



A new hominin from the Basal Member of the Hadar Formation, Dikika, Ethiopia, and its geological context

Zeresenay Alemseged^{a,*}, Jonathan G. Wynn^b, William H. Kimbel^c,
Denné Reed^d, Denis Geraads^e, René Bobe^f

^a Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology,
Deutscher Platz 6, D-04103 Leipzig, Germany

^b Department of Geography and Geosciences, Irvine Building, University of St. Andrews,
St. Andrews, Fife, Scotland, KY16 9AL, UK

^c Institute of Human Origins & Department of Anthropology, Arizona State University,
P.O. Box 874101, Tempe, AZ 85287-4101, USA

^d Department of Paleobiology, National Museum of Natural History Smithsonian Institution,
10th and Constitution Ave. NW, Washington, DC 20560, USA

^e CNRS UPR 2147, 44 rue de l'Amiral Mouchez, F-75014 Paris, France

^f Department of Anthropology, State University of New York at Buffalo, 380 MFAC Ellicott Complex,
Buffalo, NY 14261-0026, USA

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Abstract

In this paper we report for the first time hominin remains 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 fossil, DIK-2-1, is a fragment of a left mandible and associated dentition. The mandible is attributed to *Australopithecus afarensis*. However, the new fossil exhibits some metric and morphological features that have not previously been seen in the *A. afarensis* hypodigm, increasing the already impressive degree of variation in the mandibular sample of the species.

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* Corresponding author. Tel.: +49 341 35 50 353; fax: +49 341 35 50 399.

E-mail addresses: zeray@eva.mpg.de (Z. Alemseged), jonathan.wynn@st-andrews.ac.uk (J.G. Wynn), wkimbel.iho@asu.edu (W.H. Kimbel), denne@umich.edu (D. Reed), dgeraads@ivry.cnrs.fr (D. Geraads), renebobe@buffalo.edu (R. Bobe).

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 Laetoli Beds in Tanzania (where the type specimen, LH-4, was found); 2) undesignated strata near Fejej¹ 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 and White, 1988); 4) the Nachukui Formation, west of Lake Turkana, Kenya (Brown et al., 2001); and 5) informally designated "formations x and w" of the Middle Awash valley of Ethiopia (White et al., 2000). The aggregate time span of the species is at least 0.7 myr, from ca. 3.7 to 3.0 Ma (Kimbel et al., 2004).

Large hominin sample size and stratigraphic continuity at Hadar have enabled researchers to assess the contribution of sexual dimorphism (Kimbel and White, 1988; Kimbel et al., 1994, 2004) and temporal trends (Lockwood et al., 2000) to total morphological and metric variation in *A. afarensis*. However, data about *A. afarensis* and other early hominins are meager during the interval between the Hadar and Laetoli parts of the hypodigm, and fossil evidence from 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, 1998). While samples from Hadar and Laetoli are both attributed to *A. afarensis*, the morphological variation within the hypodigm is such that the older Laetoli sample is, in comparable parts of the anatomy, closer morphologically to *A. anamensis* than the younger Hadar assemblage of *A. afarensis* (Leakey et al., 1995; Lockwood et al., 2000;

Kimbel et al., 2004). Additional fossil evidence from between ca. 3.9 and 3.4 Ma is thus critically important, as it could shed light on the nature of the differences between the Hadar and Laetoli samples and the hypothesized phyletic relationship between *A. afarensis* and *A. anamensis*. Moreover, increasing the fossil sample from sediments older than 3.4 Ma will help test hypotheses about lineage diversity during the middle Pliocene (Brunet et al., 1996; Leakey et al., 2001).

The Basal Member of the Hadar Formation, which includes strata below the Sidi Hakoma Tuff (SHT; older than 3.4 Ma [Walter and Aronson, 1993]), is well exposed on the southeastern side of the Awash River adjacent to the Hadar and Gona research areas (Fig. 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 main Hadar research area (Fig. 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 1970s 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 and Tiercelin, 1980; Kalb et al., 1982; Tiercelin, 1986). Tiercelin (1986) provided 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* (A.L. 400-1; A.L. 277-1, A.L. 411-1; Johanson et al., 1982) were collected. Not since then, however, has paleontological and geological research been conducted on the southeastern side of the Awash River. The Dikika Research Project (referred as DRP

¹ As the evidence from Fejej is very fragmentary, more fossils from the site are required to confirm the taxonomic status of what has already been found.

