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Estimating origination times from the early hominin fossil record

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Abstract

The age of the earliest recovered fossil evidence of a hominin taxon is all too often equated with that taxon's origination. However, the earliest known fossil record nearly always postdates, sometimes by a substantial period of time, the true origination of a taxon. Here we evaluate the first appearance records of the earliest potential hominins (*Sahelanthropus*, *Ardipithecus*, *Orrorin*), as well as of the genera *Australopithecus*, *Homo*, and *Paranthropus*, to illustrate the considerable uncertainty regarding the actual timing of origin of these taxa. By placing confidence intervals on the first appearance records of early hominin taxa, we can better evaluate patterns of hominin diversity, turnover, and potential correlations with climatic and environmental changes.

KEYWORDS

Australopithecus, first appearance data, hominin origins, *Homo*, *Paranthropus*

1 | INTRODUCTION

In paleoanthropology, the age of the earliest recovered fossil evidence of a hominin taxon is all too often equated with that taxon's origination, as if it represented an actual evolutionary event (e.g., speciation or dispersal). Paleoanthropologists then search for an extrinsic phenomenon (e.g., a change in climate) that may coincide with the earliest evidence of that taxon. The next link in the inferential chain is a shift from the synchronic phenomenon being merely correlated with the taxon's origination to assuming they are causally related. The extrinsic phenomenon is assumed to have driven biotic change, and thus it is interpreted as being partly, or even wholly, responsible for that species' origination.[1,2] Similar arguments are also used to link extrinsic phenomena with the most recent fossil evidence of a hominin taxon to explain that taxon's extinction.[3] The observed earliest and most recent fossil evidence of hominin species are also used to estimate taxic diversity and patterns of turnover of taxa or communities over time. However, some paleoanthropologists have been aware of the perils of conflating the earliest and most recent fossil evidence of a taxon with its true origination and extinction,[4] and researchers have suggested ways of placing confidence intervals on the origin and extinction of lineages.[5–7] Without considering these confidence limits, our ability to understand important aspects of hominin macroevolution, such as speciation and extinction, any correlates between biotic and abiotic phenomena, and what drives taxic diversity and multispecies turnover, is compromised.

In the case of many hominin taxa, there may be one or more fossil specimens from a particular site. The earliest fossil evidence of that taxon at that site is the lowest record in that site's stratigraphic column. If a taxon is known from more than one site, then its observed first appearance datum (FAD) is its lowest (earliest) record in any of the stratigraphic columns. Although this overall observed FAD provides some information relevant to the origin of that taxon it all too often gets translated into the *terminus ante quem* of the true origination (Figure 1). But the earliest known representative of a species, genus, or a higher taxon, almost always postdates the true origin of

