410, 433 – 440.
- Leonard, W.R. & Hegmon, M. (1987). Evolution of P₃ morphology in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 73, 41-63.
- Lockwood, C.A., Kimbel W.H. & Johanson D.C. (2000). Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*. *J. Hum. Evol.* 39, 23-55.
- 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, Ethiopie). *C. R. Acad. Sci. D*, 275, 819-882.
- Taieb, M. & Tiercelin, J-J. (1980) La formation d'Hadar, depression de l'Afar, Ethiopie, stratigraphie, paleoenvironments sedimentaires. *Proc. VIII Pan-African Cong. Prehis. and Quaternary Studies*, pp109-114.
- Tiercelin, J.J. (1986). The Pliocene Hadar Formation, Afar Depression of Ethiopia. In (Frostick, L.E., Renaut, R. W., Reid, I., Tiercelin J.J., Eds.) *Sedimentation in the African Rift*, pp. 221-240. Geological Society Special Publication, Oxford: Blackwell Scientific.
- Reed, K.E. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.* 32, 289-322.
- Walter, R. C. & Aronson, J. L. (1993). Age and source of the Sidi Hakoma Tuff, Hadar Formation, Ethiopia. *J. hum. Evol.* 25, 229-240.

- Walter, R. C. (1994). Age of Lucy and the First Family: Single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Denan Dora and lower Kada Hadar Members of the Hadar Formation, Ethiopia. *Geology* **22**, 6-10.
- Ward, C.V., Leakey, M.G. & Walker A. (2001). Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *J. Hum. Evol.* 41, 255-368.
- Ward, C.V., Lockwood, C.A., Kimbel, W.H., Leakey, M.G. Johanson, D.C. & Rak Y.,(2003). Was *Australopithecus anamensis* ancestral to *A. afarensis*? *Am. J. Phys. Anthrop.*36 (Suppl.), 219-220.
- 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. (1985). The hominids of Hadar and Laetoli: an element-by-element comparison of the dental sample. In (Delson, E. Ed) *Ancestors: The hard evidence*, pp. 138-152 New York, Alan R. Liss.
- White, T.D., et al. 1993. New discoveries of *Australopithecus* at Maka in Ethiopia. *Nature* 366, 261-265.
- White T.D., 2003. Early Hominids-Diversity or Distortion? *Science* 229, 1994-1997.
- White, T.D., et al., 2000. Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *Am. J. Phys. Anthrop.* 111, 45-68.

Table 1. Chemical data for samples E02-1051 and E02-1067, identified as the Sidi Hakoma Tuff. Major and minor elements by EMP are in percent composition (unnormalized); Minor and trace element data by XRF data are in parts per million except K₂O, MgO and P₂O₅, which are in percent. Trace element data by ICP-MS are in parts per million, except Europium, which is in parts per billion. n/d = not detectable.

Electron Microprobe Data (EMP)

	CaO	SiO ₂	Al ₂ O ₃	Na ₂ O	K ₂ O	MgO	Fe ₂ O ₃	TiO ₂	P ₂ O ₅	MnO	F	BaO	ZrO ₂	Total	
E02-1051	0.29	70.78	11.79	4.80	2.40	0.06	1.52	0.14	0.04	0.09	0.12	0.08	0.07	92.17	<i>Avg</i>
	0.03	0.80	0.23	0.31	0.21	0.02	0.30	0.12	0.04	0.08	0.12	0.10	0.10		<i>SD</i>
	10.4	1.1	1.9	6.5	8.7	38.3	19.8	90.5	110.8	93.8	96.2	124.2	143.1		<i>% err.</i>
E02-1067	0.29	72.24	12.87	5.29	2.07	0.06	1.62	0.15	0.05	0.06	0.08	0.09	0.08	94.95	<i>Avg</i>
	0.04	0.68	0.25	0.82	0.18	0.02	0.31	0.10	0.06	0.05	0.07	0.13	0.08		<i>SD</i>
	12.4	0.9	1.9	15.6	8.6	35.8	19.0	70.9	115.2	76.6	84.1	140.8	99.9		<i>% err.</i>

X-ray Fluorescence Data (XRF)

E02-1051	Ba	Rb	Zn	Zr	Sc	Sr	Cr	Cu	F	K ₂ O	MgO	Ni	P ₂ O ₅	V
	298	100.2	80	450	4	55.3	n/d	4	267	2.057	0.438	6	0.04	66

Inductively-coupled Plasma Mass Spectrometry Data (ICP-MS)

E02-1051	Ce	Nb	Y	Ag	As	Be	Bi	Cd	Cs	Dy	Er	Eu	Ga	Gd	Ge	Hf
	169.2	82.1	72.8	n/d	1.1	5.1	0.1	n/d	1.25	12.56	7.19	1282	21	12.4	1.5	12.3
E02-1051	Ho	La	Lu	Mo	Nd	Pb	Pr	Sb	Sm	Sn	Ta	Tb	Th	U	Yb	Total
	2.75	84.44	1.13	3.9	73.46	16.7	17.38	n/d	14.01	6.6	5.8	2.2	17.2	4.4	6.84	100.

Table 2. List of DIK-2-1 specimens. All except the M3 and M2 frag fit the mandible.

DIK-2-1 a	symphyseal fragment with roots of the two central and the right lateral incisors.
DIK-2-1 b	fragment of the left corpus with the roots of the canine, P ₃ and P ₄
DIK-2-1 c	fragment of the corpus with the root of M1.
DIK-2-1 d	P ₃
DIK-2-1 e	M ₁
DIK-2-1 f	symphyseal fragment
DIK-2-1 g	M ₃
DIK-2-1 h	M ₂ fragment

Table 3. Maximum, minimum and mean values for mesiodistal and buccolingual dimensions of DIK-2-1, *A. afarensis*, *A. anamensis* and *Ar. ramidus* postcanine teeth.

Data on the three species comes from Ward et al. 2001.

		DIK-2	<i>A. afarensis</i>	<i>A. anamensis</i>	<i>A. ramidus</i>
P₃MD	Mean	11.15	9.5	9.9	7.9
	Min		7.9	9.3	7.5
	Max		12.6	9.0	8.2
P₃BL	Mean	13.8	10.5	10.9	10.7
	Min		8.9	9.5	9.9
	Max		12.6	12.0	11.5
M₁MD	Mean	14.65	13	12.74	11.1
	Min		10.1	11.5	11
	Max		14.8	13.8	11.1
M₁BL	Mean	14.03	12.3	11.99	10.3
	Min		11	10.2	10.2
	Max		14.8	13.5	10.3
M₃MD	Mean	18.1	15.1	14.63	12.7
	Min		13.4	13.7	?
	Max		17.4	17	?
M₃BL	Mean	14.7	13.4	12.75	11
	Min		11.3	11.9	?
	Max		15.3	13.4	?

