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Northern Hemisphere Glaciation, African climate and human evolution

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ABSTRACT

The hypothesis of a connection between the onset (or intensification) of Northern Hemisphere Glaciation, the stepwise increase in African aridity (and climate variability), and an important mammalian (including hominin) species turnover is a textbook example of the initiation of a scientific idea and its propagation in science. It is, however, also an example of the persistent popularity of a hypothesis despite mounting evidence against it. A critical review of key publications on the topic and statistical re-analysis of key records of global ice volume and African climate leads to three conclusions: (1) The Northern Hemisphere Glaciation was a gradual process occurring between ~3.5 and 2.5 Ma, not a single event at ~2.8 Ma or at any other time. (2) A consistent stepwise (+/−0.2 Ma) transition toward greater aridity in Africa at ~2.8 Ma does not exist; instead, there are regionally different, gradual transitions partly in connection with the intensification of the Northern Hemisphere Glaciation, but above all with the establishment of the tropical Walker Circulation after ~2 Ma. (3) Mammalian (including hominin) species turnovers at this time also appear to have been gradual, rather than stepwise.

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1. Introduction

The hypothesis of a connection between the onset (~2.4–2.5 Ma, Shackleton and Opdyke, 1977; Shackleton et al., 1984; Raymo, 1994) or intensification (~2.75 Ma, Maslin et al., 1995) of the Northern Hemisphere Glaciation (ONHG/INHG), the stepwise (+/−0.2 Ma, according to deMenocal, 2004) increase in African aridity (and climate variability) (e.g., deMenocal, 1995, 2004; Bonnefille, 2010; Antón et al., 2014; Joordens et al., 2019; Lupien et al., 2019) and an important mammalian (including hominin) species turnover (e.g., Vrba, 1995b; Bobe and Behrensmeyer, 2004; Bibi et al., 2013; DiMaggio et al., 2015) is a textbook example of the initiation of a brilliant scientific idea and its propagation in science. It is, however, also an example of the persistent popularity of a hypothesis despite mounting evidence against it (e.g., Cane and Molnar, 2001; Ravelo et al., 2004; Trauth et al., 2009; deMenocal, 2012).

The ONHG-turnover hypothesis is deeply rooted in the 1970s and 80s, when the first long Deep Sea Drilling Project (DSDP, 1968–1983) and Ocean Drilling Program (ODP, 1985–2003) paleoclimate time series appeared, reaching back several million years into Earth's history (e.g., Shackleton et al., 1984; deMenocal et al., 1991; Haug and Tiedemann, 1998; Zachos et al., 2001; Ravelo et al., 2004; Cramer et al., 2011; Mudelsee et al., 2014; Westerhold et al., 2020) (Fig. 1). At the same time, the first long records of climate change in Africa were generated, indicating a trend toward greater aridity, though there was no immediate

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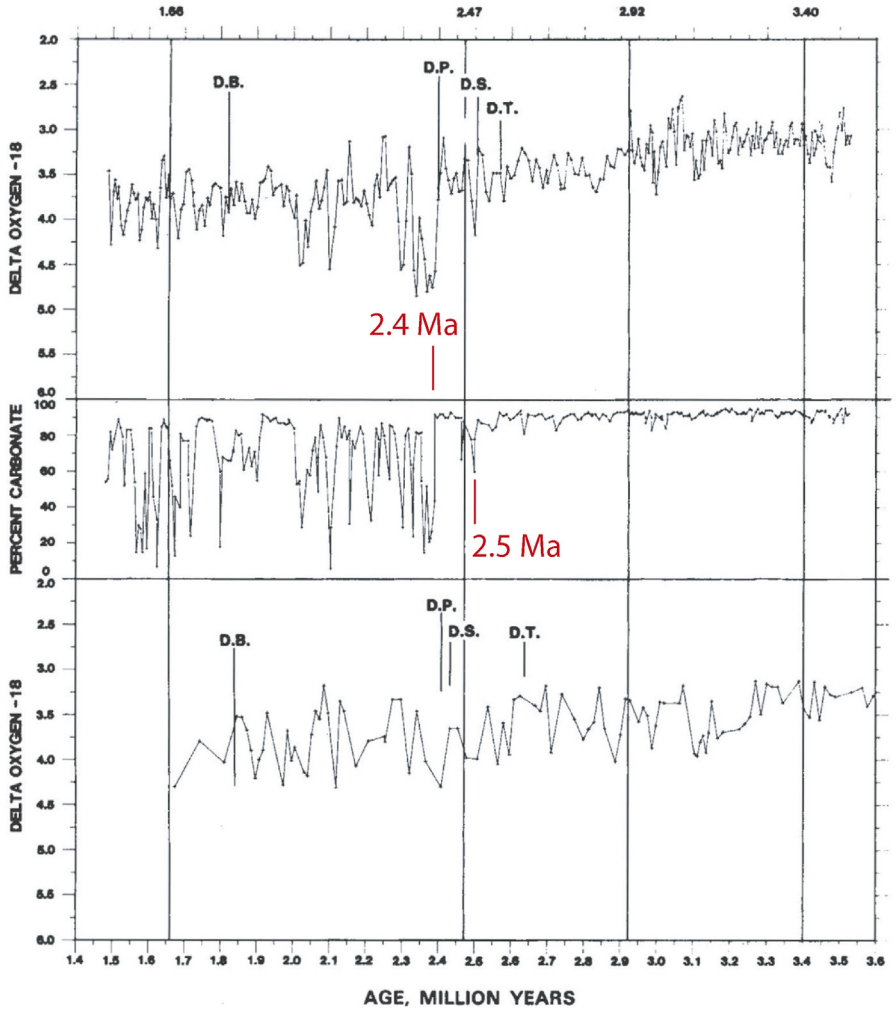


Fig. 1. Oxygen isotope record of North Atlantic ODP Site 552 A (top), carbonate content in the same interval (middle), and oxygen isotope record in Pacific core V28−179 (Imbrie et al., 1984), showing the first major horizon of ice-rafted debris occurring at ~2.4 Ma, preceded by a minor pulse of ice-rafting at about 2.5 Ma (marked by a red arrow and age by the authors of this work). The y-axis labelling DELTA OXYGEN-18 corresponds to $\delta^{18}O$ in currently common notation. The vertical lines mark magnetic subchrons used for time control with their age data valid at the time of publication. The two-letter abbreviations DT, DS, DP, and DB mark calcareous nannofossil *Discoaster* sp. extinction horizons determined in both cores. Figure modified after Shackleton et al. (1984) with permission from Springer Nature. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

consensus on its speed and cause (e.g., Cerling, 1984; Cerling et al., 2011; Trauth et al., 2005, 2007; Levin, 2015; Liddy et al., 2016; Blumenthal et al., 2017; Wood and Patterson, 2020).

The third and final piece in the formation of ONHG-turnover hypothesis came from growing archeological and fossil collections from African sites, and increasingly precise dating (e.g., Gabel, 1983; Chamberlain, 1991; Vrba, 1995b). The connection between ONHG/INHG, a stepwise increase in African aridity, and resulting species turnover was consolidated during a workshop in May 1993 in Airlie, Virginia, United States, and the subsequent publication of its proceedings in a book entitled Paleoclimate and Human Evolution (Vrba et al., 1995) (Fig. 2). Since then, the hypothesis of a turnover mediated by northern hemisphere climate change during the Plio-Pleistocene has fascinated both paleoclimatologists and paleoanthropologists (deMenocal, 1995; Cohen et al., 2016; Joordens et al., 2019; Lupien et al., 2019), and formed a basis for several large projects, including the Hominin Sites and Paleolakes Drilling Project (HSPDP) (Cohen et al., 2016). Fundamental to the support of this hypothesis is that observed stepwise (+/−0.2 Ma) changes in high latitude climate can be directly correlated to stepwise changes in African climate and faunal records (deMenocal, 1995, 2004).

This paper traces the rise and fall of the ONHG-turnover hypothesis, showing how improved geological and fossil records, in conjunction with new analytical approaches, argue that both Northern Hemisphere Glaciation and African aridification were gradual processes. As such, African aridification cannot be posited as the cause of any significant faunal turnover event at ~2.8 Ma (or at around that time). The first part of the paper deals with a comprehensive analysis of the history of the scientific idea as far back as the mid-19th century. The consequences of this idea are examined, as is its influence on subsequent scientific investigations. In the second part of the paper, we take a closer look at key data sets, statistically re-analyze some of them that have been used to propose a climatic transition in Africa at ~2.8 Ma. For this purpose, an attempt is made to understand the original interpretations behind these data sets.

2. Methods

The first part of the paper analyzes the history of the scientific idea by seeking its roots, including coincidental meetings and