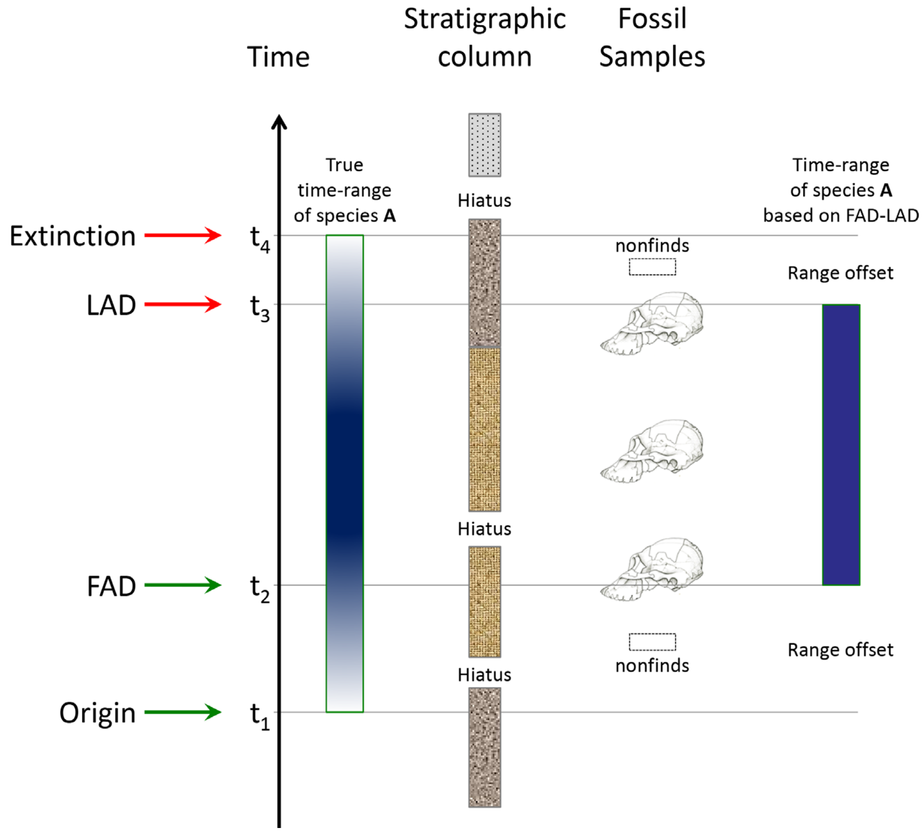

FIGURE 1 Hypothetical distribution of a species (species **A**) in a stratigraphic column in relation to its origin and extinction. The origin of this species occurred at time t_1, but this event is not detected in the known fossil record (nonfinds). The earliest known record of the species, that is, the lowest occurrence in the stratigraphic column, corresponds to time t_2, the First Appearance Datum (FAD), represented here by the lowest hominin cranium in the section. The gap between the true origin of a species and its first appearance datum can be significant, especially if the species is rare, with few specimens per sample. The species may be present in the stratigraphic column lower than the FAD, but small samples may not be sufficient to detect it (nonfinds). With increasingly large samples, the gap between t_1 and t_2 may be narrowed. Similar principles apply to the last appearance datum of a species (LAD), that is, the highest record in the stratigraphic column, represented here by the highest hominin cranium in the section. The LAD may predate the actual extinction of the species by a significant time, depending on the abundance of the species and the samples after (stratigraphically above) the LAD. Hominin cranium artwork by Vanessa Cannon

that taxon simply because it is unlikely that the fossil record will capture the origination itself.[8] When species originate, they are likely to establish themselves in peripheral habitats, and their relative abundance as reflected in terms of numbers of individuals in the fossil record may be low.[9,10] Species also undergo geographic range expansion and contraction, the details of which are unlikely to be captured at any one site.[11] Thus, unless a species is comprehensively sampled across its temporal and geographic range, and unless those samples are large, its origination may not be detected, so a species only becomes visible in the fossil record after, and perhaps long after, its actual origin. In other words, by the time represented by the earliest fossil evidence of a taxon, the evolutionary process of interest (speciation or dispersal) has already happened, most likely significantly antedating the earliest known fossil evidence. As for extinction, if a species' actual extinction is preceded by a contraction in its range and a reduction in population size, the actual extinction itself may take place long after the taxon disappears from the fossil record. This reality is recognized by the terminology used in stratigraphy. The rock sequence containing fossil evidence of a particular species is referred to as the biozone, whereas the time span between the origination and extinction of the species is referred to as the chronozone. The difference in time between the true origination of a species and its first occurrence, or between its last occurrence and its extinction, is referred to as the range offset (Figure 1).[11]

The problems associated with the presence or absence of any species from a site or stratigraphic section are magnified when we consider rare taxa. Relative abundance is a key ecological attribute of species, and the abundance distribution of species has been well studied by ecologists.[12] In most ecosystems, there are typically a few abundant species (i.e., those with the greatest number of individuals), some that are common, and many species that are rare (i.e., with very few individuals). When ecologists sample an ecosystem, they usually recover evidence of the most abundant species first, with large samples needed before rare taxa are observed.[13] Thus, for rare species in a modern ecosystem, absence of evidence is not necessarily evidence of absence. The same principle applies to the fossil record, with the added complications of time averaging and taphonomic processes.[14]

