



Connecting local environmental sequences to global climate patterns: Evidence from the hominin-bearing Hadar Formation, Ethiopia

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Abstract

Central to the debate surrounding global climate change and Plio-Pleistocene hominin evolution is the degree to which orbital-scale climate patterns influence low-latitude continental ecosystems and how these influences can be distinguished from regional volcano-tectonic events and local environmental effects. The Pliocene Hadar Formation of Ethiopia preserves a record of hominin paleoenvironments from roughly 3.5 to 2.2 Ma at a temporal resolution relevant to evolutionary change within hominins and other taxa. This study integrates the high-resolution sedimentological and paleontological records at Hadar with climate proxies such as marine core isotope, dust, and sapropel records. Consistent cycling observed both between and within fluvial and lacustrine depositional environments prior to 2.9 Ma at Hadar appears to be predominantly climatic in nature. In contrast a significant change in depositional facies after 2.9 Ma to sequences dominated by conglomerate cut-and-fill cycles indicates a strong tectonic signature related to regional developments in the Main Ethiopian Rift. While specific events seen in marine proxy records may have parallels in the Hadar environmental archive, their overall patterns of high versus low variability may be even more relevant. For example, periods of relatively high-amplitude climate oscillations between 3.15 and 2.95 Ma may be linked to noted size-related morphological changes within the Hadar *Australopithecus afarensis* lineage and a significant increase in more arid-adapted bovid taxa. Increased aridity in East Africa during this period is also indicated by peaks in eolian dust in the marine core record. Conversely, the dominant lacustrine phase at Hadar ca. 3.3 Ma coincides with the least variable period in several climate proxy records, including marine core foraminifera $\delta^{18}\text{O}$ values and eolian dust concentration. This phase is also coeval with low insolation variability and a very distinct and significant long-term period of low dust percentage in circum-Africa marine cores.

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Introduction

The degree of influence that global climate change had on events in Plio-Pleistocene hominin evolution is a matter of long-standing debate in paleoanthropology (e.g., Vrba, 1985, 1988, 1995; Vrba et al., 1989; Stanley, 1992; Potts, 1996, 1998; Behrensmeyer et al., 1997; Reed, 1997; Bobe et al.,

2002; Bobe and Behrensmeyer, 2004). A major focus of current research is on marine sediment records as proxies for changes in African climate or shifts in climate variability controlled by the Earth's orbital variation. From a paleoenvironmental standpoint there are several questions central to the climate-evolution argument. To what extent did orbital-scale climate patterns influence low-latitude continental ecosystems during the Plio-Pleistocene? If global climate is a major influence, are the geological records of hominin-bearing deposits of sufficient resolution to record such changes? In what ways can the influence of global climate be distinguished from volcano-tectonic events tied to the East African Rift

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System and other local or regional environmental effects? Once the various environmental factors are isolated, can they be used to appropriately explain trends or events in the hominin fossil and archaeological records? As resolving the issue of global climate change and hominin evolution requires multiple lines of evidence from localities spread across space and time, it is first necessary to address these questions at the scale of individual sedimentary basins. Although allowing for only a brief snapshot into the past, the hominin-bearing Hadar Formation in Ethiopia allows us to address each of these questions.

Hadar is best known for its abundant remains of the early hominin *Australopithecus afarensis* (Johanson and Taieb, 1976; Johanson et al., 1978b, 1982). While Hadar's density of fossilized fauna rivals that of other East African Plio-Pleistocene fossil sites, it is unique in the number of specimens preserved that are

attributed to a single hominin species. Hadar has yielded more than 370 specimens of *A. afarensis* from over 90 different localities (updated from Lockwood et al., 2000). These represent approximately 90% of all material attributed to the species and serve as a basis for understanding the evolution of *A. afarensis*. This extensive collection of a single taxon within such a temporally and spatially controlled context provides a rare opportunity to test hypotheses of hominin evolutionary change within a paleoenvironmental framework.

Located in the Afar region of the Main Ethiopian Rift, the Hadar Formation exposed at the Hadar site ($\sim 11^{\circ}06'N$, $40^{\circ}35'E$, 500 m) comprises a sequence of approximately 200 meters of fluvio-lacustrine sediments that preserves a high-resolution record of environmental character and change for the late Pliocene >3.45 to <2.20 Ma (Figs. 1 and 2). Often divisible