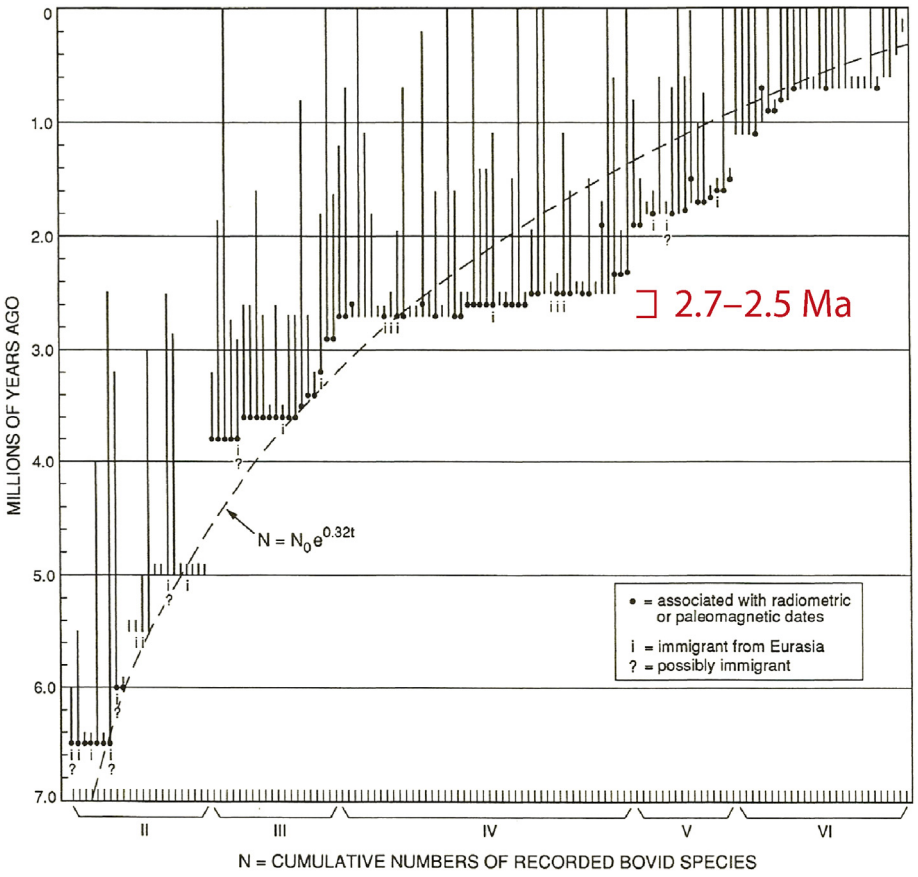


Fig. 2. Durations of African fossil boid species over the past 7 Ma according to Vrba (1995). The dashed line represents the null hypothesis of uniform speciation. According to Elisabeth Vrba's analysis a major faunal turnover marked by the first appearance of a larger number of grazers occurred at ~2.7–2.5 Ma (marked by a red arrow and age by the authors of this work), i.e. at about the same time Shackleton et al. (1984) observed the first horizons of ice-debris in both North Atlantic and Pacific oceans. This coincidence inspired her to propose a connection between the onset of Northern Hemisphere Glaciation and an important species turnover at ~2.7–2.5 Ma. Figure modified from Vrba (1995) with permission from Yale University Press. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

exchanges between scientists at project meetings, conferences, and workshops. The consequences of this idea are examined, as its influence on scientific investigations both before and after it was falsified. In the second part of the paper, we examine why the idea persists that the high latitudes have a major control on the climate of the low latitudes and thus early human evolution. For this purpose, an attempt is made to understand the original interpretation of the data, with special consideration of the composition of the scientific team and their scientific backgrounds and persuasions. Some of the key records in support of the hypothesis of a stepwise transition will be statistically re-analyzed by fitting change-point models to the time series; such models determine the chronology and statistical significance of any transitions found in the data (Fig. 3). We have used the original data from the cited sources, as found in the supplements to the papers, with the exception of the ODP data from Shackleton et al. (1995a) and Mix et al. (1995a), which were obtained from PANGAEA (https://www.pangaea.de) (Shackelton et al., 1995b; Mix et al., 1995b).

We use the benthic foraminiferal stable oxygen isotope ($\delta^{18}O$) record of ODP Site 846 as a record of global ice volume (Mix et al., 1995a,b; Shackleton et al., 1995a,b). ODP Site 846 was drilled in 1991 during Leg 138 on the southern limb of the Carnegie Ridge in the tropical Pacific Ocean (3°06′S 90°49′W, 3307 m water depth, Mix et al., 1995a,b; Shackleton et al., 1995a,b). The record goes back to ~6.1 Ma providing a median resolution of ~2.5 kyrs (Shackleton et al., 1995c). The history of increasing aridity in Africa during the last 6 Ma, in combination with the strength of the winds, and the gradual reduction in vegetation cover is traditionally reconstructed using marine records of terrestrial dust flux. The key data sets in this context include the record from ODP Site 659 offshore subtropical West Africa (median resolution ~3.7 kyrs, Tiedemann et al., 1994), ODP Site 721/722 from the Arabian Sea (median resolution ~1.6 kyrs, deMenocal et al., 1991; deMenocal, 1995, 2004), and ODP Site 967 from the eastern Mediterranean Sea (median resolution ~0.4 kyrs, Larrasoaña et al., 2003). We have already examined these data sets statistically in earlier publications (Mudelsee and Raymo, 2005; Trauth et al., 2009) and will limit ourselves to a summary of the most important results. Marine sediment cores also help to create a relatively complete vegetation history based on pollen assemblages. Here we use the ~10 Ma tree cover density from DSDP Site 231 offshore the Somali coast in the Gulf of Aden (eastern Africa) and tree pollen percentages extracted from several cores offshore the Niger delta in the Gulf of Guinea (western Africa) (Morley, 2000; Bonnefille, 2010). We used the original age model of the various ODP and DSDP Site records; using the updated age model according to Lisieck and Raymo (2005) would not change the conclusions of the paper since the statistical uncertainties are much larger than the discrepancies among the age models.

The record of stable carbon ($\delta^{13}C$) isotopes is one of the most complete but in general very complex and noisy terrestrial data sets on climate-controlled vegetation changes (e.g., Cerling, 2014). The $\delta^{13}C$ signal can be measured in soil (pedogenic) carbonate, which forms very slowly and in equilibrium with soil-respired CO2. Alternatively, the $\delta^{13}C$ signal can be found on the enamel of fossil

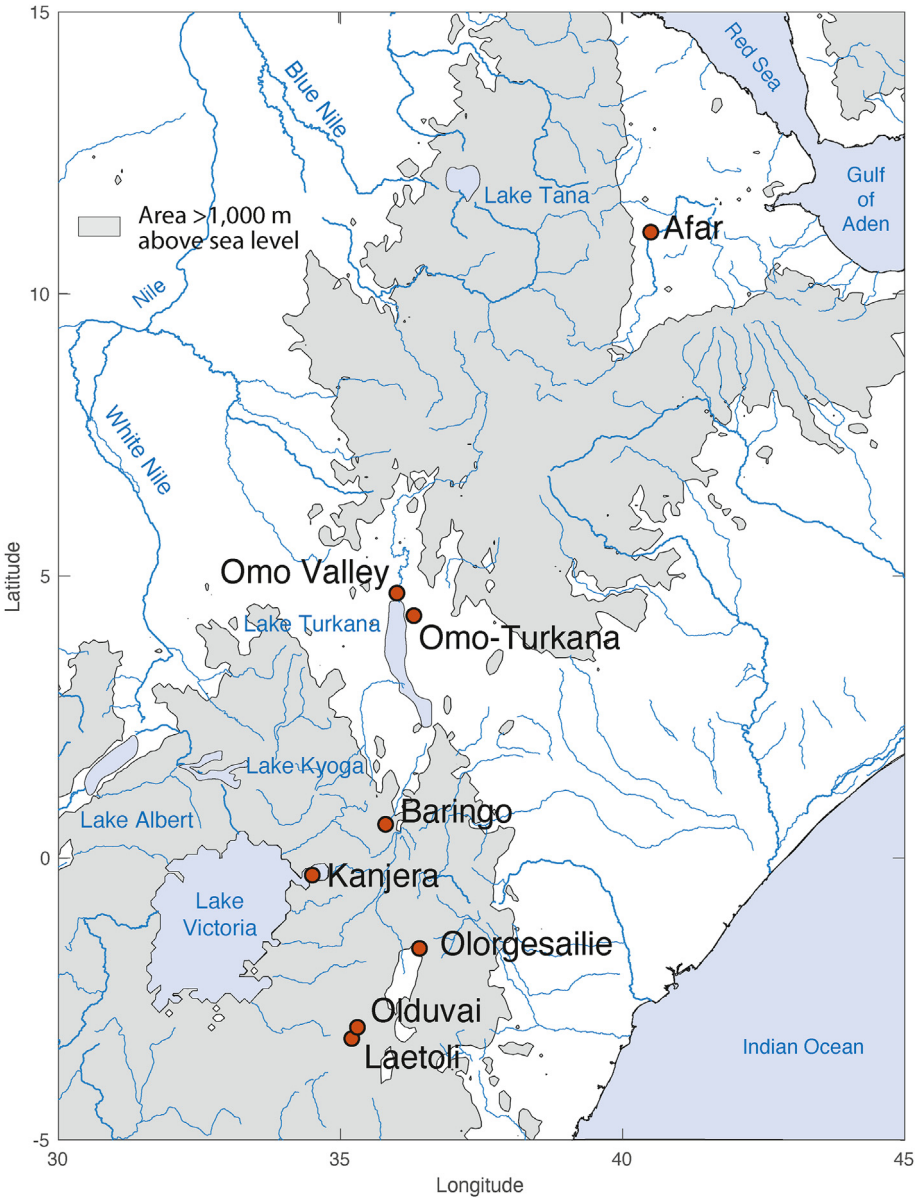


Fig. 3. Map of northeastern Africa and adjacent areas showing topography, rift faults, and key sites with records statistically re-analyzed in this study. Coastline and river polygons from the Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) (Wessel and Smith, 1996). Topography from the 1 arc-minute global relief model of the Earth's surface (ETOPO1) (Amante and Eakins, 2009).

herbivore and hominin teeth, where it reflects the composition of the diet and thus the prevailing vegetation in the environment of living beings (Cerling, 2014; Levin, 2015; Patterson et al., 2017). We use a compilation of $\delta^{13}C$ data from soil carbonates from several sites in Kenya and Ethiopia reaching as far back as ~10 Ma, with a few more data points at ~15 Ma (Levin, 2015). We also use enamel $\delta^{13}C$ records from herbivores (Bibi et al., 2013; Negash et al., 2020) and enamel $\delta^{13}C$ records from hominins from the Shungura and Usno Formations, Lower Omo Valley, Ethiopia (Wynn et al., 2020). The $\delta^{13}C$ records from other sites in Kenya and Ethiopia, such as the one from Baringo (Lupien et al., 2019) are used as a further source of information in the critical analysis of the vegetation history of eastern Africa.

We statistically re-analyzed these records for the amplitude, duration, and midpoint of a climate transition using two different methods. First, we fit a sigmoid function with $m = 4$ parameters a, b, c, and d

$$x_{\mathrm{fit}}(t) = a + \frac{b}{1 + e^{-d(t-c)}}, \text{ for } -\infty < t < +\infty$$

to the records x_i with $1 < i < n$ and n data points using nonlinear least-squares fitting. The sigmoid function (in its normalized representation) is a monotonic s-shaped curve, often referred to as a smooth version of a step function. The sigmoid function is bounded by two horizontal asymptotes $x_{\mathrm{fit}}(t) \to 0$ and 1 as $t \to -\infty$ and $+\infty$, respectively. It has a bell-shaped first derivative curve and exactly one inflection point (parameter c), which can be interpreted as the midpoint of the transition. In our analysis, we use the function fit together with fitoptions and fittype included in the Curve Fitting Toolbox of MATLAB to perform the nonlinear least-squares fitting (MathWorks, 2020) (Suppl. Fig. 1).