In this contribution, we focus on examples from the hominin fossil record. First, we provide a qualitative evaluation of how close in time the candidates for the earliest known hominin (*Sahelanthropus*, *Ardipithecus*, and *Orrorin*) might be to the true time of divergence between our lineage and that of our closest living relatives, chimpanzees and bonobos. Then, we provide a quantitative assessment of the earliest appearance in the fossil record of *Australopithecus*, *Homo*, and *Paranthropus* in relation to possible origination times. In each case, we illustrate the uncertainties associated with these first appearance records. We aim to address the following questions: (1) When and where does the focal taxon first appear? (2) How abundant is the focal taxon relative to the paleontological samples from which it derives? (3) How abundant is the fossil record prior to the first occurrence of the focal taxon? Answering these questions will help us evaluate the size of the gap between the first appearance datum of a taxon and its origination (i.e., its range offset).

2 | HOMININ ORIGINS

Molecular data provide strong evidence that the hominin clade diverged from that of chimpanzees and bonobos in the Late Miocene of Africa, between about 9 and 5 Ma (million years ago), although estimates that use older events to calibrate the molecular clock, and different assumptions about generation times, place this divergence event somewhat earlier.[15,16] Although there is broad agreement about the timing of this evolutionary divergence, and about this event having occurred in Africa,[17,18] albeit with some dissenting views[19,20] (see Cote's discussion of this topic[21]), there is considerable debate about which specimens represent the earliest species of our tribe, the Hominini.[22–25] We consider the fossil records of the species in the three genera, *Sahelanthropus*, *Ardipithecus*, and *Orrorin*, that have been suggested as being the earliest hominin. Leaving aside whether, or not, these three taxa are correctly assigned to the hominin clade, how likely is it that any of them extend further back in time? How close in time are their earliest known records to the time when hominins diverged from the other apes? To put confidence intervals on the time of origin of the earliest hominins based on the known fossil record, we use methods that rely on the abundance of the taxon under consideration and the quality of the record preceding the FAD (see Box 1).[26–28]

2.1 | *Sahelanthropus*

One of the key contenders for the earliest hominin is *Sahelanthropus tchadensis*,[29] even though there are ongoing debates about its inclusion in the hominin clade.[30,31] The fossils attributed to the only species belonging to *Sahelanthropus* come from Toros-Menalla in the Djurab desert of Chad, which is part of a larger site complex with nearly 400 listed localities.[32] The Toros-Menalla hominins derive from three localities (TM 266, TM247, TM 2992) that sample the Anthracotheriid Unit, which was originally dated through faunal correlations to between 6 and 7 Ma (Figures 2 and 3). These dates derive from comparisons of suid, elephantid, and equid specimens in Chad with those from well-dated sites in eastern Africa, particularly the Nawata Formation at Lothagam in Kenya. Subsequent work using cosmogenic nuclide dating provides ages of between 7.2 and 6.8 Ma for the Toros-Menalla sites. Thus, we consider the age of the Toros-Menalla fossils to be near 7 Ma. However, we note that questions surrounding the original context of the *Sahelanthropus* fossils add uncertainties about the geological age of the specimens.[33]

In estimating the relative abundance of hominin species, we consider species of mammals that are found in similar geological and taphonomic contexts, or similar depositional environments, or in association with hominins. There are different ways of estimating relative