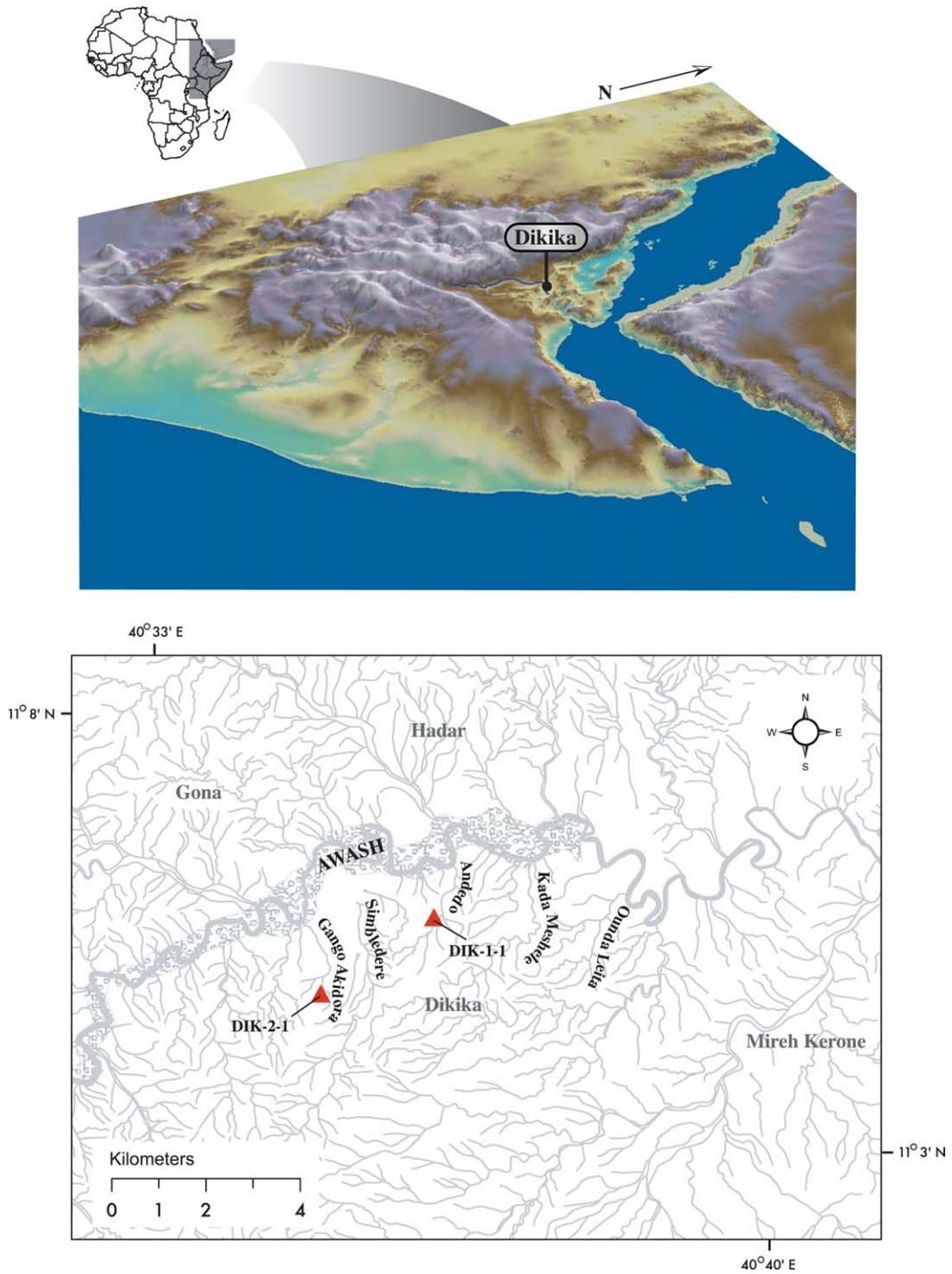


Fig. 1. Geographical location of the Dikika paleoanthropological site within the horn Africa (top); locations of DIK-2 hominin locality with in the Dikika Research Project area and major drainage patterns (bottom).

hereafter), led by the senior author, has conducted four seasons (2000, 2002, and two in 2003) of field work at Dikika, working under a permit from the Authority for Research and Conservation of Cultural Heritage (ARCCH) of the Ministry of Youth, Sports and Culture of Ethiopia.

Twenty faunal localities have been identified at Dikika through the 2003 field season. Fossils of large mammals are abundant on the surface of the deposits, and include frequent occurrences of cranial fragments and long bones of elephants, hippopotamus, rhinoceros, and other taxa.

In this paper, we describe DIK-2-1, a fragment of the left side of a hominin mandible with partial dentition of an adult individual from the Basal Member of the Hadar Formation, and discuss its taxonomic affinities and significance for the evolution of early hominins. This specimen is the first hominin recovered from the Basal Member, the oldest of the formally recognized units of the Hadar Formation. The specimen derives from a stratigraphic horizon ~20 m below the Sidi Hakoma Tuff, and so its minimum age is 3.4 Ma.