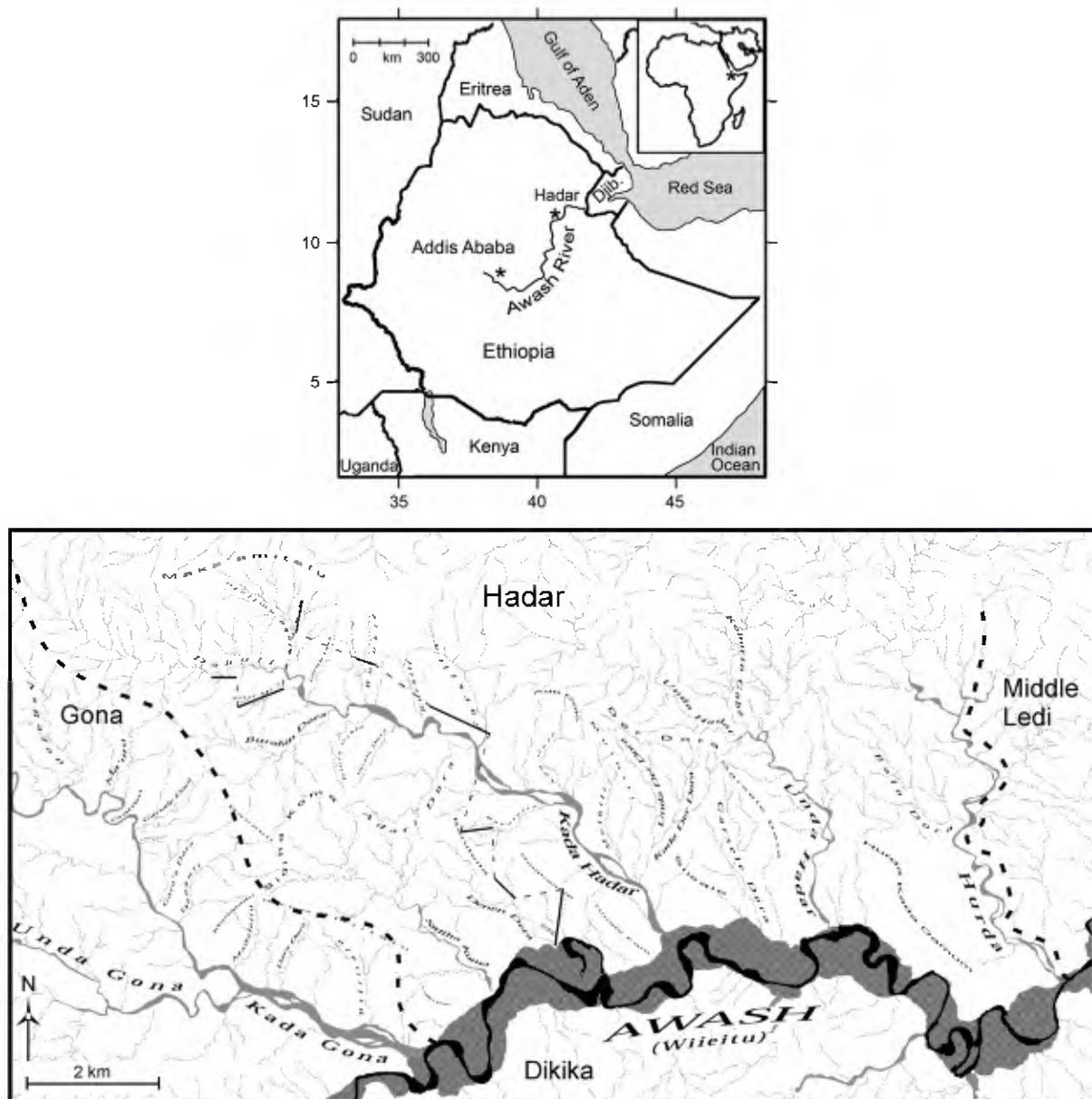


Fig. 1. Geographic location of the Hadar paleoanthropological site (top). Location of stratigraphic sections used to create the composite section at Hadar (solid lines) and approximate boundaries between Hadar and adjacent project areas (bottom). Hadar basemap provided by G. Eck.

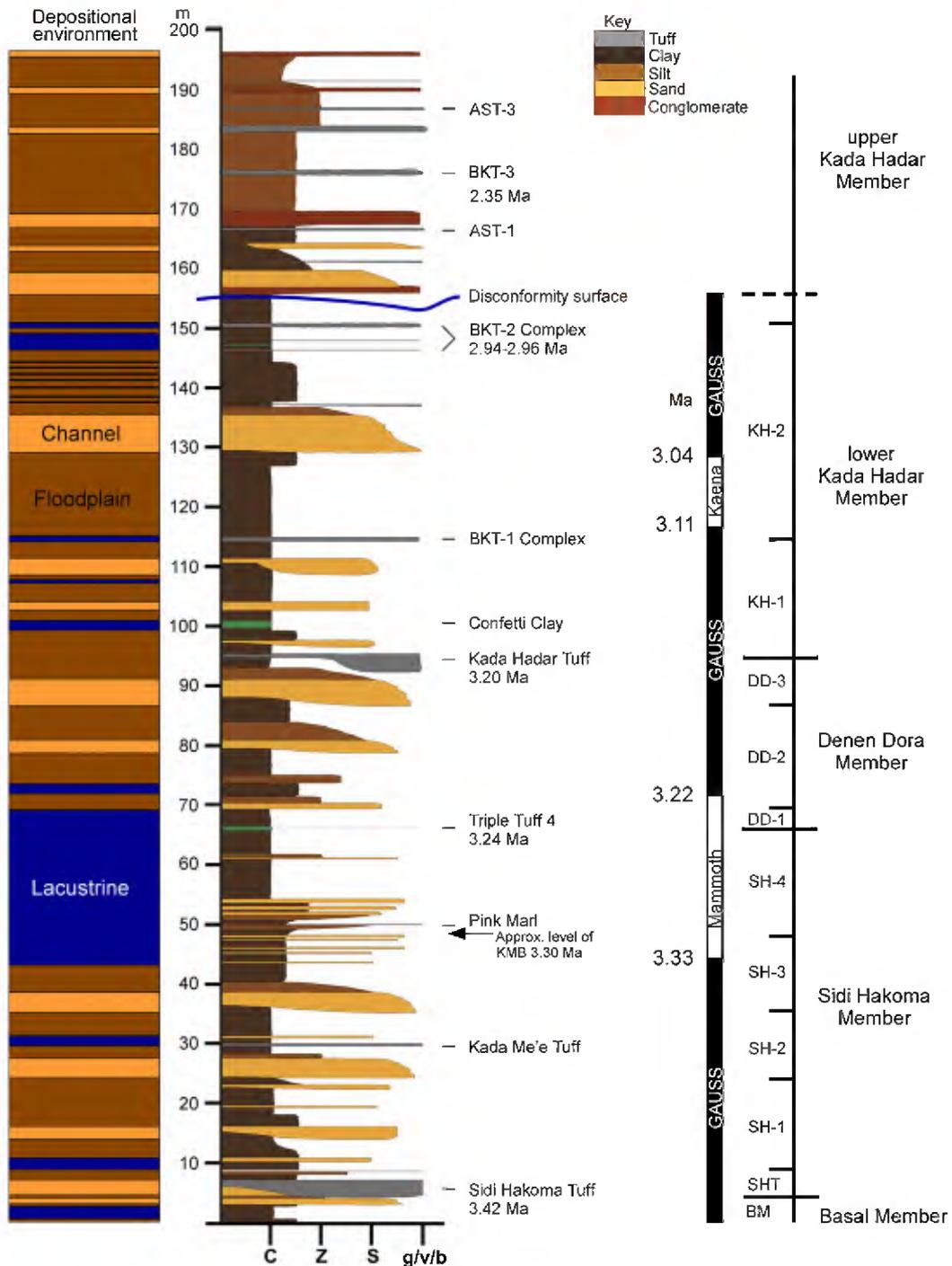


Fig. 2. Composite stratigraphic section and interpreted depositional environments of the Hadar Formation. Tuffs and major marker beds are labeled alongside the section. Submembers used for paleontological analyses (Figs. 5 and 6, Table 1) are shown within their respective member. $^{40}\text{Ar}/^{39}\text{Ar}$ dates and paleomagnetic transitions from Schmitt and Nairn, 1984; Renne et al., 1993; Walter and Aronson, 1993; Kimbel et al., 1994, 1996, 2004; Semaw et al., 1997; Walter, 1994 and unpublished data from C.J. Campisano. Compared to previous publications, the $^{40}\text{Ar}/^{39}\text{Ar}$ dates have been recalibrated to reflect the change in the age of the Fish Canyon sandstone standard (increased by approximately 0.65%).

into intervals of less than 50,000 years, the fine temporal resolution at Hadar is provided by a combination of isotopic age control on volcanics, magnetic polarity transitions, geochemically characterized vitric tephra, and numerous lithostratigraphic markers. Sedimentary deposits at Hadar are laterally extensive and relatively uninterrupted by faulting or

areas of discontinuous exposure. Combined with numerous marker beds, this provides a strong stratigraphic framework for the paleontological localities and depositional environments across the landscape.

The high rate of sediment deposition at Hadar, roughly twice that of localities of comparable age, equates to more

geologic and environmental information preserved per unit time and is largely responsible for the rich paleontological record at Hadar. For example, during the 3.42–2.90 Ma interval, the average sedimentation rate at Hadar is 30 cm/kyr, whereas rates for the Shungura, Nachukui, and Koobi Fora Formations in the Turkana Basin range from 13–18 cm/kyr (deHeinzelin and Haesaerts, 1983; Feibel, 1988; Harris et al., 1988). Although only a half-million-year geological record of paleoenvironments is preserved in the *A. afarensis*-bearing beds at Hadar, the detailed information recorded is well-suited for comparisons to global climatic records. Additionally, Hadar's abundant fossil faunal remains, including hominins, provide a means of detecting any biotic changes that could be linked to global climate patterns or change.