Second, we statistically re-analyzed these records, fitting a ramp function again with $m = 4$ parameters x_1, x_2, t_1, and t_2

$$x_{\mathrm{fit}}(t) = \begin{cases} x_1, \text{ for } t \le t_1 \\ x_1 + (t - t_1)(x_2 - x_1)/(t_2 - t_1), \text{ for } t_1 < t \le t_2 \\ x_2, \text{ for } t > t_2 \end{cases}$$

to the n data points. The monotonic ramp-shaped curve has two horizontal pieces and an inclined piece, connected by two abrupt changes of direction and with a discontinuous first derivative. The ramp function regression is implemented in the FORTRAN 77 program RAMPFIT available for download at Climate Risk Analysis (Mudelsee, 2000) (Suppl. Fig. 1). To examine the goodness-of-fit statistics we used the root mean squared error

$$RMSE = \sqrt{MSE}$$

computed from the residual *MSE*, which is in turn calculated by dividing the summed square of residuals *SSE*

$$SSE = \sum_{i=1}^{n} (x_i - x_{fit}(t))^2$$

by the degrees of freedom $v = n - m$. Both the sigmoid and ramp functions are widely used to describe transitions in climatic and environmental conditions as well as the response of the biosphere (e.g., Fleitmann et al., 2003; Mudelsee and Raymo, 2005; Crowley and Hyde, 2008; Grove, 2015).

To ensure the comparability of the results, we consider the time period between 4 and 1 Ma before present, even if some of the records do not completely cover this time period and others are much longer. Unfortunately, the various time series also differ considerably in terms of the quality of the age model, the temporal resolution, the number of replicate measurements at the same points in time, and the signal-to-noise ratio. All of this makes the interpretation of the results difficult and some of the differences found in the timing of climate transitions may be entirely due to these uncertainties. Therefore, it is mandatory to interpret midpoint timings (and deviations between records) with the help of the 2-sigma (~95 %) confidence bounds as an approximation and generic uncertainty measure for the midpoint timings, which are also supplied by the methods. After analyzing the period between 4 and 1 Ma concerning possible climate transitions, we explore the entire time series and try to critically examine the interpretations of the data sets by the original authors.

2.1. Chronology of the emergence, establishment, and decline of a scientific hypothesis

Following Darwin's (1871) early speculations about the evolution of bipedalism accompanying an arboreal to terrestrial transition, the savanna hypothesis associates the evolutionary divergence of hominins and other great apes, and the emergence of bipedalism, with a proposed forest-savanna transition. Though contentious (see Domínguez-Rodrigo, 2014, and other authors' comments therein), the savanna hypothesis has influenced the search for shifts towards drier climates and their association with events in human evolution at all time scales (e.g., deMenocal, 1995; Potts, 1998; Sepulchre et al., 2006; Carto et al., 2009; Domínguez-Rodrigo, 2014).

The first putative African fossil hominin was found at Olduvai Gorge, in an expedition led by Hans Reck in 1913 (Reck, 1925). Reck excavated a human skeleton from early Pleistocene beds at Olduvai that he claimed showed the presence of anatomically modern humans deep into the African past (Leakey, 1928). Though it would later be shown as an intrusive burial that was early Holocene in age (Leakey et al., 1933), Reck's discovery came at a time when most scholars sought human origins in Europe or Asia, and so his find kindled contention and debate over the possibility of human origins in Africa. In 1925, Raymond Dart described the first true fossil hominin from the continent, a juvenile skull from Taung, South Africa, that he named Australopithecus africanus (Dart, 1925). Besides presenting the new find (which was also received with much contention), Dart put forth the idea that open and dry tropical habitats must have played a causal role in the evolution of human intellect.

The second half of the 20th century would bring the pioneering work of Mary and Louis Leakey at Olduvai (Leakey et al., 1961, 1964) and Laetoli (Leakey and Hay, 1971), to be followed by discoveries in the Afar and the Turkana Basin (e.g., Leakey, 1970; Fitch and Miller, 1970; Curtis et al., 1975). Together, the growing assemblage of hominin fossils, stone tools, and fossilized footprints, showed that Australopithecus species were in fact bipedal, but had small brains and lacked tools. This forced the realization that different human features, such as large brains, tool use, and upright walking, must have evolved at different times, and put to rest any notion that the divergence of humans from their ape cousins took place in a single event. The savanna hypothesis adapted to the new reality of 'mosaic evolution', and, for its proponents, would have taken on broader meaning associating human evolution with a general opening up of habitats, rather than any particular event (see Domínguez-Rodrigo, 2014).

At around the same time as the Laetoli discoveries in the 1970s, Elisabeth Vrba suggested turnovers in the South African fossil record might be associated with environmental change events: "The bovid data suggest that an environmental change may have been responsible for the faunal change, at least in the Sterkfontein Valley. It is thus not entirely idle speculation to consider whether the change from gracile australopithecines (…) to robust forms (…) may be environmentally correlated" (Vrba, 1976: 302). Vrba wondered whether the event might be recognized across the continent: "is it a coincidence that an East African proliferation of bovids adapted to open country [here citing as yet unpublished data by A. Gentry and J. Harris] seems to coincide temporally with the analogous South African development? It could be possible that such change in faunal tribal representation, mirroring a change in environmental exploitation, marked the boundary (…) elsewhere in Africa as well" (Vrba, 1976). In 1981, C.K. Brain explicitly examined the potential role of 'low temperature episodes' on human evolution in Africa, specifically considering a link between the onset of Northern Hemisphere Glaciation between 3.2 and 2.6 Ma and the evolution of Homo from Australopithecus at this time (Brain, 1981).

Vrba's work on the question of global climate change and evolution continued, and in 1985 she argued for a causal role for the spread of open habitats in the evolution of Homo from Australopithecus (Vrba, 1985). In this study, Vrba found that the faunal change she first recognized in the South African record was continentally extensive and sought correlation with the newly developing global climate proxy record. Critical here was the new oxygen isotope ($\delta^{18}O$) record of Shackleton et al. (1984) from North Atlantic deep-sea sediments, which provided paleontologists with a quantitative global paleoclimatic proxy against which to compare their fossil records. Vrba correlated the faunal turnover event with a global drop in temperatures recorded around 2.4 Ma, and which Shackleton et al. (1984) had identified as the time of onset of major north Atlantic glaciation, and a shift in the Earth's climatic cyclicity to higher variability (Figs. 1 and 2). This effectively marked the beginning of the side-by-side comparisons of climatic and paleontological records that would become so commonplace in the African paleoanthropological literature. Over time, this global drop in temperatures would come to be identified as the onset of Northern Hemispheric Glaciation, and both it and the turnover

events ascribed to it would be shifted back in time to ~2.8 Ma as the chronology of deep-sea cores and fossil sites improved.

In the late 19th/early 20th century, as adroitly summarized by Kingston and Hill (2005), John W. Gregory's observation of low moraines on Mt. Kenya (Gregory, 1894) and high shorelines in the rift valley (Gregory, 1896) came at a time when it was common to correlate traces of climate change worldwide with the chronology of ice ages in the European Alps (Brooks, 1914). The pluvials, a term introduced by Hull (1885), were then introduced by Leakey (1952) to establish a relative chronological framework for paleontological and archeological assemblages. This approach had already been questioned by Gregory, who noted that tectonic and volcanic signals in the geologic record may complicate such correlations, and also later by others such as Bishop and Clark (1967). Systematic radiocarbon dating of depositional sequences and shorelines in several basins by Butzer et al. (1972), and later also by Gasse (1977), led to the retirement of the pluvial-interpluvial scheme. Instead, the highest lake levels in eastern Africa seem to have occurred during interglacial times, probably as a consequence of maximum low-latitude insolation during minimum precession (Kutzbach and Street-Perrott, 1985).

Beyond the radiocarbon time scale, systematic K–Ar and Ar–Ar dating of volcanic ash layers associated with mammalian (including hominin) fossils started in 1960 in the Olduvai Gorge (Leakey et al., 1961) and the late 1960s in the Turkana Basin (e.g., Leakey, 1970; Fitch and Miller, 1970; Curtis et al., 1975). A few years later Cerling et al. (1977) analyzed $\delta^{18}O$ values of pedogenic and groundwater carbonates in the two basins, suggesting that rainfall decreased significantly in the Lake Turkana region 2.0–1.8 Ma, and in the Olduvai Gorge region 0.6–0.5 Ma ago. A few years later, Cerling and Hay (1986) proposed that three major periods of climatic change in the Olduvai Gorge occurred at about 1.67 Ma, 1.3 Ma, and 0.6 Ma. Cerling (1984) and Cerling (1992) used $\delta^{13}C$ values to estimate the fraction of C4 plants in local flora, suggesting a gradual increase in the proportion of biomass using the C4 photosynthetic pathway over the last 10 Ma, with relatively pure C4 grassland appearing at around 1 Ma.

After the establishment of calcitic foraminifera shell $\delta^{18}O$ for the reconstruction of glacial cycles, Shackleton and Opdyke (1977) applied this technique to the Pacific Ocean sediment core V28–179 spanning the last 3.4 Ma. Their observation of a correlation between $\delta^{18}O$ variations and Berggren's (1972) ice-rafted detritus (IRD) in the North Atlantic yielded an age for the onset of Northern Hemisphere Glaciation (ONHG) at ~2.4 Ma (Shackleton and Opdyke, 1977). According to Shackleton et al. (1984), the first IRD events in a DSDP core from the North Atlantic Ocean occurred at 2.4 Ma, with a previous minor event at ~2.5 Ma (Fig. 1). In contrast to this earlier work, Raymo et al. (1989) and Raymo et al. (1994), however, showed using data on published DSDP and ODP $\delta^{18}O$ records that the Northern Hemisphere Glaciation was established gradually, rather than abruptly, between 2.9 and 2.4 Ma.