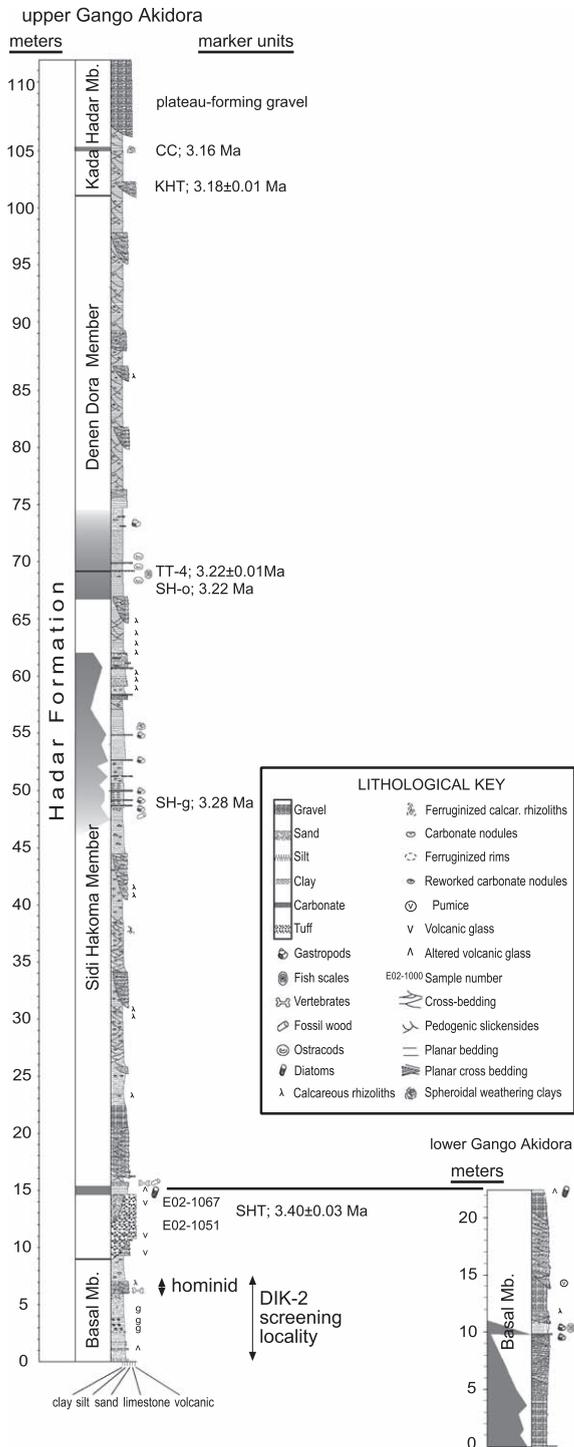
Stratigraphic, sedimentary and paleoenvironmental context of the DIK-2 hominin fossil

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 Fig. 2) in the headwaters of the Gango Akidora stream (Fig. 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 the 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 stable lacustrine sedimentation, no part of the regional section indicates a permanent lake existing over periods longer than a few tens of thousands of years. 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/kyr, which is comparable to that calculated for the type section at Hadar (32 cm/kyr), but lower than that calculated at Andedo and Simbildere to the east (43 cm/kyr), and lower still than the 87 cm/kyr 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. Terrestrial vertebrates from this locality include the tortoise *Geochelone*, an 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

Fig. 2. Stratigraphic section of the Hadar Formation at upper and lower Gango Akidora, showing the provenance of the DIK-2 hominid fossils, the area of section screened for fossils, and prominent marker units exposed. SHT = Sidi Hakoma Tuff; SH-g = Sidi Hakoma Member gastropodite (lowermost unit used as a marker); SH-o = Sidi Hakoma Member ostracodite (lowermost unit used as a marker); TT-4 = Triple Tuff-4; CC = Confetti Clay. Age of SHT is defined by its correlation to the Tulu Bor Tuff (Brown, 1982) and by Walter and Aronson (1993). Age of TT-4 is from Walter (1994). Other stratigraphic markers are calculated from stratigraphic scaling within geochronologically constrained sections. Intervals of lacustrine sedimentation are marked in gray.

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 from XRF 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	100.1

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

The specimen was found on the 12th of December 2000 by the senior author. Specimen DIK-2-1 consists of a fragment of the left mandibular corpus and a portion of the symphyseal region. The P₃, M₁, M₃, and part of the M₂ crown were also recovered (Table 2). 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 crown, which joins 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 crown fragment, all mandibular pieces and teeth join cleanly.

Preservation

The mandible is preserved irregularly up to about the distal level of the M₁ posteriorly (Fig. 3D). Laterally, the corpus surface is abraded

and pitted, with cortex missing in some areas (Fig. 3A). However, based on our comparison of DIK-2-1 with Hadar mandibles of *A. afarensis*, this abrasion did not appreciably affect the corpus dimensions as reported here (ca. 0.5–1.0 mm). The roots of the canine, the two premolars, and the first molar are preserved. The mesiobuccal face of the canine root is exposed (Fig. 3A). The 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 (Fig. 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 (Fig. 3B). The corpus is complete to the basal margin level below M₁, but this margin is missing below C-P₄ (Fig. 3B). The alveolar bone is appreciably abraded.