BOX 1 By the numbers

There are several methods to place confidence intervals on the origination of species in the fossil record (for a recent review, see Marshall 2019[99]), and some of these methods have been applied to hominins.[81] For the earliest hominins (*Sahelanthropus tchadensis*, *Ardipithecus kadabba*, and *Orrorin tugenensis*) we rely on the published literature and take a qualitative approach to assess the likelihood of the taxon occurring in deposits preceding its first appearance datum, FAD. The data available for these earliest hominins is not sufficient to apply the quantitative approach outlined here. For *Australopithecus*, *Homo*, and *Paranthropus*, we follow a method used by Barry et al.[28] to estimate the probability P_i of finding a focal taxon i in an interval with a sample size of r fossil mammals preceding the genus' first appearance:

$$P_\mathrm{i} = 1 - (1 - n/m)^r.$$

We estimate the relative abundance of the focal taxon as n/m, with n = the number of specimens (NISP) of the focal taxon during its range, and m = the total number of mammals (NISP) during that range. We set P_i to 0.8 and examine the abundance of the fossil record in the first interval preceding the FAD. If P_i is less than 0.8, we add to r the abundance of the fossil record in the next consecutive interval preceding the focal taxon's FAD, and so on successively until reaching at least $P_\mathrm{i} = 0.8$.

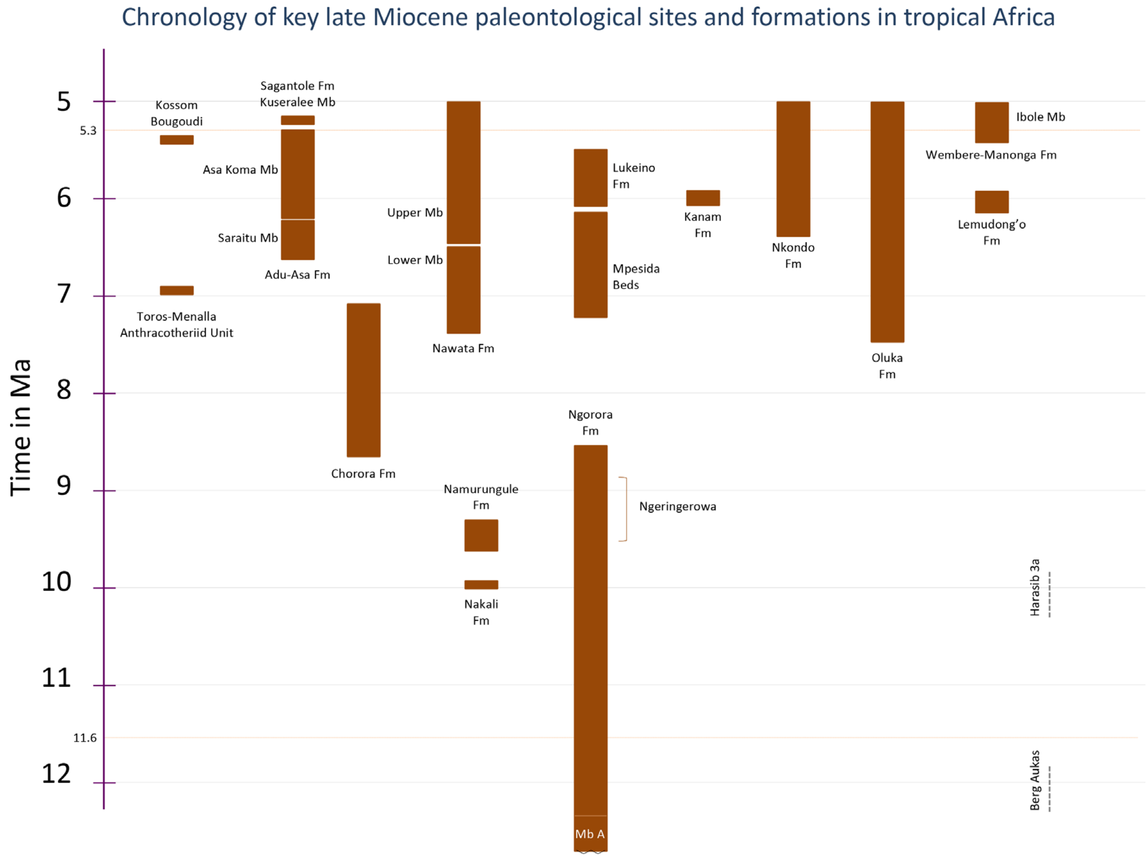

FIGURE 2 Chronology of late Miocene paleontological sites and formations in tropical Africa from ~12 to 5 Ma. The figure illustrates the time span of the Anthracotheriid Unit at Toros-Menalla in the Chad Basin, the Asa Koma Member of the Adu-Asa Formation in the Afar Region, and the Lukeino Formation in the Tugen Hills in the Kenya Rift. Other formations discussed in the text are also illustrated. Figure modified from Bobe and Reynolds, Forthcoming, which provides a full list of references[100]