In 1995, Vrba (1995b) published an analysis of a compilation of first and last appearance dates for African bovid species (Fig. 2), finding further support for a major pulse of speciation associated with the ONHG at 2.7–2.5 Ma (Vrba, 1995a, 1995b, 1995c, 1995b), now also using Shackleton's (1995d) new data from the eastern equatorial Pacific spanning the last 6 Ma. Vrba's work on faunal turnovers goes back to the early 1980s when she formulated the turnover pulse hypothesis (TPH) (Vrba, 1980, 1985, 1993, 1994, 1995b, 1995b), which is based in part on the theoretical foundations of punctuated equilibrium (Eldredge and Gould, 1972). The TPH argued that most faunal turnover (speciation, extinction, immigration, and emigration) was synchronized across diverse lineages and was associated with pronounced changes in the physical environment. The TPH addresses the patterns of (and underlying processes behind) large-scale turnover in the fossil record and is applicable to any time interval, though in many people's minds the TPH has come to be associated specifically with the proposed ONHG-Turnover at 2.7–2.5 Ma. Vrba herself consistently identified the presence of several turnover pulses in the African Neogene mammal record, most notably those at ~2.8 Ma and ~1.9 Ma (e.g., Vrba, 1995b, 1995c, 2000).

Interestingly, Vrba (1995b) proposed the link between the ONHG, an increase in African aridity, and a faunal turnover (at ~2.7–2.5 Ma) more than five years after the hypothesis of an abrupt ONHG (~2.4 Ma) had been replaced by the one of a more gradual (~2.9–2.4 Ma) change (Raymo et al., 1989; Raymo, 1994). Moreover, there was a change in terminology – originally onset of the Northern Hemisphere Glaciation (ONHG) was used to describe the initiation of the large Northern Hemisphere ice sheet around 2.4 Ma (e.g., Shackleton et al., 1984) until the early 1990s. Due to the recognition that Greenland had glaciated much earlier, possibly in the Miocene (e.g., Jansen and Sjøholm, 1991), the term intensification of Northern Hemisphere Glaciation (INHG) was adopted from the early 1990s onward (e.g., Maslin et al., 1996). A few years later, Haug and Tiedemann (1998) describe the intensification of the Northern Hemisphere Glaciation as a gradual process lasting from 3.1 to 2.5 Ma as a consequence of the closure of the Isthmus of Panama between 13 and 1.9 Ma (Keigwin, 1978, 1982, 1982; Keller et al., 1989; Haug and Tiedemann, 1998). Three years later, Cane and Molnar (2001) proposed that the closure of the Indonesian seaway initiating at about 5 Ma, not that of the Isthmus of Panama, was the cause of Plio-Pleistocene eastern African aridification, and even of the INGH.

In the early 1990s, deMenocal et al. (1991) used the ODP Site 721/722 dust record as an archive of climate change in Africa, describing a shift from predominantly precession to obliquity cyclicities at ~2.4 Ma. In the Airlie volume, deMenocal and Bloemendal (1995) used the same data set, and again in deMenocal (1995, 2004) to propose a stepwise (±0.2 Ma) shift in the dust flux, but now at 2.8 Ma, due to cold northern Atlantic Ocean sea-surface temperatures (SSTs) associated with the ONHG. At the same time, the continent also shifted from low-latitude insolation forcing due to the Earth's orbital precession to an obliquity-controlled variability after the shift (deMenocal, 1995). The climate transition at 2.8 Ma, and others at 1.7 Ma and 1.0 Ma, were suggested to be linked with major steps in the evolution of hominins and other vertebrates in Africa that may have been climatically mediated (deMenocal, 1995). Trauth et al. (2005) analyzed eastern African lake sediments and found, in contradiction to deMenocal (1995, 2004), that there was a humid period between 2.7 and 2.5 Ma, without any sign of a stepwise trend toward greater aridity.

In an analysis of species diversity in the Turkana Basin, Kenya, and Ethiopia, Behrensmeyer et al. (1997) found that, when collection bias was accounted for, overall diversity between 3.0 and 2.0 Ma remained relatively stable. No distinct turnover pulse is seen between 2.8 and 2.5 Ma; instead, the most significant period of elevated faunal turnover is identified between 2.1 and 1.7 Ma (Behrensmeyer et al., 1997). These authors concluded that Plio-Pleistocene eastern Africa was affected by the cumulative ecological consequences of cooler, drier, and more variable climate conditions rather than by a sudden change toward open habitats (Behrensmeyer et al., 2017). Bobe et al. (2002) and Bobe and Behrensmeyer (2004) analyzed a compilation of first and last appearances of bovids, suids, cercopithecids, and hominins in the Turkana Basin, proposing that global-scale shifts in climate at 2.8–2.5 Ma, including a transition to a 41-ka orbital cycling in the tropics, provided the driving force behind the radiation of the bovids and the hominins.

Ravelo et al. (2004) published a paper on the development of the

modern Walker Circulation stating that the ONHG did not result in fundamental changes in tropical conditions. It occurred when tropical conditions were stable and El Niño-like, about a million years after an initial, possibly tectonically driven change due to the closing of the Indonesian seaway, and about a million years before the establishment of strong Walker Circulation between 2.0 and 1.5 Ma (Ravelo et al., 2004). Mudelsee and Raymo (2005) proposed based on statistical change-point analyses of 45 marine $\delta^{18}O$ records that the dynamics of Northern Hemisphere Glaciation were gradual between 3.6 and 2.4 Ma. Sarnthein et al. (2009) confirmed that the INHG was a long process, but identified three stepped changes centered at 3.25 Ma, 2.95 Ma, and 2.75 Ma. Sepulchre et al. (2006) used numerical modeling to assess both climate and biosphere responses to topographic changes linked to eastern and southern African uplifts. These authors found that tectonic uplift, along with landscape fragmentation linked to asynchronous uplift events, must be considered as a dominant cause of change in the Late Neogene climate of eastern Africa, rather than as a background factor (Sepulchre et al., 2006).

Trauth et al. (2009) re-analyzed published records of terrigenous dust flux from marine sediments off the coast of subtropical West Africa (Tiedemann et al., 1994), the eastern Mediterranean Sea (Larrasoañ et al., 2003), and the Arabian Sea (deMenocal, 1995) for possible stepwise (+/−0.2 Ma) increases in African climate variability and aridity near 2.8 Ma, 1.7 Ma, and 1.0 Ma, coincident with the onset and intensification of high-latitude glacial cycles. Their analysis falsified the existence of a transition near 2.8 Ma, and hence no support for a possible link with the INHG at ~2.75 Ma (or any other climate event near that time) (Trauth et al., 2009). Trauth et al. (2009), however, found breakpoints in the slopes of the dust records at 1.9−1.4 Ma, possibly linked with the intensification of the Walker Circulation between 2.0 and 1.5 Ma (Ravelo et al., 2004). This change coincides with the second transition near 1.7 Ma according to deMenocal (1995, 2004), but does not have a stepwise (+/−0.2 Ma) character. Bonnefille (2010) reported a decline of tree cover density in a core off the shore of the Niger river at 2.7 Ma, which is a series of stepwise changes in vegetation at 3.3 Ma, 3.0 Ma, and 2.7 Ma, which could agree with the steps observed by Sarnthein et al. (2009). A similar transition was found in the Gulf of Aden record (Bonnefille, 2010).

Cerling et al. (2011) analyzed the $\delta^{13}C$ record covering the last 6 million years from 1300 paleosoil sections adjacent to two hominin sites in the Omo-Turkana Basin and the Awash Valley, suggesting that habitats with low woody cover (i.e., open habitats) have been present at eastern African hominin sites for at least 6 Ma (Cerling et al., 2011). The late Pliocene and early Pleistocene (~3.6−1.4 Ma) show the persistence of, or even increases, in wooded habitats, with decreases in woody cover in the Awash Valley after only ~2.9 Ma, but after 1.9 Ma ago in the Turkana Basin (Cerling et al., 2011). Surprisingly, Cerling et al. (2011) conclude from their observations that the savanna hypothesis is a viable scenario for explaining the context of the earliest bipedalism. The temporal resolution of the record is very low and the error bars of the results are large, as Fig. 4 of the paper by Cerling et al. (2011) shows. Additionally, White et al. (2010) and Suwa and Ambrose (2014) articulated several potential problems with the modern reference data set used to identify woody cover percentage from fossil paleosols, as well as inferring habitat usage by hominins using paleosols, as these might have been sampled kilometers away from sites where hominins and fauna are found.

At the 2012 AAAS Annual Meeting, deMenocal (2012) proposed that the expansion of grasslands in eastern Africa occurred between 1.6 and 2.0 Ma, probably as a consequence of the establishment of the zonal Indian SST gradient at around 2.0 Ma. In contrast, Levin (2015) proposed that variations in soil carbonate isotope compositions of the last 10 Ma from northeastern Africa are the result of a combination of high-latitude ice distributions, sea-surface temperatures, and low-latitude orbital forcing modulated by local basin dynamics. At about the same time, DiMaggio et al. (2015) published a paper on the Late Pliocene environmental context of early Homo from the Lee Adoyta region, Afar, Ethiopia, in which they proposed that the faunal changes of this region are in accordance with the hypothesis that global climate change at ~2.8 Ma, and resultant increases in African climatic variability and aridity, have spurred cladogenetic events in various mammalian lineages, including hominins.

DiMaggio et al. (2015) reference the oldest fossil currently attributed to the genus Homo, a left mandible designated LD 350−1, found in the Lee Adoyta region of the Ledi-Geraru research area (Villmoare et al., 2015); another broadly contemporary partial dental specimen from the upper Tulu Bor Member at Koobi Fora (KNM-ER 5431) may represent the same early taxon. The 2.84−2.58 Ma old fossil and hominin-bearing sediments in the Ledi-Geraru area of Afar, Ethiopia, suggest a faunal turnover indicative of more open and arid habitats after ~2.8 Ma (DiMaggio et al., 2015). However, Bibi et al. (2017) analyzed bovids from Ledi-Geraru and concluded that the increase in open habitats (and presumably aridity) observed there, in contrast to the underlying Hadar Formation, was part of a longer-term, gradual change in the Afar Basin going back to at least 4 Ma. Liddy et al. (2016) published a 5.2−2.2 Ma terrestrial vegetation record from DSDP Site 213 and found that there is no shift near 2.7 Ma (Liddy et al., 2016: 434). The combined hydrogen isotopic composition of terrestrial plant waxes (δDwax) and pollen data suggest an aridity shift at 4.3 Ma, but no major changes between 3.3 and 2.7 Ma when high-latitude cooling led to the first major glaciation of the Northern Hemisphere (Liddy et al., 2016).