Sex and age

A large canine root combined with a large P₃ (see below) indicate that DIK-2-1 is a male. The exposed root of 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.

Comparative material

For this study, comparisons of the new fossil were made with specimens that are roughly contemporaneous with it, namely those of *A. afarensis* and *A. anamensis*. The proposed early hominin taxa *Kenyanthropus platyops* and *Australopithecus bahrelghazali* also supply specimens that come from time periods roughly contemporaneous with that from which DIK-2-1 derives. No mandible can be attributed to *K. platyops* with certainty. Leakey et al. (2001) pointed out that even if KNM-WT 8556 was attributed to *A. afarensis*

Table 2

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

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

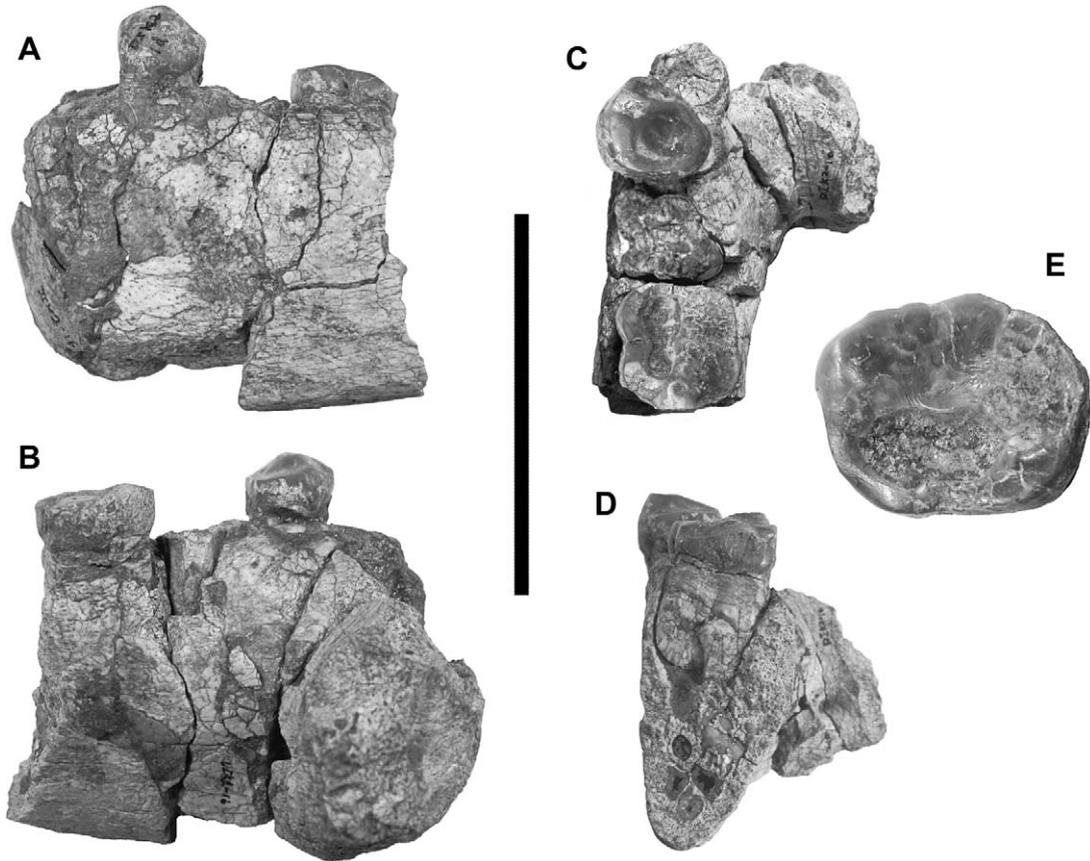


Fig. 3. DIK-2-1 hominin specimens, left mandibular corpus in lateral (A), medial (B), occlusal (C), and posterior (D) views; occlusal view of the left lower third molar, mesial side is facing left (E). Scale bare = 5 cm.

(as suggested by Brown et al., 2001), affiliation of this mandible with the *K. platyops* type is not contradicted by its molarized P_4 . But the same authors recognized that the size of the molars is not consistent with this interpretation. Moreover, 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 a 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, based on published information and our examination of a cast of the mandible, there is nothing to prevent this specimen from being accommodated within the range of mandibular and dental variation in *A. afarensis*.

Description and comparisons

Mandible

Lateral aspect (Fig. 3A)

There is no hint of a lateral prominence below M_1 as there is in most *A. afarensis* specimens; instead this surface is flat and rises vertically from the base of the corpus, at least in the preserved part. The lateral corpus hollow in DIK-2-1 is vertically oriented and very narrow anteroposteriorly. Thus, the Dikika jaw does not display the typical *A. afarensis* morphology, in which the hollow is anterosuperiorly elongated and bordered by the root of the ramus posteriorly, the anterosuperiorly sweeping basal marginal torus inferiorly, and the swollen alveolar region superiorly. We

infer that the root of the ramus would have been more posteriorly located than in all or most 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 anterosuperiorly, as is common in *A. afarensis*.