Methods and materials

The basic stratigraphy of the pre-disconformity Hadar Formation and the broad-scale reconstructions of depositional environments have changed little since the 1980s. For the most part, subsequent geological work has focused on refinements of the geochronological framework and interpretations of depositional environments and overall paleoenvironments. Building upon this prior geological research at Hadar (e.g., Taieb et al., 1976; Johanson et al., 1978a, 1982; Taieb and Tiercelin, 1979, 1980; Aronson and Taieb, 1981; Tiercelin, 1986), detailed stratigraphic sections measured by the authors were used to construct a composite section of the Hadar Formation and a record of its depositional environments (Fig. 2). A total of seven stratigraphically successive sections were used to construct the composite section. These sections were measured in the central and western portions of the Hadar region in a roughly continuous northwest trajectory from Keini'e Koma to the Maka'amitalu Basin (Fig. 1). Although these individual sections do not incorporate details in lateral variation that existed across the landscape, they are considered appropriate representations of the regional stratigraphy. Additionally, these sections are in association with the majority of the fossil fauna localities and consistent with the location of previously measured sections (e.g., Johanson et al., 1978a).

Depositional environments were interpreted using the general categories of channel (primarily fluvial), floodplain, and lacustrine (including ephemeral floodplain lakes). It should be noted that, due to the spatial variation of strata thickness across the Hadar landscape, the geographic placement of stratigraphic sections does influence the timing and duration of specific depositional environments in our timescaled sequence. For example, because the depocenter was to the east of the Hadar site, strata in the far eastern portion of Hadar preserve more lacustrine-dominated facies compared to those further west. The stratigraphic sections used in this study were measured in the central and western portion of Hadar, which better record the timing and extent of individual transgression events. Fortunately, numerous lithostratigraphic markers and the lateral continuity of the Hadar strata allow for the tracing of depositional environments between the eastern and western exposures. Although details of the

lithostratigraphy may vary between temporally equivalent but geographically separate stratigraphic sections, the overall sequence and patterns in depositional environments presented in this study are, for the most part, consistently preserved across the Hadar region.

For more accurate age determinations, as well as for comparison to the orbitally tuned marine record, ages for the Sidi Hakoma Tuff (SHT), the Kada Damum Basalt (KMB), Triple Tuff 4 (TT-4), the Kada Hadar Tuff (KHT), and the Bouroukie Tuffs 2L and 2U (BKT-2L and -2U) that had been published using the former Fish Canyon (FC) sanidine standard age of 27.84 Ma (Deino and Potts, 1990) were recalibrated using the revised standard age of 28.02 Ma (Renne et al., 1998) by multiplying the former age by 1.0065 (and supported by unpublished $^{40}\text{Ar}/^{39}\text{Ar}$ analysis by C.J.C.). This standard date is also in closer accordance to the suggested FC age based upon orbitally tuned evidence (e.g., Hilgen et al., 1997; Kuiper et al., 2004). These recalibrated ages, noted in Fig. 2, will also be used throughout the text.

To construct a timescaled stratigraphic sequence, pre-disconformity strata were subdivided into eight temporal segments using the nine geomagnetic and isotopic dates for the Hadar Formation (Fig. 2). The thicknesses of these individual segments were then scaled according to their temporal duration using a linear sedimentation rate (Fig. 3). These temporal segments are not to be confused with the formal stratigraphic submember divisions (also noted in Fig. 2) used in the paleontological analyses discussed later. We acknowledge the fact that sedimentation rates are likely to differ between different depositional environments preserved within any temporal segment, and that this is likely to have some influence on the accuracy of our age model within certain temporal segments. However, we believe that the highly-resolved chronology of the Hadar Formation minimizes the overall degree of error introduced, and that our age model for depositional environments is appropriate for the level of analysis in this study.

The timescaled depositional environment sequence was compared to several proxies of regional and global climate (Fig. 3). Oxygen isotope records of planktonic foraminifera are a common paleoclimatic proxy, as they relate to near sea surface conditions, including temperature and salinity in addition to global ice volume. The oxygen isotope record of the planktonic foraminifera species *Globigerinoides ruber* from Lourens et al. (1996) was used since it could be directly related to the sapropel record from the Eastern Mediterranean (Emeis et al., 2000); both studies are tuned to the same insolation record (Laskar et al., 1993). For a more global "type section" climate proxy record, the recent LR04 stack of benthic $\delta^{18}\text{O}$ records of Lisiecki and Raymo (2005) was used. The percentage of eolian dust from ODP sites 721/722 in the Arabian Sea was used as a proxy for East African climate change, specifically aridity and patterns in arid-humid climate cycles (deMenocal, 1995, 2004). Eccentricity modulated precession and summer solar insolation (July, 15° N) were calculated from Berger and Loutre (1991).

Univariate and multivariate analyses were conducted using a subset of the Hadar paleontological database maintained by