Rose et al. (2016) developed a northeast African hydroclimate and vegetation proxy record for two 100 kyr-duration windows near 3.05 Ma and 1.75 Ma at ODP Site 967 in the eastern Mediterranean basin, where sedimentation is dominated by eastern Sahara dust input and Nile River runoff. They do not find a difference in the monsoonal paleohydrological or paleovegetational response to monsoonal circulation for these two time intervals, which bracket the onset of the Northern Hemisphere glaciation after 2.8 Ma as well as the shift toward more open C4-dominated landscapes in eastern Africa (Rose et al., 2016). Uno et al. (2016) published a paleovegetation record from West Turkana, showing that carbon isotope ratios from biomarkers indicate a highly dynamic vegetation structure between 2.3 and 1.7 Ma, with an overall shift toward more C4 vegetation on the landscape after about 2.1 Ma. Blumenthal et al. (2017) presented a revised aridity index for quantifying water deficit in terrestrial environments using tooth enamel $\delta^{18}O$ values. Using this index, the authors do not find a long-term trend in aridity in the Omo-Turkana Basin, suggesting that the abundance of C4 grasses and grazing herbivores have been decoupled from aridity (Blumenthal et al., 2017).

This review shows how scientific knowledge propagates with a significant time lag between the different scientific fields, such as marine and terrestrial paleoclimatology, paleontology, and paleoanthropology.

2.2. Reviewing available data, their analysis and interpretation of the time between 4 and 1 Ma

Here we revisit key publications that have proposed a link between the Northern Hemisphere Glaciation, an associated increase in aridity, an expansion of more open grasslands at the expense of woodlands, and an important mammalian (including hominin) species turnover (Suppl. Table 1). Some of the key records in

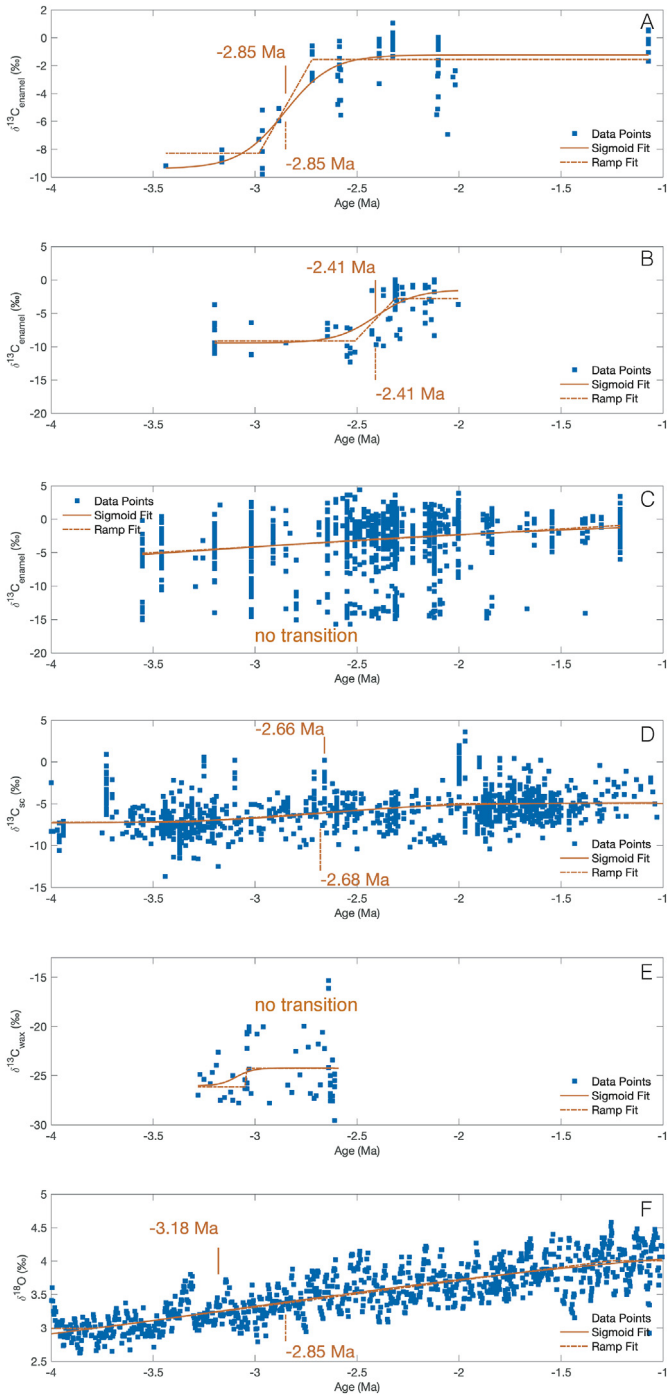


Fig. 4. Results of nonlinear least-squares fitting of a sigmoid function (red line) and a ramp function (blue line) to key records of global ice volume and African climate: (A) enamel stable carbon isotopes ($\delta^{13}C_{enamel}$) record from herbivores from the Shungura Formation of the Lower Omo Valley (data of the 3.53–1.00 Ma interval from Bibi et al., 2013); (B) enamel stable carbon isotopes ($\delta^{13}C_{enamel}$) record from hominins from the Shungura and Usno Formations in the Lower Omo Valley (data of the 4–1 Ma interval from Wynn et al., 2020); (C) enamel stable carbon isotopes ($\delta^{13}C_{enamel}$) record from herbivores from the Shungura Formation of the Lower Omo Valley (data of the 4–1 Ma interval from Negash et al., 2020); (D) soil carbonate carbon isotopes ($\delta^{13}C_{sc}$) record from Afar, Omo-Turkana, Kanjera, Baringo, Olorgesailie, Laetoli, and Olduvai (data of the 4–1 Ma interval compiled by Levin, 2015); (E) carbon isotopic composition of leaf wax biomarkers ($\delta^{13}C_{wax}$) from a drill core from the Chemeron Formation from Baringo (data of the 4–1 Ma interval from Lupien et al., 2019); (F) benthic foraminiferal stable oxygen isotope ($\delta^{18}O$) record of ODP Site 846 as a record of global ice volume (data of the 4–1 Ma interval from Mix et al., 1995a,b; and Shackleton et al., 1995–d). The original data were obtained from the cited references, as found in the supplements to the papers, with the exception of the ODP data from Shackleton et al. (1995a) and Mix et al. (1995a), which were obtained from PANGAEA (https://www.pangaea.de) (Shackelton et al., 1995b; Mix et al., 1995b). Please note that the direction of the x-axis is physically correct, i.e. from the past (with negative ages) to the present (zero). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

support of the hypothesis of a stepwise transition will be statistically re-analyzed by fitting a sigmoid function and a ramp function to the time series to determine the midpoint and duration of the transition (Fig. 4, Table 1).

2.2.1. Fossil evidence for an important species turnover

The first of these key data sets and analyses is Vrba's (1995b) classic paper on bovid speciation. Fig. 2.7.4 therein shows the durations of African fossil bovid species over the past 7 million years, with lines connecting the first and last appearance dates (Fig. 2). The appendix of the paper contains the raw data used to generate the figure, incuding species and site names, ages and references. Even within the uncertainties of the presented age dates, significant clusters of new species are visible at ~3.6 Ma, ~2.7–2.5 Ma, ~1.8 Ma and ~0.6 Ma. Another key data set includes a compilation of first and last appearance data of bovids, suids, cercopithecids, and hominids in the Turkana Basin (Bobe et al., 2002; Bobe and Behrensmeyer, 2004). In that study, the proposed shift is a long-term trend, starting at 2.8 Ma and lasting until ~2.0 Ma (Fig. 7 in Bobe et al., 2002), which is consistent with the long-term cooling trend associated with the Northern Hemisphere Glaciation and the establishment of the Walker Circulation on African climate after ~2.0 Ma, rather than an abrupt transition (Ravelo et al., 2004; Mudelsee and Raymo, 2005).

2.2.2. Marine records of terrestrial dust flux

The compilation of terrigenous (eolian) detritus in marine cores from western and eastern African offshore sites has been used to propose a stepwise (+/−0.2 Ma) increase in African climate variability and aridity near 2.8 Ma, 1.7 Ma, and 1.0 Ma (deMenocal, 1995, 2004). Trauth et al. (2009) used a running Mann-Whitney and Ansari-Bradley test and a parametric, nonlinear regression technique called breakfit regression (Mudelsee, 2014) on dust flux records to analyze published records of terrigenous dust flux from marine sediments off the coast of subtropical West Africa (ODP Site 659, Tiedemann et al., 1994), the Arabian Sea (ODP Site 721/722, deMenocal et al., 1991; deMenocal, 1995), and the eastern Mediterranean Sea (ODP Site 967, Larrasoaña et al., 2003) (Fig. 5). The most important result of this study was that the most dramatic change in aridity and variability in Plio-Pleistocene African climate occurred between 1.4 and 1.9 Ma and hence after the intensification of the Walker Circulation (Trauth et al., 2009: 407) and not, as previously suggested by deMenocal (1995, 2004), at 2.8 (±0.2) Ma, 1.7 (±0.1) Ma, or 1.0 (±0.2) Ma (Fig. 5).

A comprehensive interpretation of the dust flux records in terms of landscape variability in the Saharo-Arabian desert, together with their comparison with lake, pollen, and isotopic records of African climate variability, indicate that the hydrological cycle in tropical Africa is mainly controlled by low-latitude heating via its impact on monsoon dynamics (Trauth et al., 2005, 2007, 2009, 2007; Maslin et al., 2014). An examination of the fossil record indicates that the key junctures in hominin evolution reported nowadays at 2.6 Ma, 1.8 Ma, and 1 Ma coincide with 400 kyr eccentricity maxima, which in turn suggests that periods with enhanced speciation and extinction events coincided with periods of maximum climate variability on high moisture levels (Trauth et al., 2005, 2007) (Fig. 5). In agreement with these results, a connection between global and regional climate change was proposed by deMenocal (2012), suggesting that the influence of zonal temperature

Table 1
Compilation of the results of nonlinear least-squares fitting of a sigmoid function and a ramp function to environmental records from the tropical Pacific Ocean and eastern Africa. Sources are [1] Mix et al. (1995a,b); [2] Shackleton et al. (1995a–c); [3] Bibi et al. (2013); [4] Levin (2015); [5] Lupien et al. (2019); [6] Wynn et al. (2020); [7] Negash et al. (2020). The original data were obtained from the cited references, as found in the supplements to the papers, with the exception of the ODP data from Shackleton et al. (1995a) and Mix et al. (1995a), which were obtained from PANGAEA (https://www.pangaea.de) (Shackelton et al., 1995b; Mix et al., 1995b).