Medial aspect (Fig. 3B)

A prominent superior transverse torus dominates the lingual aspect, which is separated from the weak inferior transverse torus by a shallow subalveolar fossa. As in *A. afarensis*, but unlike the condition 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 medial aspect of the alveolar process is damaged.

Anterior aspect

Anteriorly, the symphyseal region is flat and mildly inclined posteriorly. The substantial posterior 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. It is more similar to the morphology found in the Hadar sample. 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,” as in A.L. 288-1 and MAK-VP-1/12, to rounded and bulbous, as in A.L. 266-1 and A.L. 438-1. Specimen DIK-2-1 approximates the morphology of A.L. 400-1a in having a rather flat anterior external corpus, but is similar to A.L. 417-1 in a more vertical orientation of the symphyseal contour.

Posterior aspect (Fig. 3C)

What remains of the post-incisive planum is biconcave, as is the case in most *A. afarensis* mandibles. The planum is much shorter and more vertically disposed than in the *A. anamensis*

mandible KNM-KP 29281. Specimen DIK-2-1 has a well-developed superior and mildly developed inferior transverse torus, similar to that of A.L. 400-1a and MAK-VP-1/12. The genioglossal fossa is well defined and circular in outline.

Occlusal aspect (Fig. 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 long axis of 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 from the corpus to the symphysis, 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). What is preserved of the lateral margin of the alveolar process is straight. The alveolar process in this view is oriented anterolaterally, as it is in most *A. afarensis* mandibles, and unlike the condition in *A. anamensis*, where the alveolar process is straight and aligned with the dental row.

Basal aspect

The narrowness of the corpus base below M₁ is remarkable, but can be matched in Hadar specimen A.L. 266-1. The preserved part of the Dikika corpus base demonstrates moderate lateral eversion, as is commonly encountered in Hadar mandibles of *A. afarensis*.

Mandibular corpus cross section

The mandibular corpus cross section at M₁ shows that DIK-2-1 has a very flat lateral surface and a lateral extension of a pronounced superior transverse torus medially (Fig. 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

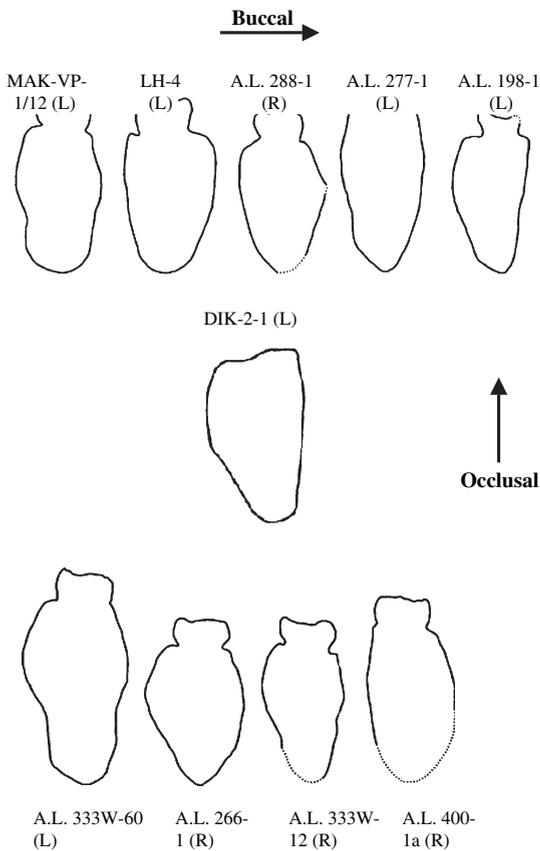


Fig. 4. Mandibular corpus cross section at M_1 perpendicular to the lingual alveolar margin of DIK-2 and other *A. afarensis* mandibles. M_1 not included in the section for DIK-2-1. Cross sections for *A. afarensis* specimens adopted from White et al. (2000). Not to scale.

superior transverse torus compared to DIK-2-1. Even though there is no trace of a lateral prominence below M_1 , 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%). The mean value for *A. afarensis* is 58%, with a range of 48% to 69%. Overall dimensions of the Dikika mandible compare favorably to those of the larger mandibles from Hadar (Fig. 5).

Dentition

P_3

The crown of the DIK-2 left P_3 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 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 position 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* P_3 s. 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). In most *A. afarensis* P_3 s, the prominence of the metaconid results in a bulging lingual face that partly overhangs the alveolar margin. This aspect of the P_3 crown is even more pronounced in DIK-2-1. This feature separates DIK-2-1 and most *A. afarensis* P_3 s, 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 P_3 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* P_3 s 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 P_3 is morphologically similar to most *A. afarensis* P_3 s. 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.