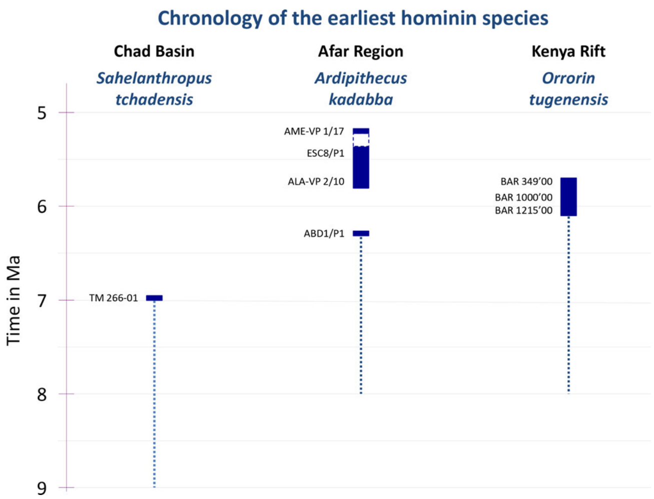

FIGURE 3 Chronology of the earliest hominin species: *Sahelanthropus tchadensis*, *Ardipithecus kadabba*, and *Orrorin tugenensis*. The temporal distribution of each taxon is represented by a solid rectangle. The first appearance datum (FAD) is the earliest (stratigraphically lowest) record of each taxon. The dashed vertical lines represent confidence intervals on the origin of the taxon. Some of the key specimens for each taxon are noted on the left of the columns

abundances. We use one of the simplest measures, the Number of Identified Specimens (NISP), because it facilitates comparisons across sites and provides results that are usually equivalent to those that use Minimum Number of Individuals (MNI).[34] Brunet and colleagues listed nine specimens as belonging to *Sahelanthropus*.[29,35] More recently, a femur has been published as likely belonging to *Sahelanthropus*,[30] so now 10 specimens are attributed to the earliest hominin taxon.

How abundant is *Sahelanthropus* compared with the other mammals found at Toros-Menalla? In 30 well-documented localities at Toros-Menalla there is a total sample of 5450 mammalian specimens.[36] Thus, the relative abundance of *Sahelanthropus* would be about 0.2% of the mammalian fauna (10 fossils attributed to *Sahelanthropus*/5450 fossils attributed to mammals). This simple calculation provides only a rough estimate of the relative abundance of *Sahelanthropus*, but it does indicate that this taxon is rare among the Toros-Menalla fossils.

2.2 | *Ardipithecus*

Two potential earliest hominins are known from eastern Africa, *Ardipithecus kadabba*[37,38] and *Orrorin tugenensis*.[39] The sample of *Ar.*

kadabba derives from sediments of the Adu-Asa Formation in the Middle Awash and Gona research areas of the Afar Region (Figures 2 and 3). A single tooth from Gona attributed to cf. *Ar. kadabba* dates to about 6.3 Ma, but most of the sample (21 specimens) dates from 5.8 to 5.4 Ma, and a single toe bone from the Sagantole Formation dates to ~5.2 Ma.[40,41] Six localities in the Middle Awash (Alayta, Asa Koma, Saitune Dora, Digiba Dora, Asa Koma, Amba East) and four in the Gona area (ABD1, ESC2, ESC3, ESC8) have yielded specimens of *Ar. kadabba*. These specimens are chronologically well constrained by radiometric dates, paleomagnetism, and faunal correlations.[40,42] The earliest specimen attributed to *Ardipithecus* is a single lower premolar (p4), well dated to 6.3 Ma, but only tentatively assigned to *Ardipithecus kadabba*.[40] Specimens dating from 5.8 to 5.4 Ma, including the holotype, are more securely attributed to *Ar. kadabba*.[43]