Site	Location	Lat	Lon	Climate Proxy	Sigmoid Fit		Ramp Fit		Reference
					Inflection (Ma)	Duration (Ma)	Inflection (Ma)	Duration (Ma)	
ODP Site 846	Pacific Ocean	3.1°S	90.8°W	Benthic foraminiferal $\delta^{18}O$	1–4 Ma: **3.18 (1.75, 4.6)** 1–6.1 Ma: **2.19 (2.10, 2.28)**	1–4 Ma: **>3** 1–16 Ma: **~3.5**	1–4 Ma: **2.85 (2.76, 2.95)** 1–6.1 Ma: **2.24 (2.08, 2.40)**	1–4 Ma: **2.55** 1–16 Ma: **3.13**	1,2
Omo Valley	Ethiopia	4.7°N	36.0°E	Herbivore enamel δ13C	**2.85 (2.73, 2.96)**	**1.1**	**2.85 (2.76, 2.95)**	**0.26**	3
Afar	Ethiopia	11.1°N	40.5°E	Soil carbonate $\delta^{13}C$	1–4 Ma: **2.66 (2.43, 2.89)** 1–16 Ma: **1.47 (1.35 ,1.59)**	1–4 Ma: **2.0** 1–16 Ma: **3.0**	1–4 Ma: **2.68 (2.19, 3.16)** 1–16 Ma: **1.57 (1.36, 1.78)**	1–4 Ma: **1.35** 1–16 Ma: **1.16**	4
Omo-Turkana	Kenya	4.3°N	36.3°E						
Kanjera	Kenya	0.3°S	34.5°E						
Baringo	Kenya	0.6°N	35.8°E						
Olorgesailie	Kenya	1.6°S	36.4°E						
Laetoli	Tanzania	3.2°S	35.2°E						
Olduvai	Tanzania	3.0°S	35.3°E						
Baringo	Kenya	0.6°N	35.8°E	Plant wax $\delta^{13}C$	**insignificant**	–	**insignificant**	–	5
Omo Valley	Ethiopia	4.7°N	36.0°E	Hominin enamel $\delta^{13}C$	**2.41 (2.31, 2.50)**	**1.0**	**2.41 (2.36, 2.47)**	**0.20**	6
Omo Valley	Ethiopia	4.7°N	36.0°E	Herbivore enamel $\delta^{13}C$	**no transition**	–	**no transition**	–	7

gradients associated with the establishment of Walker Circulation had a greater impact on long-term changes in climate in Africa.

2.2.3. Marine and terrestrial pollen records of vegetation change

Since long terrestrial and continuous pollen-based paleo-vegetation records from Africa are not available, the reconstruction of past vegetation changes of the last 10 Ma by Bonnefille (2010) is based mainly on marine records, one from western Africa (at the mouth of the Niger river) and the other from the Gulf of Aden (Bonnefille, 2010) (Fig. 6). For the period of interest here (~3.5–2 Ma), Bonnefille (2010) links a decline of pollen taxa at ~2.7 Ma with the ONHG, acknowledging that this shift was much more pronounced in western than in eastern Africa. In the analysis of Bonnefille (2010), describing relative shifts in vegetation, one should consider, however, that the tree pollen sums used as a common moisture indicator for the western and eastern sides of the continent reflect a rather complex interplay of humidity, temperature, and solar radiation which is characteristic in the different source region of all these tree taxa (Fig. 6). Furthermore, Bonnefille (2010) links the abundance of salt-tolerant plants such as Chenopodiacea-Amaranthaceae (C/A) covering lowlands and sabkhas expanding in the course of a significant drop in sea level at ~2.7 Ma, which has not yet been shown for the time of the ONHG (e.g. Raymo et al., 2018). Considering the different, sometimes coarse temporal resolutions of the time series in western and eastern Africa, as well as some discrepancies in the paleosol carbonate and leaf-wax $\delta^{13}C$ values in her Fig. 7B, the evidence for a significant and abrupt African-wide vegetation change at ~2.7 Ma is not so convincing in light of the total record Bonnefille (2010) presents.

2.2.4. Stable carbon isotope records from herbivore and hominin enamel

Several papers on stable isotopes from fossil enamel propose a strong link between presumed transitions (or change points) in their data and the ONHG/INHG near ~2.8 Ma (e.g., Bibi et al., 2013; Negash et al., 2020). At the same time, other studies conclude that there are transitions, abrupt or gradual, from woodland to grassland, but at times that do not suggest a connection with the ONHG/INHG (e.g., Bibi and Kiessling, 2015; Wynn et al., 2020).

Using enamel stable carbon isotopes ($\delta^{13}C$) record from the Shungura Formation of the Lower Omo Valley, Bibi et al. (2013) found unexpectedly large increases in C4 dietary intake at around 2.8 Ma, without connecting the proposed shift to the Northern Hemisphere Glaciation. Using a nonlinear least-squares fitting of a sigmoid function we indeed find a transition from −9.3 to −1.3 ‰ between 3.5 and 2.4 Ma with an inflection point at ~2.85 Ma with a 95 % confidence interval (2.73 Ma, 2.95 Ma) (Fig. 4A). The RMSE is 1.63 ‰ and therefore relatively small compared to the ~8 ‰ shift, suggesting that the sigmoidal model accurately describes the record of $\delta^{13}C$ measurements. Fitting a ramp function to the same data set we find a similar transition from −8.3 to −1.6 ‰ between 2.98 and 2.72 Ma with a midpoint at ~2.85 (2.76, 2.95) Ma. This transition agrees in its nature and timing with recent assessments of the gradual buildup of the Northern Hemisphere ice sheets (e.g., Raymo et al., 1989; Mudelsee and Raymo, 2005).

Two studies from the Shungura Formation in the Lower Omo Valley investigate the environmental context of Paranthropus boisei using stable carbon isotopes measured on hominin samples and herbivores from the Shungura and Usno Formations in the Lower Omo Valley (Wynn et al., 2020; Negash et al., 2020). Wynn et al. (2020) find that an important hominin dietary shift toward C4 foods occurred at ~2.37 Ma, postdating the ONHG/INHG. Using the same statistical technique applied to the data set of Bibi et al. (2013), we find a long-term −9.4 to −1.6 ‰ transition between ~2.7 and 2.0 Ma with an inflection point at ~2.41 (2.31, 2.50) Ma with an RMSE of 2.62 ‰ using the sigmoid fit and 2.41 (2.36, 2.47) Ma from −9.1 to −2.8 ‰ between 2.51 and 2.31 Ma using the ramp fit; these numbers agree with the result of Wynn et al. (2020) (Fig. 4B).

Negash et al. (2020) find two major change points in the proportion of grazers relative to mixed feeders at ~2.7 and at ~2.0 Ma,

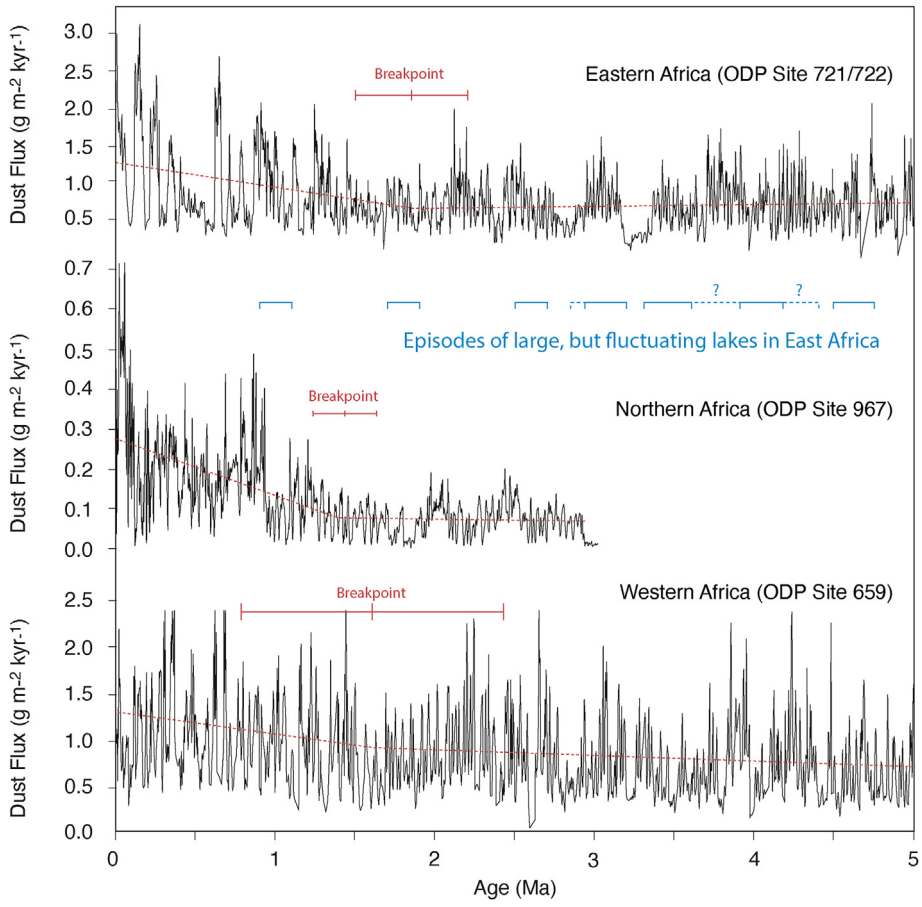


Fig. 5. Breakfit regression analysis of marine records of terrestrial dust indicating significant breakpoints in the trends in the dust values at 1.86 ± 0.44 Ma (ODP Site 721/722), 1.44 ± 0.20 Ma (ODP Site 967) and 1.62 ± 0.82 Ma (ODP Site 659) but not at the proposed time of ONHG/INHG at 2.5–2.8 Ma (redrawn from Trauth et al., 2009). Whereas the dust flux records of western Africa (ODP Site 659, Tiedemann et al., 1994) and eastern Africa (ODP Site 721/722, deMenocal, 1995, 2004) are overprinted by dust transport mechanism effects, the dust flux of northern Africa (ODP Site 967, Larrasoaña et al., 2003) is the only long marine record that provides a pristine view on wet/arid cycles in the Saharo-Arabian desert belt (SADB) in response to monsoon dynamics. The Site 967 dust flux correlates with Plio-Pleistocene humidity changes as recorded by East African rift lakes (Trauth et al., 2005, 2007).