M_1

The DIK-2 M_1 measures 14.7 mesiodistally and 14.0 buccolingually. The protoconid and hypoconid are heavily worn and connected by an hourglass shaped dentine exposure measuring

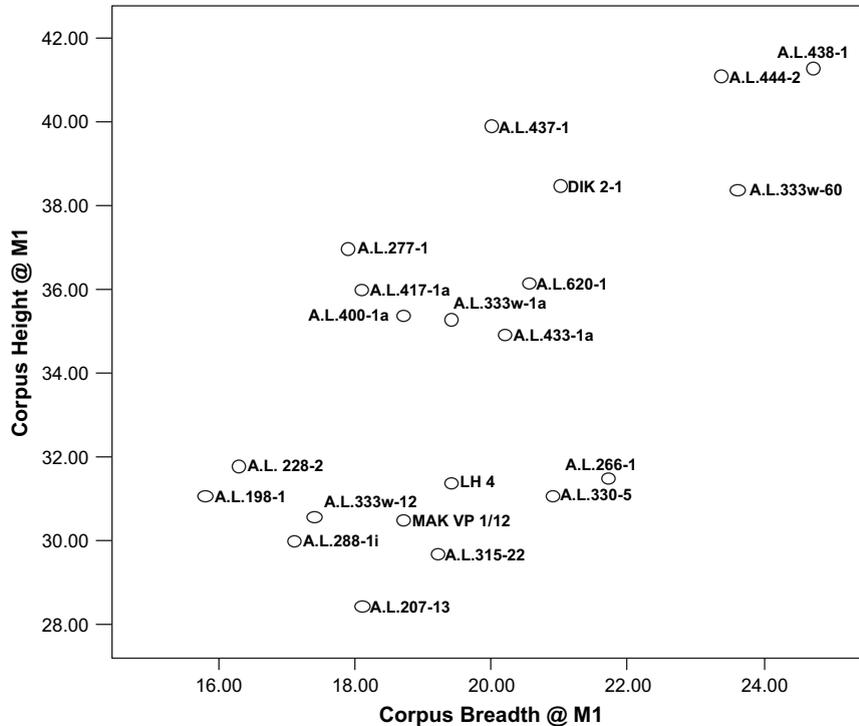


Fig. 5. Corpus height and breadth of *Australopithecus afarensis* mandibles at M₁.

9.5 mm mesiodistally and 4.2 mm (maximally) buccolingually. One mm diameter dentine pits are exposed on the tips of the metaconid and hypoconulid; the entoconid shows just a very small area of dentine exposure. Overall, the morphology and wear pattern are similar to those of MAK-VP-1/12, but the DIK-2-1 tooth is square, 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 (Fig. 3E)

The DIK-2 M₃ is heavily worn and measures 18.1 mesiodistally and 14.7 buccolingually. The protoconid and hypoconid are connected by an area of exposed dentine 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 of the occlusal profile posteriorly. 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 an occlusally projecting metaconid, but the entoconid rims are less marked than in the Maka M₃.

Dental metrics

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

the maximum for *A. anamensis* ($n = 5$) (Fig. 6; Table 3). The buccolingual dimension surpasses that of all P_3 s 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 hypodigm by about 3 mm (Fig. 7; Table 3). This creates a relatively low crown shape index [(0.82), compared to Hadar mean of 0.89 ($n = 21$)]—i.e., a buccolingually expanded crown—but one that is similar to some Hadar specimens, such as A.L. 417-1a (0.82), A.L. 440-1 (0.83), and A.L. 288-1 (0.84), and to MAK-VP-1/12 (0.84). 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 that of LH-24 (0.87).

The mesiodistal dimension of the Dikika M_1 (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 (14.8) (Fig. 8). In buccolingual breadth, DIK-2 falls within the range of variation for *A. afarensis* but surpasses all *A. anamensis* specimens (Fig. 9). For M_3 , the mesiodistal length of DIK-2 falls above the range for *A. afarensis* teeth (by 0.9 mm; A.L. 487-1), but it is within the range for buccolingual breadth, exceeded only by A.L. 188-1 and A.L. 620-1 (Figs. 10 and 11). For M_1 and M_3 , DIK-2-1 surpasses all *A. anamensis* specimens in both mesiodistal and buccolingual dimensions (Figs. 8–11).

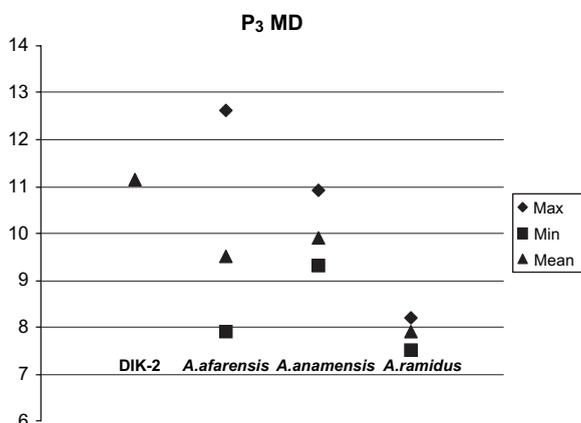


Fig. 6. Mesiodistal dimensions of DIK-2-1 P_3 and that of *A. afarensis*, *A. anamensis*, and *A. ramidus*.