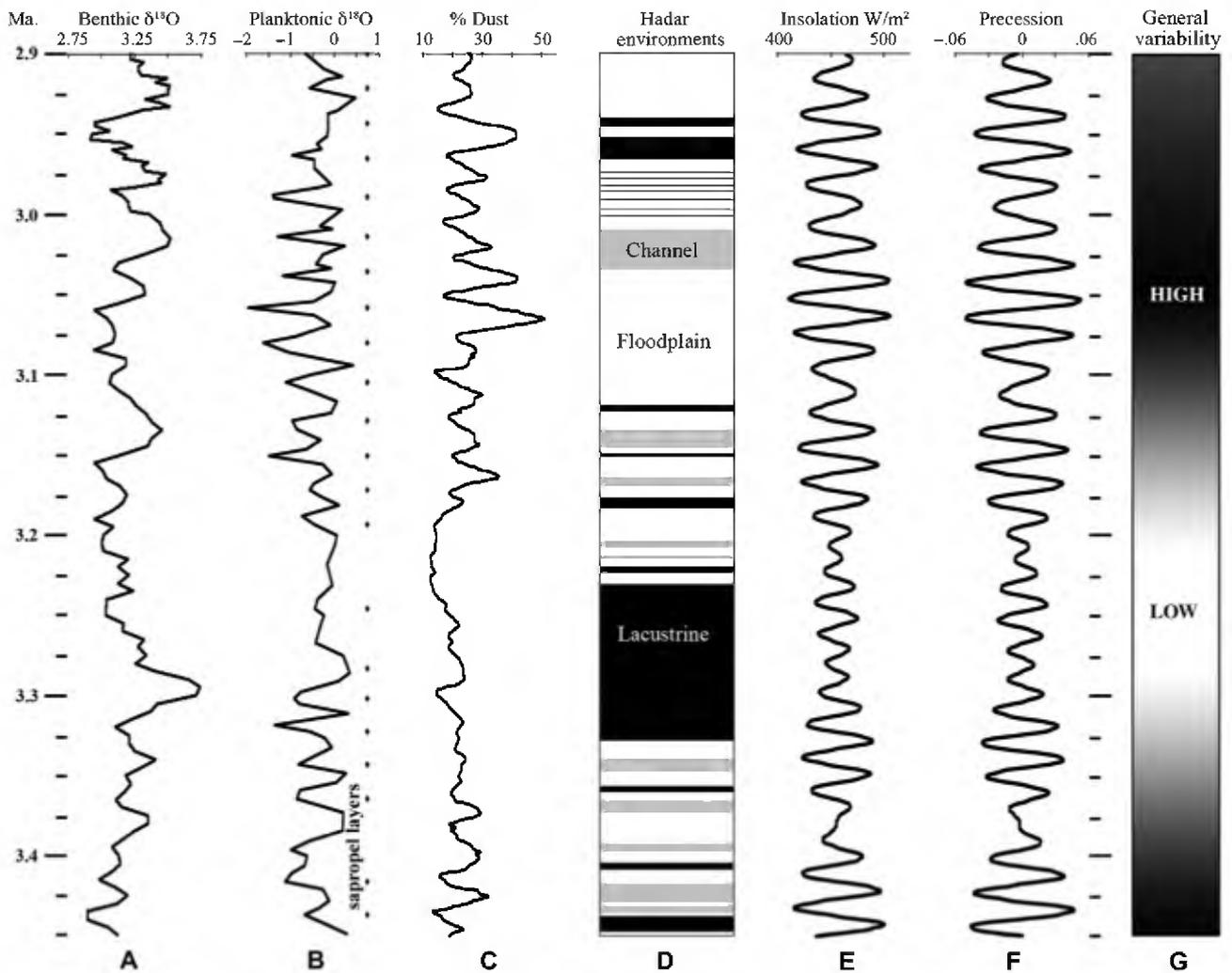


Fig. 3. Geologic and climatic records discussed in the text from 2.9–3.45 Ma. A) Composite record of benthic foraminifera $\delta^{18}\text{O}$ values from the LR04 stack (Lisiecki and Raymo, 2005). B) Record of planktonic foraminifera $\delta^{18}\text{O}$ values from the Mediterranean (Lourens et al., 1996) and sapropel record of the Eastern Mediterranean (Emeis et al., 2000). C) Record of eolian dust deposition at ODP sites 721/722 in the Gulf of Aden (deMenocal, 1995). D) Timescaled sequence of depositional environments of the pre-disconformity Hadar Formation. E) Summer (July) solar insolation record at 15°N . (Berger and Loutre, 1991). F) Record of eccentricity modulated precession (Berger and Loutre, 1991). G) Generalized pattern of climate variability between 2.9–3.45 Ma.

Dr. G. Eck and the Institute of Human Origins at Arizona State University. During collection, paleontological specimens were assigned to stratigraphic submembers (e.g., SH-2 = Sidi Hakoma 2 submember), the position of which are shown in Fig. 2. Here, we focused only on the family Bovidae, as they are the most abundant and continuous mammalian family in the Hadar record. Only bovid specimens with unambiguous submember stratigraphic position were included in the analytical dataset. In addition to their abundance, bovinds are an ecologically diverse and speciose family with many taxa being relatively habitat specific, making them particularly useful for reconstructing paleoenvironments and tracking environmental change through time (Kingdon, 1982; Greenacre and Vrba, 1984; Vrba, 1985; Shipman and Harris, 1988; Estes, 1991; Kappelman et al., 1997; Bobe and Eck, 2001). The identification of bovid remains to the tribe level in this analysis was almost exclusively based on craniodental evidence, particularly teeth and horn cores. In calculating abundance data,

multiple fossil specimens that were believed to represent the same individual at the time of collection were counted as a single occurrence; unassociated or isolated specimens were taken to represent separate individuals. Table 1 displays abundance data for bovid tribes for each submember and an approximate midpoint age for the submember.

A simple method utilized in this study to indicate “closed” versus “open” habitats using the proportion of different bovid tribes is the alcelaphine plus antilopine criterion (AAC) developed by Vrba (1980). Using modern bovid data from 16 game parks and reserves, Vrba observed that the percentage of alcelaphines plus antilopines never exceeded 30% of the total bovid population in areas with a high proportion of bush and tree cover (i.e., “closed”) and always exceeded 60% in areas with a low proportion of bush and tree cover (i.e., “open”). Vrba (1980) used the AAC method to evaluate the paleoenvironments of South African Plio-Pleistocene sites, while others have subsequently applied it to East African sites (e.g., Potts,

Table 1
Abundance data of bovid tribes from the Hadar submembers. Dates (in Ma) are approximate midpoint ages for the submembers using recalibrated $^{40}\text{Ar}/^{39}\text{Ar}$ dates as discussed in the text. The stratigraphic range of the submembers is shown in Fig. 2

	BM	SHT	SH-1	SH-2	SH-3	SH-4	DD-1	DD-2	DD-3	KH-1	KH-2
	3.43	3.42	3.41	3.39	3.35	3.28	3.23	3.22	3.21	3.14	3.02
Aepycerotini	12	7	9	6	4	7	9	38	21	8	17
Alcelaphini	11	1	2	4	9	6	1	14	39	8	37
Antilopini	1	2	2	1	1	0	0	2	2	4	40
Bovini	16	4	4	9	5	5	2	10	13	7	17
Cephalophini	0	0	2	0	0	1	0	0	0	0	0
Hippotragini	2	0	0	1	1	1	0	2	0	1	3
Neotragini	0	0	2	1	0	1	0	0	1	0	2
Ovibovini	0	0	0	0	0	0	0	1	0	0	0
Reduncini	0	0	2	2	5	11	7	123	28	5	7
Tragelaphini	9	5	5	5	8	10	6	33	14	9	21
Total	51	19	28	29	33	42	25	223	118	42	144

1982; Kappelman, 1984; Shipman and Harris, 1988). However, the AAC method relies on the principle of taxonomic uniformitarianism, that bovid tribes occupy the same general habitat today that they did millions of years ago. Although “taxon-free” methods, such as stable carbon isotope analysis of fossil tooth enamel or ecological functional morphology (ecomorphology), have become increasingly popular and useful in reconstructing hominid paleoenvironments, the Hadar paleontological assemblage has yet to be systematically analyzed by these methods. While this study relies on the concept of uniformitarianism, other studies directly comparing carbon isotope or ecomorphology results to AAC values have identified similar overall trends in paleoenvironmental communities between the methods (e.g., Plummer and Bishop, 1994; Sponheimer and Lee-Thorp, 2003).

Cluster and correspondence analysis (CA) were performed using the program MVSP (Multi-Variate Statistical Package v.3.13; Kovach Computing Services, 2002) to identify similarity or differences between submember bovid assemblages and to understand the controlling factors of the patterns observed. Cluster analysis is an exploratory technique for identifying groups and subgroups in a multivariate dataset based on the overall similarity of samples to one another. In ecological studies, results will ideally display group structure based on the composition of taxa from multiple samples (e.g., submembers) that can be interpreted in terms of ecological similarity/difference. The cluster analysis incorporated all 10 bovid tribes identified at Hadar and was calculated using the UP-GMA clustering method. In order to minimize potential sample size bias between submembers, nonparametric Spearman’s rank order was used to measure similarity/distance.