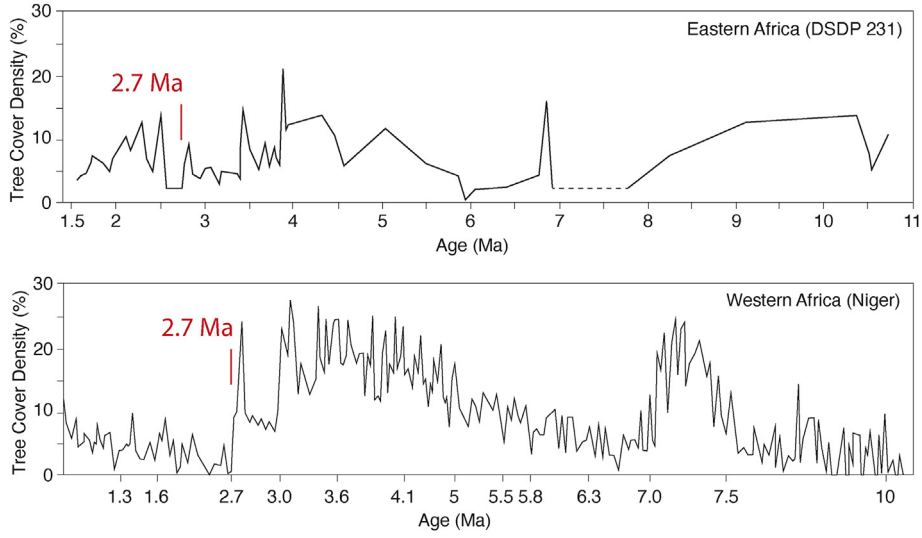


Fig. 6. Tree cover density in tropical Africa vegetation, estimated from percentages of tree and shrubs pollen (Arboreal Pollen AP) calculated versus total pollen sum in the Niger (western Africa) and the Gulf of Aden (DSDP 231, eastern Africa) marine pollen sequences (redrawn from Bonnefille, 2010). For the period of interest here (~3.5–2 Ma), Bonnefille (2010) links a decline of pollen taxa at ~2.7 Ma with the ONHG, acknowledging that this shift was much more pronounced in western than in eastern Africa.

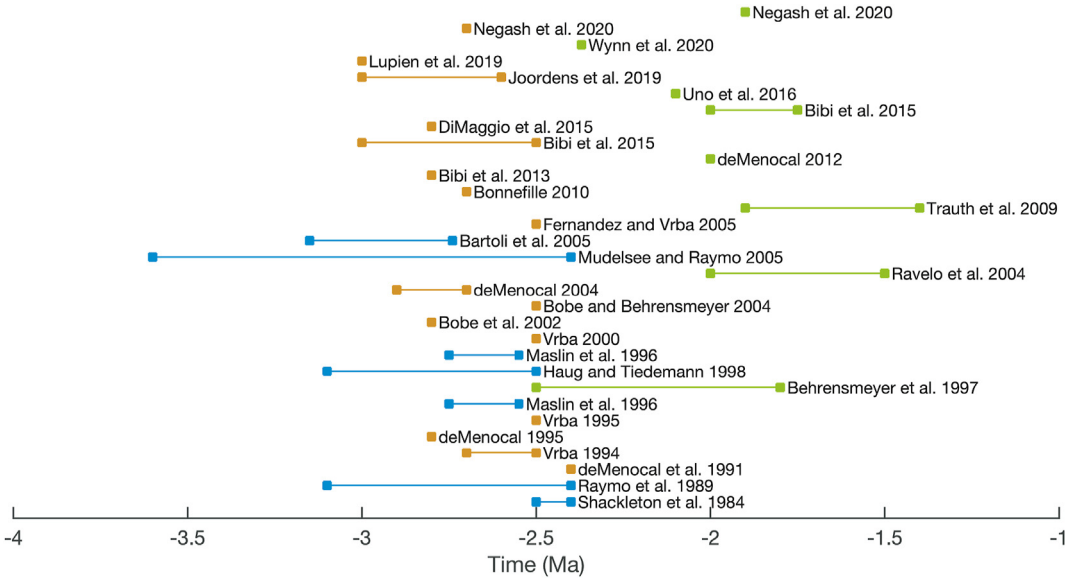


Fig. 7. Compilation of proposed transitions (using data from Supplementary Table 1) in a record of global ice volume (in blue) and African climate with a possible link with the onset (or intensification) of Northern Hemisphere Glaciation (NHG) (in orange), and the establishment of the Walker Circulation (WC) (in green). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

which could correlate with both the conventional date for the ONHG/INHG at ~2.75 Ma (e.g., Maslin et al., 1995; Haug and Tiedemann, 1998) and the establishment of the modern Walker Circulation after ~2.0 Ma (e.g., Ravelo et al., 2004). Fitting a sigmoid function to the data, however, we find a long-term trend toward higher $\delta^{13}C$ values with a slope of ~1.6 ‰/Ma between 3.55 and 1.21 Ma rather than a stepwise transition (Fig. 4C). The RMSE of ~4.00 ‰ is in the same order of magnitude as the difference between the maximum value (~5.1 ‰) and minimum value (−0.94 ‰) within the time interval under consideration and therefore the sigmoid model fit is insignificant. The fit of a ramp function is also unsuccessful, providing the midpoint 2.38 Ma between the first and the last point in time as a result, which suggests that no stepwise transition exists within the time interval of 3.55–1.21 Ma.

2.2.5. Stable carbon isotope records from soil carbonate, leaf waxes, and lignin phenols

The latest studies on stable isotopes from soil carbonates, plant waxes, and lignin phenols as indicators for the change in vegetation, partly with the use of statistical methods, do not agree in terms of the number and time of the inflection points between 4 and 1 Ma ago (e.g., Levin, 2015; Liddy et al., 2016; Rose et al., 2016; Uno et al., 2016; Lupien et al., 2019). Analyzing the $\delta^{13}C$ data from soil carbonates between 4 and 1 Ma, which Levin (2015) compiled, we find a transition from ~7.2 to ~5.0‰ with an RMSE of ~2.1 ‰ between 3.5 and 1.5 Ma with an inflection point at ~2.66 (2.43, 2.89) Ma using the sigmoid fit and between 3.35 and 2.00 Ma with a midpoint at 2.68 (2.19, 3.16) Ma using ramp fit (Fig. 4D). However, extending the observed period to the entire time series between ~15 and 0 Ma, we find a much more pronounced transition between 3 and 0 Ma with an inflection point at ~1.47 (1.35, 1.59) Ma from −6 to −2‰ and an RMSE of 2.5 ‰ when fitting a sigmoid function and between 2.15 and 0.99 Ma with a midpoint at 1.57 (1.36, 1.78) Ma fitting a ramp function to the data (Suppl. Fig. 2A). As a second example of an isotope study, Lupien et al. (2019) find a ~10 % increase in C4 vegetation at ~3.04 Ma based on carbon isotopic composition of leaf wax biomarkers ($\delta^{13}C_{wax}$), which predates the conventional date of the ONHG/INHG at ~2.75 Ma (e.g., Maslin et al., 1995; Haug and Tiedemann, 1998). Fitting a sigmoid function to the $\delta^{13}C_{wax}$ record of Lupien et al. (2019), we find a −26 to −24.3 ‰ transition and an RMSE of 3.1 ‰ suggesting that the transition is insignificant. This is in agreement with the results from fitting a ramp function, as a standard error of 2.54 ‰ exceeding the 1.88 ‰ shift suggests (Fig. 4E).

2.2.6. Stable oxygen isotope records of benthic foraminifera

Finally, we explore the benthic foraminiferal stable oxygen isotope ($\delta^{18}O$) record of ODP Site 846 as a record of global ice volume (Mix et al., 1995a,b; Shackleton et al., 1995a,b). The record goes back to ~6.1 Ma providing a resolution of ~2.5 kyrs (Mix et al., 1995a,b; Shackleton et al., 1995a–c). Fitting a sigmoid function to the 4–1 Ma interval we find a rather long (>3 Ma) transition with an inflection at 3.18 (1.75, 4.6) Ma with a relatively large confidence interval from 3 to 4‰ with an RMSE of 0.24 ‰ (Fig. 4F). Using RAMPFIT we find a transition between 3.8 and 1.3 Ma and a midpoint at 2.85 (2.76, 2.95) Ma. Similar to the data set of Levin (2015), the transition is part of a long-term trend since ~3.5 Ma ago, culminated at 2.19 (2.10, 2.28) Ma according to the fit of a sigmoid function and 2.24 (2.08, 2.40) Ma according to the fit of a ramp function (Suppl. Fig. 2B).

3. Discussion

By reanalyzing published work and key data sets dealing with African climate we attempt to better understand the emergence, propagation, and decline of the hypothesis of a connection between the onset (or intensification) of the Northern Hemisphere Glaciation (ONHG/INHG), an associated stepwise increase in aridity, and species turnover in Africa (Figs. 7 and 8). Based on the prevalence of this hypothesis in current literature, against the backdrop of increasing evidence that for a gradual rather than a step-like change across the Plio-Pleistocene transition, we think that it is important to reexamine this hypothesis.

The history of the hypothesis begins in the mid-1970s when the ONHG was identified in both $\delta^{18}O$ records from foraminifera shells (Shackleton and Opdyke, 1977) and ice-rafted detritus (IRD) in the North Atlantic spanning the last ~3 Ma (Berggren, 1972). At about the time when Elisabeth Vrba surveyed the entire African bovid

record (Vrba, 1995b), the accepted date for the ONHG was 2.4 Ma, with a minor IRD event at ~2.5 Ma according to Shackleton et al. (1984). Though the dates for both the ONHG, then called the INHG, and the faunal turnover later shifted closer to 2.8 Ma, the observation of an important species turnover at the time of the ONHG helped lead to the formulation of the turnover pulse hypothesis (TPH), which is independent of any particular transition, but which was designed using this example (Vrba, 1995b).