Table 3

Maximum, minimum, and mean values for mesiodistal and buccolingual dimensions of DIK-2-1, *A. afarensis*, *A. anamensis*, and *A. 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>
P_3 MD	Mean	11.2	9.5	9.9	7.9
	Min		7.9	9.3	7.5
	Max		12.6	9.0	8.2
P_3 BL	Mean	13.8	10.5	10.9	10.7
	Min		8.9	9.5	9.9
	Max		12.6	12.0	11.5
M_1 MD	Mean	14.7	13.0	12.7	11.1
	Min		10.1	11.5	11.0
	Max		14.8	13.8	11.1
M_1 BL	Mean	14.0	12.3	12.0	10.3
	Min		11	10.2	10.2
	Max		14.8	13.5	10.3
M_3 MD	Mean	18.1	15.1	14.6	12.7
	Min		13.4	13.7	?
	Max		17.4	17.0	?
M_3 BL	Mean	14.7	13.4	12.8	11.0
	Min		11.3	11.9	?
	Max		15.3	13.4	?

Discussion

The new Dikika specimen possesses some of the suite of mandibular and dental traits that have been suggested to distinguish *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 posteriorly projecting superior transverse torus and a rounded, basally set inferior transverse torus. The DIK-2-1 P_3 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 a mesiolingually directed anterior fovea that opens inferiorly only part way toward the cervix (Ward et al., 2001). In addition, DIK-2-1 has a more vertically oriented symphyseal region than in *A. anamensis*. However, the Dikika specimen differs from most *A. afarensis* mandibles in the placement of the lateral corpus hollow

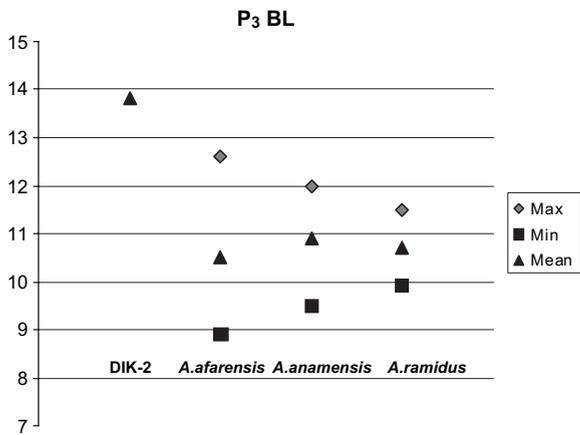


Fig. 7. Buccolingual dimensions of DIK-2-1 P₃ and that of *A. afarensis*, *A. anamensis*, and *A. ramidus*.

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, especially buccolingually, and its M₃ is more rectangular rather than tapering posteriorly. On balance, the weight of the morphological evidence favors an assignment of DIK-2-1 to *A. afarensis*.

There is a broad consensus concerning the assignment of hominins from Hadar and Laetoli to *A. afarensis* (see Kimbel et al., 2004, for a recent summary). However, many questions related to

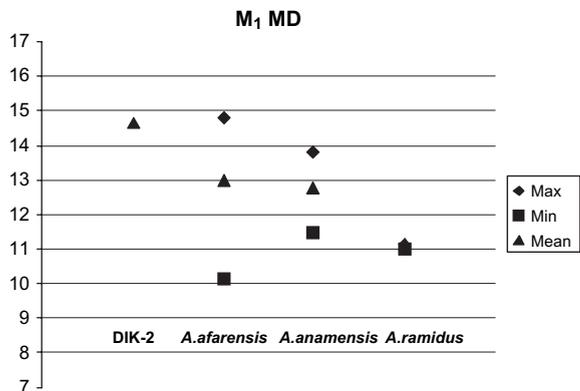


Fig. 8. Mesiodistal dimensions of DIK-2-1 M₁ and that of *A. afarensis*, *A. anamensis*, and *A. ramidus*.

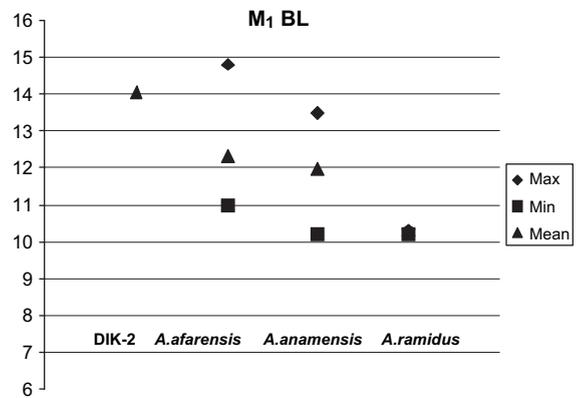


Fig. 9. Buccolingual dimensions of DIK-2-1 M₁ and that of *A. afarensis*, *A. anamensis*, and *A. ramidus*.