In the Middle Awash, there are 17 specimens belonging to *Ar. kadabba* (NISP) in the Asa Koma Member of the Adu-Asa Formation, in an assemblage that includes about 2025 mammals.[44] Thus, the relative abundance of *Ardipithecus* in the Asa Koma Member is ~0.8% of the mammalian fauna. The paleontological sample from Gona remains to be fully published, so at present we cannot estimate the relative abundance of *Ar. kadabba* in that area. If the <1% relative abundance of *Ardipithecus* in the Asa Koma Member is typical, *Ar. kadabba* is a rare component of the late Miocene mammalian fauna.

2.3 | *Orrorin*

Fossils attributed to *Orrorin tugenensis*, the only species in the genus, derive from the Lukeino Formation in the Tugen Hills of Kenya, a sedimentary sequence with a maximum age of 6.2 Ma and a minimum age of about 5.7 Ma based on radioisotopic analyses (Figures 2 and 3).[45] The potential earliest hominins from the Lukeino Formation, which were found in four localities (Cheboit, Kapsomin, Kapcheberek, Aragai) among 44 documented paleontological sites, consist of the 13 fossils (NISP), from a minimum of five individuals (MNI), in the original description of the species, plus eight additional specimens published more recently.[46] The earliest specimen of *Orrorin* is a femoral fragment from Aragai dated to 6.1 Ma, with other specimens dating to about 5.8 Ma.[45]

The *Orrorin tugenensis* hypodigm was part of a sample of 1275 fossil vertebrates from the Lukeino Formation, but we have no further details about how this abundance is distributed among the major vertebrate groups, including mammals.[47] Thus, a rough estimate of *Orrorin*'s relative abundance would be ~1% of the vertebrate fauna, but the published record does not allow us to estimate relative abundance among mammals. Although these numbers are only rough approximations, they give an indication that late Miocene potential hominin fossils are rare. It remains to be determined if this rarity is due to taphonomic processes, life history patterns, low abundance in the paleolandscapes, or a combination of these factors. But the rarity of these fossils has implications for our assessment of when the hominin clade first emerged in Africa.

2.4 | How abundant is the African fossil record prior to the first appearance of possible hominins?

The three contenders for the earliest hominin species, *S. tchadensis*, *Ar. kadabba*, and *O. tugenensis*, have first occurrences dating between 6 and 7 Ma (Figure 3). But how good is the fossil record, both locally and regionally, prior to these earliest occurrences?

In the Chad Basin, there are no Miocene records reported with ages older than the Anthracotheriid Unit at Toros-Menalla (Figure 2). Furthermore, there are no sites with Miocene mammals elsewhere in Central Africa. Thus, if *Sahelanthropus* had been present in the region prior to its first occurrence at about 7 Ma, there is no fossil record to detect its presence. If we broaden our geographic focus beyond Central Africa, the nearest fossil sites antedating the Toros-Menalla deposits are in the Maghreb, where the Beglia and Ségui Formations (>9 Ma)[48] place constraints on the origination of *Sahelanthropus*. But the late Miocene sites in the Maghreb have not yielded any hominoids. There is a late Miocene site in Niger with a fossil hominoid, but its geological context has not been studied and its age remains poorly constrained.[49]

In the Afar, the Adu-Asa Formation, where *Ardipithecus* has been found, represents the oldest Miocene fossiliferous sequence both in the Middle Awash[50] and Gona[51] research areas. There are fossiliferous deposits in the Saraitu Member of the Adu-Asa Formation (>6 Ma), but these contain primarily aquatic vertebrates and are thus do not sample the types of environments where hominins are likely to be found.[50] Thus, if *Ardipithecus* was present in these areas prior to its earliest known record, we do not have fossil samples to detect it.