In contrast to cluster analysis, which attempts to organize entities (e.g., submembers) into discrete groups, ordination techniques, such as CA, attempt to organize entities along a continuum (Ludwig and Reynolds, 1988; Hammer and Harper, 2006). As one of the few multivariate methods of analysis that is designed for noncontinuous data, correspondence analysis has been used on extant bovid assemblages to characterize bovid tribe habitat preference (e.g., Greenacre and Vrba, 1984; Alemseged, 2003). Although complicated by the biased

representation of taxonomic abundance in a fossil assemblage, CA has also been applied to fossil bovid assemblages to characterize the paleoenvironments of fossil localities through time (e.g., Bobe and Eck, 2001; Alemseged, 2003). As used in this study, when applied to a contingency table containing frequency counts of bovid tribes in different submembers (Table 1), samples with similar taxonomic compositions will be placed close to each other on the CA plot, and taxa with similar distributions across samples will be placed close to each other. While cluster analysis shows a similar pattern of similarity/difference between submembers, CA has the advantage of also showing which bovid tribes are generally responsible for the associations between submembers. Additionally, the distribution of submembers in relation to bovid tribes on the CA graph provides a level of paleoenvironmental information for each submember. In this study, the correspondence analysis excluded the exceptionally rare bovid tribes (Neotragini, Cephalophini, and Ovibovini) and was calculated using the cyclic Jacobi algorithm with no species weighting.

Cyclicality in the Hadar sedimentary record

A major disconformity in the Hadar sequence just above the 2.94 Ma BKT-2U divides the youngest member at Hadar, the Kada Hadar, into “upper” and “lower” components. This disconformity marks a dramatic shift in facies character, stratigraphic completeness, and accumulation rates (Vondra et al., 1996; Yemane, 1997). Sediments below the disconformity have yielded numerous specimens of *Australopithecus afarensis*, while the upper Kada Hadar Member has yielded material attributed to *Homo* aff. *H. habilis* and Oldowan stone tools (Kimbel et al., 1996, 1997). Sediments of the upper Kada Hadar Member are coeval with the lowermost strata of the newly designated Busidima Formation in the adjacent Gona region (Quade et al., 2004). However, due to the discontinuous and poorly preserved nature of these sediments at Hadar, we have yet to formally adopt the formation-level designation.

Strata below the disconformity at Hadar are composed of fluvial sands, well-developed claystone paleosols (dominantly vertisols), and several brief lacustrine transgressions

(including ephemeral floodplain lakes). The depocenter during Hadar Formation times was located just east of Hadar, as evidenced by lacustrine-dominated facies in the easternmost regions of Hadar and the adjacent Middle Ledi region. Detailed analysis of the Hadar deposits indicates a strong cyclicity in the fluvial system with regular intercalations of fully lacustrine, lake-margin, or ephemeral floodplain lake-facies. Although variably higher during lacustrine versus fluvial regimes, the sedimentation rate in the central region at Hadar during this time is remarkably linear with an average of ca. 30.1 cm/kyr (Fig. 4). This suggests that either an empty Hadar Basin was filled in linearly, or that basin subsidence and sediment influx were well-balanced with accommodation space continually and consistently being formed and filled. While there is some evidence to suggest that the initial sedimentation in the Hadar Basin (ca. 3.8 Ma) was rapid and lacustrine-dominated (Wynn et al., 2006), we believe that the sedimentation rate pattern indicates a balance between basin subsidence and sediment influx by at least 3.4 Ma.

While continuous basin subsidence is tied to the tectonic development of the rift, there is as yet no evidence for any major tectonic events during pre-disconformity times in the Hadar or Middle Ledi regions that could explain the cyclicity in Hadar's depositional environments. This suggests that the periodicity observed in the depositional environments at Hadar was predominantly climatically controlled. While there may have been periodic tectonic activity along the Western Ethiopian Escarpment, recent kinematic evidence indicates that approximately 85% of crustal extension in the Afar occurred before 3.2 Ma and less than 12% occurred after 2.9 Ma (Redfield et al., 2003). Such evidence provides little support for major subsidence of the Hadar region during of after Hadar Formation times, an argument that has been used to interpret paleoclimate trends, particularly regarding paleotemperature (Redfield et al., 2003, contra Aronson and Taieb, 1981; Bonnefille et al., 1987). Additionally, in combination with the global climatic context discussed below, we believe this evidence does not support the suggestion that the cyclicity in depositional environments at Hadar was controlled by rapid

periodic basin subsidence resulting from displacement along major normal faults bounding the Ethiopian Rift (cf. Vondra et al., 1994; Yemane, 1997).

The disconformity at Hadar may represent some 200,000 years, from ca. 2.9–2.7 Ma (Quade et al., 2004). Following the disconformity, sediment preservation in the upper Kada Hadar Member is highly localized and strata are composed primarily of cut-and-fill channel conglomerates and silt-dominated paleosols. The thickness of post-disconformity sediments thins in a general west to east direction across the Gona, Hadar, and Middle Ledi regions. Yemane (1997) attributed the cobble conglomerates to braided-stream alluvial fan deposits resulting from western margin uplift, while Quade et al. (2004) attributed them to deposition by the ancestral Awash River associated with a period of major erosion following the drying of the sub-disconformity lake. Recent work by Wynn et al. (2006) has suggested that deposition in the Hadar Basin ceased after 2.9 Ma and that the Hadar Formation strata were uplifted from a depositional position by normal faults. Although Wynn et al. (2006) do not expand on the details of the origin and depositional environment of the conglomerates, they propose that the sediments of the Busidima Formation (=upper Kada Hadar Member) were subsequently deposited in the Busidima half-graben located between the Hadar Basin and the edge of the western escarpment. While this cessation of sediment accumulation at Hadar is broadly corroborated, our recent research suggests that the process outlined by Wynn et al. (2006) was gradual and potentially episodic, with minor accumulation (ca. 40 m) in the Hadar Basin persisting well into the early Pleistocene.

We have previously suggested that the facies shift is the result of tectonic reorganization within this segment of the Main Ethiopian Rift, most likely reflecting the initiation of down-rift translation of the primary terminal depocenter (Feibel and Campisano, 2004; Campisano and Feibel, 2005). This explanation is an extension of Kalb et al.'s (1982) proposal that the Hadar Formation generally reflects a northeastwards migration of the Awash deposystem from the Middle Awash region during the Pliocene. Such a translation would have a similar effect as described by Yemane (1997), increasing the gradient between the western margin and the depocenter, and could have occurred with or without coeval uplift along the Ethiopian Escarpment. This interpretation fits the volcano-tectonic model of Lahitte et al. (2003) which documents the northward migration of central Afar volcanism between 3 and 1 Ma, linked to the northward propagation of the Gulf of Aden Ridge. It is also supported by the identification of a thick lacustrine sequence ca. 40 km northeast of Hadar dated to ca. 2.8 Ma (Campisano, unpublished data).

While climatic factors may still have influenced post-disconformity sedimentary patterns contemporary with the origins and early evolution of the genus *Homo*, the incomplete nature of the stratigraphic record in the Hadar region makes such identifications difficult. As such, the rest of this discussion will focus on the pre-disconformity sequence at Hadar prior to 2.9 Ma.