the tempo and mode of evolution of this species are not yet fully understood, although some progress toward their elucidation has been made (Leonard and Hegmon, 1987; Lockwood et al., 2000; Ward et al., 2003). There remains a time gap between the Hadar and Laetoli site-samples. While it has been suggested that *A. afarensis* exhibits stasis throughout its temporal range (Johanson and White, 1979; White et al., 1993; Kimbel et al., 1994), temporal trends in dental and mandibular dimensions have also been documented (Leonard and 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,

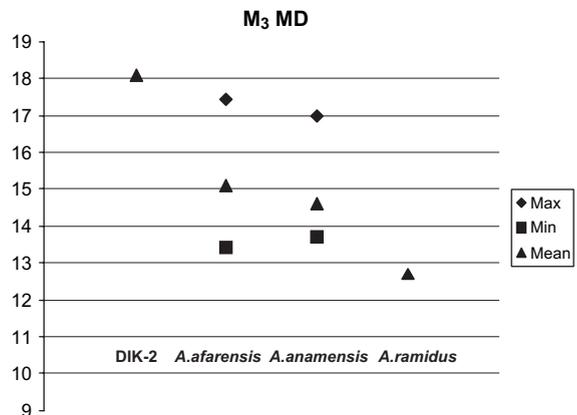


Fig. 10. Mesiodistal dimensions of DIK-2-1 M₃ and that of *A. afarensis*, *A. anamensis*, and *A. ramidus*.

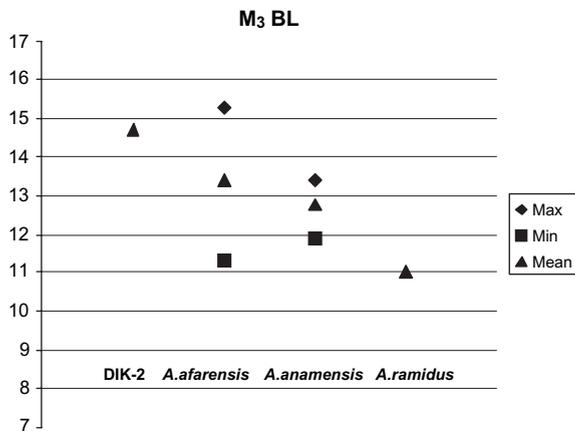


Fig. 11. Buccolingual dimensions of DIK-2-1 M_3 and that of *A. afarensis*, *A. anamensis*, and *A. ramidus*. Data in Figs. 6–11 comes from Ward et al., 2001.

and the increase in mandible size in the upper part of the *A. afarensis*-bearing sequence at Hadar. The Dikika P_3 is the largest in the *A. afarensis* sample, with a crown area of 152 mm², which exceeds the means for both Laetoli (115.2 mm², s.d. = 12.8) and Hadar (96.4 mm², s.d. = 10.8) samples. The large mesiodistal dimension in DIK-2 is more similar to P_3 s from Laetoli than to specimens from Hadar, which are smaller in this regard. However, in the Laetoli sample, the large P_3 mesiodistal dimension is associated with a relatively small buccolingual dimension compared to Hadar homologs, whereas in the Dikika jaw, the large mesiodistal dimension is accompanied by marked buccolingual expansion, rendering the MD/BL ratio close to that observed in the Hadar sample. This results in a crown shape index for DIK-2-1 of 82%, which is outside of the range for the Laetoli P_3 sample.

Corpus dimensions place DIK-2-1 among the larger *A. afarensis* mandibles from Hadar (Fig. 5). The geometric mean of corpus breadth and height measured at M_1 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 towards a large corpus size in the “upper” Kada Hadar Member at Hadar

(< 3.18 Ma). DIK-2-1, the oldest Hadar Formation hominin mandible, appears to counter this trend. However, the Dikika mandible is marginally smaller than the A.L. 333w-60 mandible, which derives from sediments in the middle of the Hadar sequence (Denen Dora Member). As the geometric mean of corpus height and breadth of the Dikika jaw falls in between the “upper” Kada Hadar sample value (30.1, n = 4) and the remaining Hadar sample (“lower” Kada Hadar, Denen Dora, and Sidi Hakoma) value (25.1, n = 15), but within the range of both, the impact of the new specimen on the overall trend identified by Lockwood et al. (2000) is not clear. 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 interval between the Laetoli and Hadar hypodigms of *A. afarensis*.

Recent discoveries from different parts of Africa suggest 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. Specimen 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 variation in *A. afarensis* might exceed that observed in the existing hypodigm. The extensive size variation in the *A. afarensis* mandible sample suggested earlier on the basis of the Hadar and Laetoli parts of the hypodigm (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 of qualitative and quantitative variation hold true for the pre-3.4 Ma time period in the Afar basin and elsewhere. Additional specimens would also help to address important questions

concerning temporal patterns of early hominin diversity. The DRP hopes to recover more hominin remains relevant to these issues.

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