In the Tugen Hills, the Lukeino Formation—the source of evidence for *Orrorin*—rests on top of the Mpesida Beds, a sequence dating from 7.29 to 6.2 Ma. Only ~350 fossil vertebrates, including fishes, turtles, crocodiles, and mammals,[47] have been reported, so even if *Orrorin* was present in the Mpesida Beds, the present sample of fossil mammals would be too small to detect this rare taxon. Lower down in the stratigraphic columns of the Tugen Hills area, the Ngorora Formation (13.3–8.5 Ma)[52] would provide some constraints on the appearance of hominins, but the faunal record from this sequence remains to be fully published and total numbers of specimens are not available.[53–56] Elsewhere in the East African Rift, the Nawata Formation at Lothagam in Kenya has sediments and some fossils dating to the late Miocene, but the bulk of the abundant fossil mammals from Lothagam are younger than 7 Ma, and the Lothagam hominins KNM-LT 2230 and KNM-LT 25935 are younger than 6.5 Ma (Figure 2).[57] The main sedimentary sequence in tropical Africa with a significant fossil record from the interval between 7 and 9 Ma is the Chorora Formation, between the Afar Triangle and the Main Ethiopian Rift (Figure 2).[58] The upper levels of the Chorora Formation date from *c*.7.5 to 7 Ma, but the published fossil record lists only about 30 specimens of fossil mammals (10 species).[59] Chorora has older fossiliferous deposits that date from 8.5 to 8 Ma, and these consist of about 100 specimens of fossil mammals from 26 different species, including the hominoid *Chororapithecus abyssinicus*.[18] Thus, the African fossil record for the interval from nearly 9 to 7 Ma derives mostly from the Chorora Formation with less than 150 specimens of fossil mammals. This is a sparse fossil record from the second largest continent. The time from 10 to 9 Ma is somewhat better sampled, with fossiliferous sites in Kenya including the Tugen Hills (Ngorora Formation), Samburu Hills (Namurungule Formation), and Nakali.[53,60–63] The combined fossil record from these sites, which includes the hominoids *Samburupithecus kiptamali* and *Nakalipithecus nakayami*, does help constrain the first appearance of hominins.

2.5 | How well constrained is the origin of the hominini?

If we make the debatable assumption that *S. tchadensis* represents the earliest hominin,[22,23,30] how well constrained is the temporal origination of the hominin clade? If hominins were present in the Chad region prior to 7 Ma, we have no fossil record to show either their presence or their absence. Thus, the possible origin of hominins in the Chad region is poorly constrained by older fossil evidence.

Were hominins present elsewhere in Africa between 9 and 7 Ma? Fossil sequences prior to the first appearance of *Ar. kadabba* and *O. tugenensis* provide meager evidence of mammals in that time period. A simple qualitative assessment suggests that hominins may not have been found in sediments prior to 7 Ma simply because the African fossil record from 9 to 7 Ma is so sparse. The 150 or so fossil specimens from the Chorora Formation sample only a small proportion of the mammal lineages evolving in Africa during the time between 9 and 7 Ma. Thus, the absence of potential hominins during this interval is probably an example of the traditional aphorism "absence of evidence is not evidence of absence," something that is especially true for rare species. Estimates of divergence times based on molecular evidence have their own problems and uncertainties,[15,16,64–66] but the true origination of hominins is also poorly constrained by the known fossil record, and it would be unwise to use the latter to pick and choose among molecular estimates. Likewise, given the uncertain timing of hominin origins, it would be imprudent to attempt chronological correlations between such a poorly-constrained 'event' and much better-constrained signals from the paleoclimate record, or evidence of other biotic developments that are informed by much larger faunal samples.