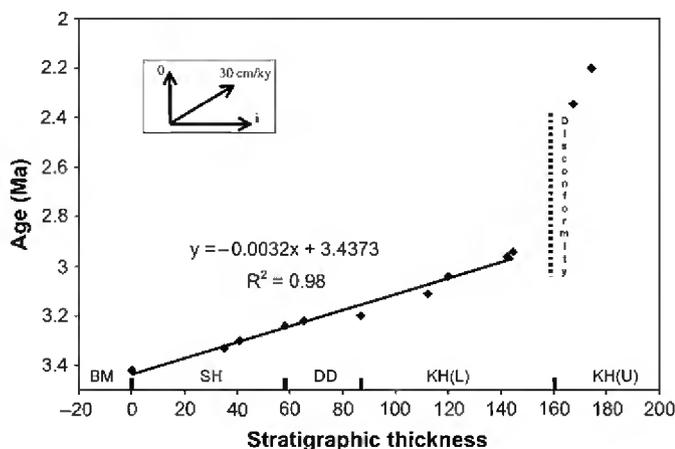


Fig. 4. Sedimentation rate model (age vs. depth) for the Hadar Formation. Trendline equation is for pre-disconformity values only.

Global climate cycles and the local sedimentary record

The marine record of climatic variability indicates that prior to 2.8 Ma, subtropical African climate was dominated by precessional cycles of 23–19 kyr, which are tied to changes in solar insolation and reflected in the strength of the African monsoon system (deMenocal, 1995). The amplification of low-latitude summer insolation results in the intensification of East African monsoon rainfall leading to increased flow of the Nile River and subsequent sapropel formation in the Eastern Mediterranean Basin (Rossignol-Strick, 1985). After 2.8 Ma, African climate varied primarily at the longer 41-kyr obliquity-dominated cycles, synchronous with the onset of high-latitude ice sheets and cooling of the subpolar oceans (deMenocal, 1995, 2004). While the relationship between this shift in orbital cyclicity dominance and African faunal evolution at ca. 2.8 Ma has been the subject of considerable debate (e.g., Vrba, 1995, 1999; Bobe et al., 2002; Bobe and Behrensmeyer, 2004), little research has focused on the potential influence of paleoclimatic variability during precession-dominated times, which encompasses the entire pre-disconformity sequence at Hadar. Palynological evidence for climatic and vegetational variability at Hadar has been suggested to correlate well with global records (Bonnefille et al., 2004). In order to further evaluate the potential influence of global climate patterns on Hadar paleoenvironments, we integrate Hadar depositional environments and changes in faunal assemblages into various global climate proxy records.

East African climate patterns are the result of a complex interaction of factors. While orbital parameters are likely to have influenced East African paleoenvironmental change, the extent of this influence and the mechanisms involved are still being investigated. While there may be some connection between orbital precession cycles and the cycling of fluvial and lacustrine depositional environments at Hadar, there is no consistent one-to-one relationship between the phenomena such as has been observed in lacustrine sequences in the hominid-bearing Chemeron Formation of the Tugen Hills, Kenya (Deino et al., 2006). While some lacustrine events at Hadar correlate with orbital precession maxima, not all do, nor do all precession maxima correlate with a lacustrine phase or transgression. Similarly, as both the Awash River and the Blue Nile have their source in the Ethiopian highlands, it should be expected that Pliocene environments at Hadar would also have been influenced by sapropel forming processes, but consistent correlations with the sapropel record are difficult to establish. As mentioned earlier, such fine-scale correlations (or lack thereof) are influenced by the exact location of stratigraphic sections and the degree of potential error in comparing a complex depositional timescale derived from geomagnetic and $^{40}\text{Ar}/^{39}\text{Ar}$ age estimates (with associated errors) to insolation solutions or astronomically calibrated timescales. While the sedimentation patterns at Hadar do appear to be climatically influenced, it is likely that the dynamic nature of the local controls on sedimentation obscure the consistent recording of precessional cycles, even if there were no errors in the age model.

During relatively long-term stable conditions in the depositional environments, such as existed during the upper Sidi Hakoma and lower Denen Dora lacustrine phase, ca. 20-kyr precessional cycles do appear to be present. For example, a ca. 60-kyr section of lacustrine clay deposits (3.30–3.24 Ma) records three packages of sediment, the lower two of which are identical pair sets. Each of these two sets are composed of an identical series of three-colored clay sequences that transition upward from dark grayish brown to very dark gray to dark olive-gray. Both the thickness of the two sets as well as the thickness of corresponding units between the two sets are comparable. The very dark gray and dark olive-gray units are of similar thickness to each other, but thinner than the grayish brown unit. Pedological analyses have not yet been conducted to identify any other differences amongst the clay sequences, but it is possible that the color variation represents differences in lake levels. The transitions from the oxidized brown clays to the reduced dark gray and olive-gray clays may represent cycles of shallower, more oxygenated lake conditions transitioning to deeper water conditions. If correct, then this section may not only suggest that precessional scale cycles are recorded at Hadar, but potentially sub-precession-scale cycles as well. Isotopic values of mollusks (Hailemichael et al., 2002) and the periodic formation of paleosols during this lacustrine-dominated phase also provide evidence for short-term cycles of lake-level fluctuations that may be climatic in nature. Recent investigations by one of us (C.J.C.) in the lacustrine-dominated Middle Ledi deposits immediately east of Hadar also show sedimentological cyclicity, the temporal framework of which is being analyzed.

The influence of eccentricity-modulated “variability packets”

Terrigenous dust volume and isotopic data from marine cores off Africa indicate that during precession-dominated times, orbital eccentricity modulation of precession produced “variability packets” of high- and low-amplitude African paleoclimate variability lasting 10,000 to 100,000 years in duration (Berger, 1978; deMenocal, 2004). While detailed orbital climatic cycles may not be consistently chronicled in the Hadar strata, these larger-scale regional/global patterns do appear to be recorded (Fig. 3).

The upper Sidi Hakoma and lower Denen Dora lacustrine sequence, documenting the most persistent lake phase at Hadar, has been thought to be the result of tectonic factors (Vondra et al., 1994; Yemane, 1997). However, when viewed in the global climatic context, this lacustrine stage roughly coincides with the most stable period in both the oxygen isotope and terrigenous sediment flux records from marine cores during the Hadar sequence (Fig. 3, columns A–D). Climatologically, this distinct long-term period of very low dust percentage indicates less arid (i.e., more humid and/or wet) conditions. Although isotopic values of Mediterranean planktonic forams are enriched, indicative of cooler conditions, the Mediterranean record still preserves several sapropel horizons indicating the continuation of strong summer monsoonal precipitation

(Emeis et al., 2000). Similar situations of humid periods during cool stages are also recorded in the Levant during the Pleistocene (Almogi-Labin et al., 2004). Isotopic evidence from the LR04 stack shows that while the beginning of this lacustrine phase overlaps with the abrupt and short-lived glacial excursion of marine isotope stage M2, it rapidly returns to warmer and less variable conditions for the rest of the lacustrine phase (Fig. 3, column A). This lacustrine period also roughly coincides with the period of lowest-amplitude climate variability during Hadar times as indicated by insolation and eccentricity-modulated precession.