The idea of a connection between the glaciations in the high latitudes and climate change in tropical eastern Africa has a long tradition, as the pluvial hypothesis suggests (Leakey, 1952). The hypothesis of a link between a drier climate and the evolution of mammals (including hominins) is also rooted in the savanna hypothesis (Darwin, 1871; Dart, 1925, 1953). The Climate: Long range Investigation, Mapping, and Prediction (CLIMAP) program of the 1970s further cemented the assumption that the lower latitudes were strongly influenced by the high latitudes (CLIMAP, 1976, 1981). One of the most important conclusions of the global project on temperature construction was that at the time of the Last Glacial Maximum (LGM) the temperature in the tropics was ~2 °C colder than in the Holocene, whereas the North Atlantic Ocean was at least 5 °C colder during the LGM (CLIMAP, 1976, 1981).

There is also a scientific social-cultural aspect that has to be considered when examining the dominance of the theory that high latitude changes influence the tropics (Fig. 8). Much of the early paleoclimatic research in the 1970s and 1980s was focused on understanding the causes of the glacial-interglacial cycles. Even tropical marine sites were used to obtain global records of the waxing and waning of the ice ages (Shackleton, 1967; Hays et al., 1976). This strong focus on the ice age of the high latitudes and the realization of the scale of the changes, with huge ice sheets over North America and Eurasia (Denton et al., 1986) and sea level drops of 120 m (Fairbanks, 1989), meant there was a perception that these significant changes must have influenced, if not controlled, the rest of the world's climate. In fact, after the role of the tropics attracted more attention in the 1990s (e.g., Kerr, 2001), and at times even upset the Milankovitch theory (e.g., Broecker, 1992), the results obtained from the new millennium onward suggest that climate changes in the low and high latitudes are more likely the result of complex interactions in both directions, fueled by fluctuations in solar radiation across the globe (e.g., Cane and Molnar, 2001; Ravelo et al., 2004; Trauth et al., 2007, 2009; deMenocal, 2012).

Although the view of the Northern Hemisphere Glaciation as a gradual trend rather than a stepwise transition is well supported in the literature (Raymo et al., 1989; Raymo, 1994; Maslin et al., 1996; Haug and Tiedemann, 1998; Mudelsee and Raymo, 2005), both Vrba (1995b) and deMenocal (1995, 2004), as well as many other scientists working on the topic more recently (e.g., Bobe and Behrensmeyer, 2004; Bonnefille, 2010; Bibi et al., 2013; DiMaggio et al., 2015; Joordens et al., 2019; Lupien et al., 2019; Negash et al., 2020) continue to use the abrupt model for the build-up of the Northern Hemisphere ice sheets to explain changes in the environment and flora/fauna assemblages in Africa (Fig. 7). The critical examination of key data sets, including a statistical recalculation, however, shows that none of these conclusions are tenable. Instead, all data sets show either no (e.g., deMenocal, 1995, 2004; Negash et al., 2020) or a very indistinct (e.g., DiMaggio et al., 2015; Lupien et al., 2019) transition, which only in one case covers a temporal interval as short as 0.2 Ma (Wynn et al., 2020) (Table 1).

The transitions also lie in a very wide range between 3.5 and 2.4 Ma and therefore do not in their entirety contradict a gradual build-up of the northern hemisphere ice sheets as a possible factor in the increasing aridity in Africa (e.g., Bibi et al., 2013; Levin, 2015; Lupien et al., 2019; Wynn et al., 2020). Interestingly, a slight trend between 2.8 and 2.5 Ma can be seen in the proposed inflection points in the stepwise aridification of Africa (e.g., deMenocal et al., 1991, deMenocal, 1995; Bobe et al., 2002; Bonnefille, 2010; DiMaggio et al., 2015; Lupien et al., 2019), corresponding to the shift in the established time of the ONHG/INHG from 2.4 to 2.5 Ma (Shackleton et al., 1984) to 2.7–2.8 Ma (Raymo et al., 1989, 1994; Maslin et al., 1996; Haug and Tiedemann, 1998) (Fig. 5). Some of the more recent time series show further, or partly also exclusively, transitions after 2.2 Ma and thus suggest the establishment of Walker Circulation as a more likely reason (e.g., Behrensmeyer et al., 1997; Trauth et al., 2009; Bibi and Kiessling, 2015; Uno et al., 2016; Negash et al., 2020). Especially with the numerous isotope data sets it can be observed that the signal-to-noise ratio decreases the more samples are measured, which is very obvious

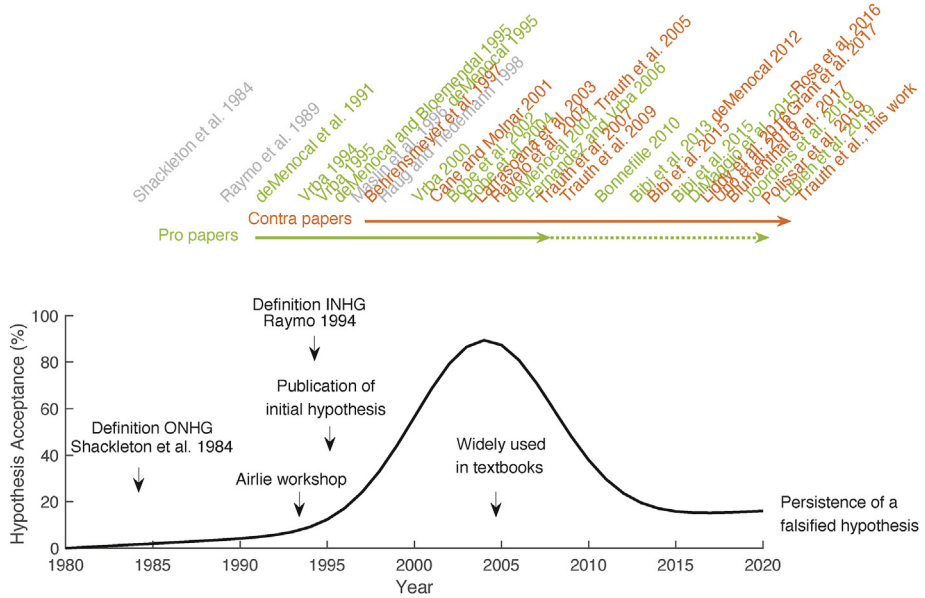


Fig. 8. History of the hypothesis of a connection between the onset (or intensification) of Northern Hemisphere Glaciation (NHG), the stepwise increase in African aridity (and climate variability) and an important mammalian (including hominin) species turnover (using data from Supplementary Table 1).

by comparing the results from early works by Cerling et al. (1977) and Cerling (1984) with that of Levin (2015) and Negash et al. (2020).

The absence of a widespread stepwise climate transition in Africa at ~2.8 Ma is no surprise since it would require a strong nonlinear (threshold-like) response from the African climate to a gradual (~1 Ma long, Mudelsee and Raymo, 2005) build-up of the continental ice sheet in the Northern Hemisphere and its effects in the ocean and the atmosphere. On the other hand, such an abrupt transition in environmental conditions in Africa would have provided important support for hypotheses on the relationship between climate and evolutionary turnover, above all the TPH (Vrba 1985, 1995b, 1995b). The series of climate events around 2.8–2.5 Ma, however, cannot account for this, as our current understanding of the ONHG/INHG and its possible influence on African climate suggests. The examination of a possible connection between a single or multi-stage establishment of Walker Circulation at ~1.9 Ma, more or less abruptly, and its influence on human evolution could be a worthwhile goal for future research. In contrast to the falsified connection between the ONHG/INHG, African climate, and evolution, however, this would not be a connection between high and low latitudes, but an internal development operating within the lower latitudes.

4. Conclusions

A critical review of key publications that have proposed a connection between a stepwise (+/−0.2 Ma) onset of the Northern Hemisphere Glaciation, an associated increase in aridity, an expansion of more open grasslands at the expense of woodlands, and an important mammalian (including hominin) species turnover leads to three conclusions: (1) Northern Hemisphere Glaciation is a gradual process between ~3.5 and 2.5 Ma, not an abrupt onset, neither at ~2.5 Ma, nor at ~2.8 Ma, or any other time in the Late Cenozoic Era, (2) the trend toward greater aridity in Africa during this period was also gradual, not stepwise in the sense of a consistent transition of a duration of $\leq$0.2 Ma, and (3) accordingly, a stepwise change in environmental conditions cannot be used to explain an important mammalian (including hominin) species turnover.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author statement

Martin H. Trauth: Funding acquisition; conceptualization of the work; compilation (equal) of the history of the scientific hypothesis; statistical analysis (equal)—MATLAB; visualization of the results; writing—original draft of the entire manuscript. Asfawossen Asrat: Compilation of the history of the scientific hypothesis—paleoclimatology; visualization of the results—validation; writing—review & editing. Nadine Berner: Contribution to conceptualization of the work; selection of suitable statistical methods and discussion of the results; validation; writing—review & editing of the entire manuscript. Faysal Bibi: Compilation (equal) of the history of the scientific hypothesis—paleoanthrology and paleoclimatology; writing—original draft on paleoanthropology (equal); writing—review & editing of the entire manuscript. Verena Foerster: Compilation (equal) of the history of the scientific hypothesis—paleoclimatology; validation; writing—review & editing of the entire manuscript. Matt Grove: Compilation (equal) of the history of the scientific hypothesis—paleoanthropology and archeology; validation; writing—review & editing of the entire manuscript. Stefanie Kaboth-Bahr: Compilation (equal) of the history of the scientific hypothesis—paleoceanography; reviewing the paleoceanographic evidence; validation; writing—review & editing of the entire manuscript. Mark A. Maslin: Conceptualization of the work (equal); compilation (equal) of the history of the scientific hypothesis—paleoceanography; reviewing the paleoceanographic evidence; validation; writing—review & editing of the entire manuscript. Manfred Mudelsee: Conceptualization of the work (equal); statistical analysis (equal)—RAMPFIT; validation; validation; writing—review & editing of the entire manuscript. Frank Schäbitz: Reviewing paleovegetation evidence; writing—original draft on paleovegetation; validation; writing—review & editing of the entire manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2021.107095.

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