Recent research in other Plio-Pleistocene East African lacustrine basins have suggested that prolonged lacustrine sequences are related to eccentricity maxima and thus precessional insolation amplitude and summer monsoon strength (Deino et al., 2006; Trauth et al., in this issue). However, the specific influence of insolation patterns on East African climate and its potential interaction with other factors is not yet fully understood and could be expected to vary regionally. For example, not only does the main lacustrine sequence at Hadar occur during a period of eccentricity minima, but high resolution analyses of the Chemeron Formation correlate some, but not all, eccentricity maxima to lacustrine intervals (Deino et al., 2006). Combined with the other proxy data, particularly the extended period of low marine core dust concentrations, we believe that the main Hadar lacustrine interval is climatically driven, coinciding with a relatively long and stable period of wet conditions tied to equable rainfall and modest seasonality. Unfortunately, the relatively short temporal record preserved at Hadar precludes us from determining if other periods of low-amplitude climate variability are associated with lacustrine sequences.

Global climate proxies and the Hadar paleontological record

To what degree can the influence of global climate change be observed in the fossil record of hominins and other mammalian taxa at Hadar? Unfortunately, unlike other hominin localities in Africa, Hadar does not have the paleontological record to test for a ca. 2.8 Ma event in African faunal evolution. It is also unlikely that any Pliocene locality would have sufficient data to record ca. 23-kyr variability in fossil mammalian communities. However, eccentricity modulated precession “variability packets” may play a role in changes evident in the paleontological record at Hadar. These extended periods of paleoclimatic stability and instability as a mechanism for natural selection are a key component of the Variability Selection Hypothesis of faunal adaptation and evolution (Potts, 1996, 1998). In contrast to habitat-specific hypotheses, the Variability Selection Hypothesis acknowledges that variability is inherent across all timescales, but emphasizes the importance of periods of environmental instability over long durations as a mechanism for introducing genetic variance. It states that certain adaptations fostering adaptability can evolve as a response to long-term patterns of environmental

variability in selective conditions over the course of a lineage, not just a few generations (Potts, 1998).

A period of high-amplitude climatic variability related to eccentricity-modulated precession is evident in the dust and oxygen isotope record in marine cores from ca. 3.15 to 2.90 Ma, with particularly high variability in the interval between ca. 3.07 and 2.93 Ma (Fig. 3). This increase in climatic variability coincides with a distinct change in Hadar paleoenvironments as indicated by the fossil bovid community around 3.0 Ma. Moreover, palynological evidence from Hadar indicates that while pre-disconformity conditions were both cooler (by ca. 6.4 °C) and wetter than present, there is a stronger seasonal contrast at ca. 2.95 Ma than at any earlier or modern sampled interval for the Hadar record (Bonnefille et al., 2004).

Bovoid fossils from the KH-2 submember of the Kada Hadar Member derive from a major fluvial system (channel and overbank) just prior to ca. 3.0 Ma and are dominated by the tribes Alcelaphini and Antilopini. Extant alcelaphines (e.g., hartebeests and wildebeests) are the archetypal plains antelopes, preferring to live in the open savanna with short grasses. Alcelaphines have very hypsodont teeth and are specialist bulk-grazers that are able to go without drinking for varying intervals and have cursorial limb bones adapted for open country running. Extant antilopines (e.g., springboks and gazelles) are specialized for arid biomes with hypsodont teeth and cursorial limbs. They are gleaners (grain picking) and selective feeders on both foliage and herbage, but typically on vegetation that occurs in dry and open environments. This feeding strategy allows antilopines to subsist in areas too dry and nutrient-poor to support larger roughage eaters (Kingdon, 1982; Estes, 1991). Cluster analysis and correspondence analysis of Hadar bovid tribes clearly indicates the distinction between the KH-2 bovinds and those from earlier intervals which is a result of the submember’s high proportion of antilopines and alcelaphines; 53% of all bovinds identifiable to tribe (Figs. 5 and 6). While the KH-2 AAC percentage would not technically place it in the open country category according to Vrba (1980), it is significantly higher than the other submember values, which are all below 35%, indicating that it at least represents the most open and arid habitat present at Hadar between 3.42 and 2.90 Ma. This KH-2 transition is also reflected in other mammalian lineages at Hadar and includes the first appearances of several arid-adapted bovid and nonbovid taxa (Campisano and Reed, 2007). Although beyond the range of this discussion, the limited faunal evidence from above the disconformity (ca. 2.2–2.4 Ma) also indicates open/arid habitats (Eck and Reed, 1996), possibly reflecting the global trend towards increased aridity documented after 2.8 Ma (e.g., deMenocal, 1995, 2004).

While the dataset is not as robust, there may also be a correlation between the timing of this high-amplitude period and a significant size increase in *A. afarensis*. Six individuals from the KH-2 submember suggest an overall larger size than from earlier deposits as evident in some dental, mandibular, and forelimb dimensions (Lockwood et al., 2000; Drapeau et al., 2005). While the increase in mandibular dimensions is statistically significant and the dentition shows directional temporal

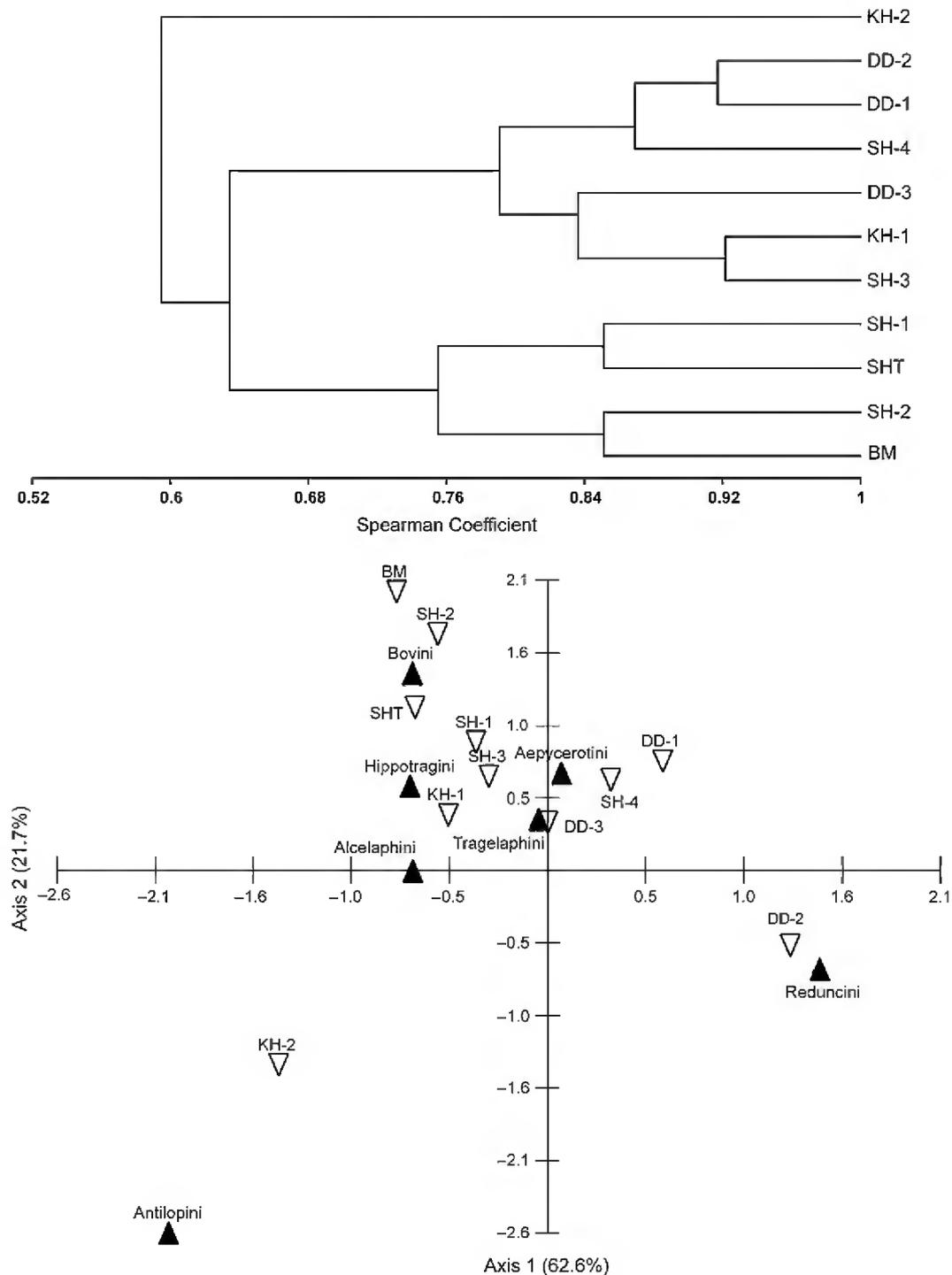


Fig. 5. Cluster analysis (top) and correspondence analysis (bottom) of Hadar submember bovid tribe abundance indicating the outlier position of the KH-2 sub-member. Axes 1 and 2 account for 84% of the variation in the correspondence analysis. DD-2 bovinds are distinct in their high number of edaphic grassland-adapted Reduncini coinciding with a unique delta plain type environment.

trends in a few dimensions, the increase in forelimb size is based upon the analysis of only one KH-2 individual. If this marked size increase continues to be supported by more fossil evidence, then it may be possible to suggest that the size increase in *A. afarensis* is an adaptive response to a more variable environment. Suggested advantages of larger body size include the improved ability to escape predation, greater

reproductive success (sexual selection), expanded size range of acceptable food, extended individual longevity (life span relates broadly to body size), and improved thermal efficiency (Damuth and MacFadden, 1990; Pagel, 2002). A possible test of this hypothesis may include the examination of other Hadar mammalian fauna to see if they, too, follow any trends towards larger body size in this time interval. However, further

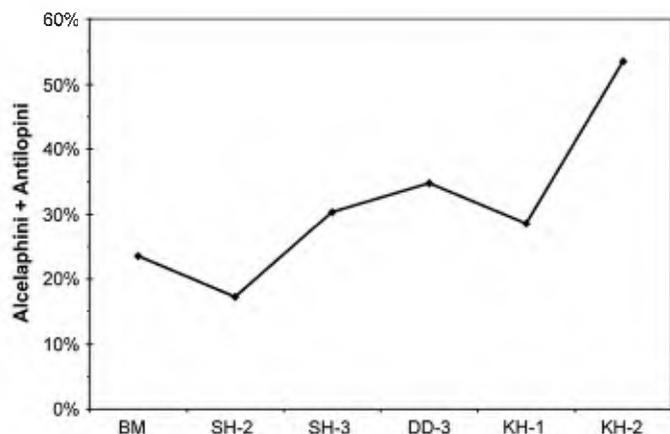


Fig. 6. Alcelaphini plus Antilopini as a percentage of all bovid tribes across fluvial-dominated submembers at Hadar.

investigation would still be required to attempt to identify a causal connection between the size increase and environmental events, not just a temporal correlation.

Determining whether this morphological change in *A. afarensis* continues beyond the KH-2 submember as well as attempts to identify the cause(s) of the species' extinction at Hadar are currently prohibited by the lack of strata preserved between roughly 2.7–2.9 Ma. It is unlikely that the true last appearance datum (LAD) of *A. afarensis* at Hadar is within the KH-2 submember (ca. 3.0 Ma), even though it is relatively contemporaneous with the taxon's LAD in the Shungura Formation (ca. 2.95 Ma; Grine et al., 2006). Although the KH-2 submember reflects probably the most dramatic environmental change recorded at Hadar, the proportion of *A. afarensis* in the KH-2 reaches its second highest submember level as opposed to decreasing (Campisano and Reed, 2007). It seems likely that if it was not for the disconformity, additional *A. afarensis* specimens would be found above BKT-2.

Summary and conclusions

Numerous regional and global paleoclimate proxy records have provided a wealth of data relevant to East African hominin sites. These records, often from the marine realm, provide an important context for the reinterpretation of terrestrial paleoenvironmental reconstructions. However, the extent to which the influences of orbital-scale global climate change can be recognized and subsequently incorporated into the East African record must be carefully determined on a site-by-site basis. While particular terrestrial intervals in East Africa may be of sufficient resolution to preserve a record of these short-term climate changes, they are typically the exception as opposed to the norm. For the Hadar record, it may be more useful to look for correlations to the larger patterns of regional and global climate change than to any particular event.

Correlations to circum-Africa climatic patterns, tectonic evidence, and stability in the sedimentation rate throughout the Hadar pre-disconformity sequence (>2.9 Ma) suggest that consistent oscillations between fluvial and lacustrine depositional

environments are predominantly climatically controlled. Although there is no reason to assume global climate patterns did not influence post-disconformity paleoenvironments, any potential climate signatures have been obscured by major changes in the Hadar depositional system and sediment preservation related to regional tectonics and paleogeography. While precessional patterns in global climate may be recorded in the Hadar terrestrial record, they are commonly overshadowed by local sedimentary and environmental dynamics. In contrast to specific one-to-one correlation of events, packets of climate variability may be an equally important and more recognizable influence on Hadar paleoenvironments. For example, periods of high- and low-amplitude climate variability appear to be manifested in the Hadar sedimentary record, particularly the major lacustrine transgression coinciding with a significant low-amplitude period.

Over the course of its duration at Hadar, *A. afarensis* persisted through a variety of changes in local paleoenvironments, some of which were manifestations of global climate change and patterns. In the paleontological record, a significant high-amplitude period of climate variability coincides with a shift towards more arid-adapted bovid taxa after 3.11 Ma, as indicated by the abundance of alcelaphines and antilopines in the KH-2 submember. This period of climatic variability may also be connected to size increases observed in *A. afarensis* dental, mandibular, and postcranial elements. To test whether such a size increase is, in fact, ecologically related may depend on the recognition of similar patterns in other mammals and the recovery of additional hominin material. Fortunately, the fossil-rich Hadar sediments, which continue to yield such specimens, may be one of the few localities with the ability to provide answers to such questions.

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