3 | THE ORIGIN OF *AUSTRALOPITHECUS*

The genus *Australopithecus* is pivotal in human evolution, appearing in the Pliocene and extending into the early Pleistocene, and likely giving rise to both *Homo* and *Paranthropus*.[67,68] The earliest species of *Australopithecus*, *Australopithecus anamensis*, is known from the Turkana Basin and the Afar Region of eastern Africa. The earliest record is from Kanapoi, southwest of Lake Turkana in Kenya, dating to *c*.4.2 Ma (Figures 4 and 5),[69,70] and by 4.1–4.0 Ma there is also evidence of *Au. anamensis* at Allia Bay,[69] Fejej,[71] Galili,[72] and Asa Issie.[73]

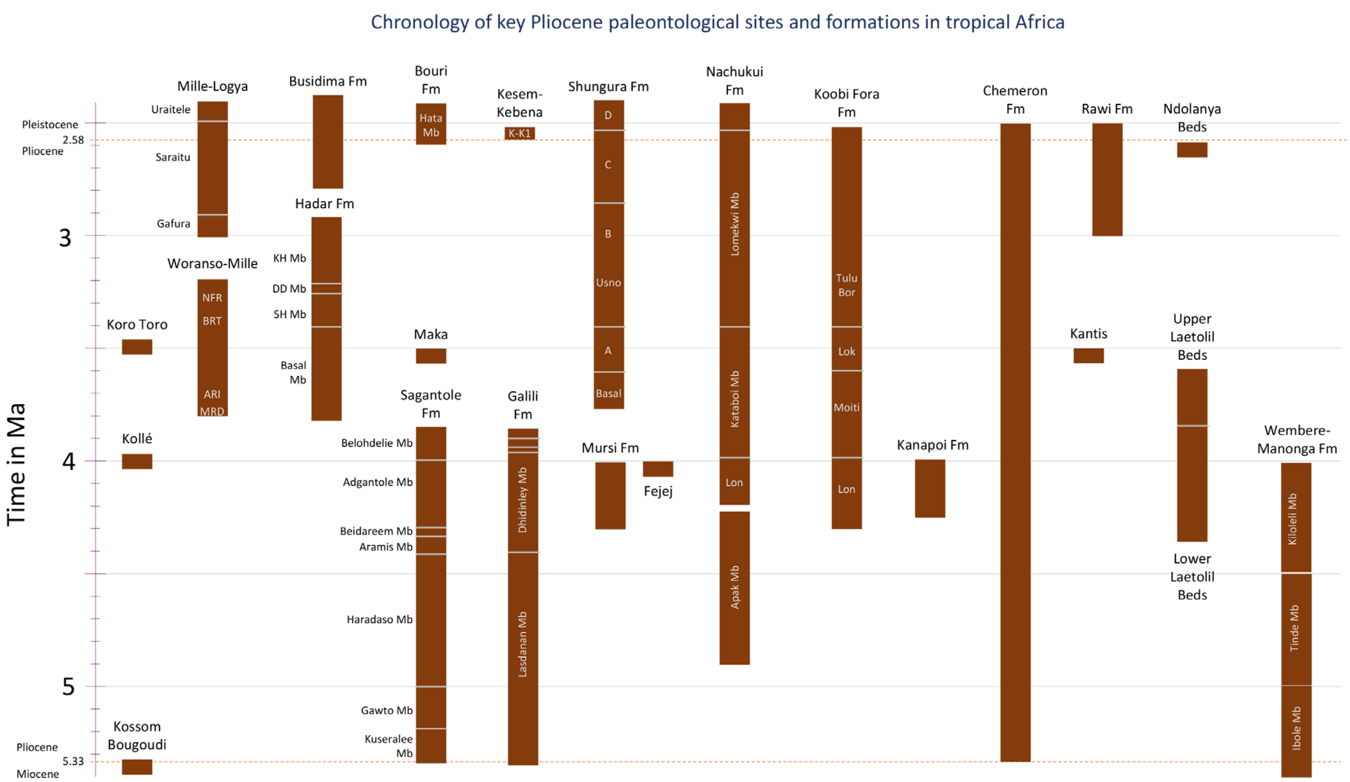

FIGURE 4 Chronology of key Pliocene paleontological sites and formations in tropical Africa discussed in the text. Figure modified from Bobe and Reynolds, Forthcoming, which provides a full list of references[100]

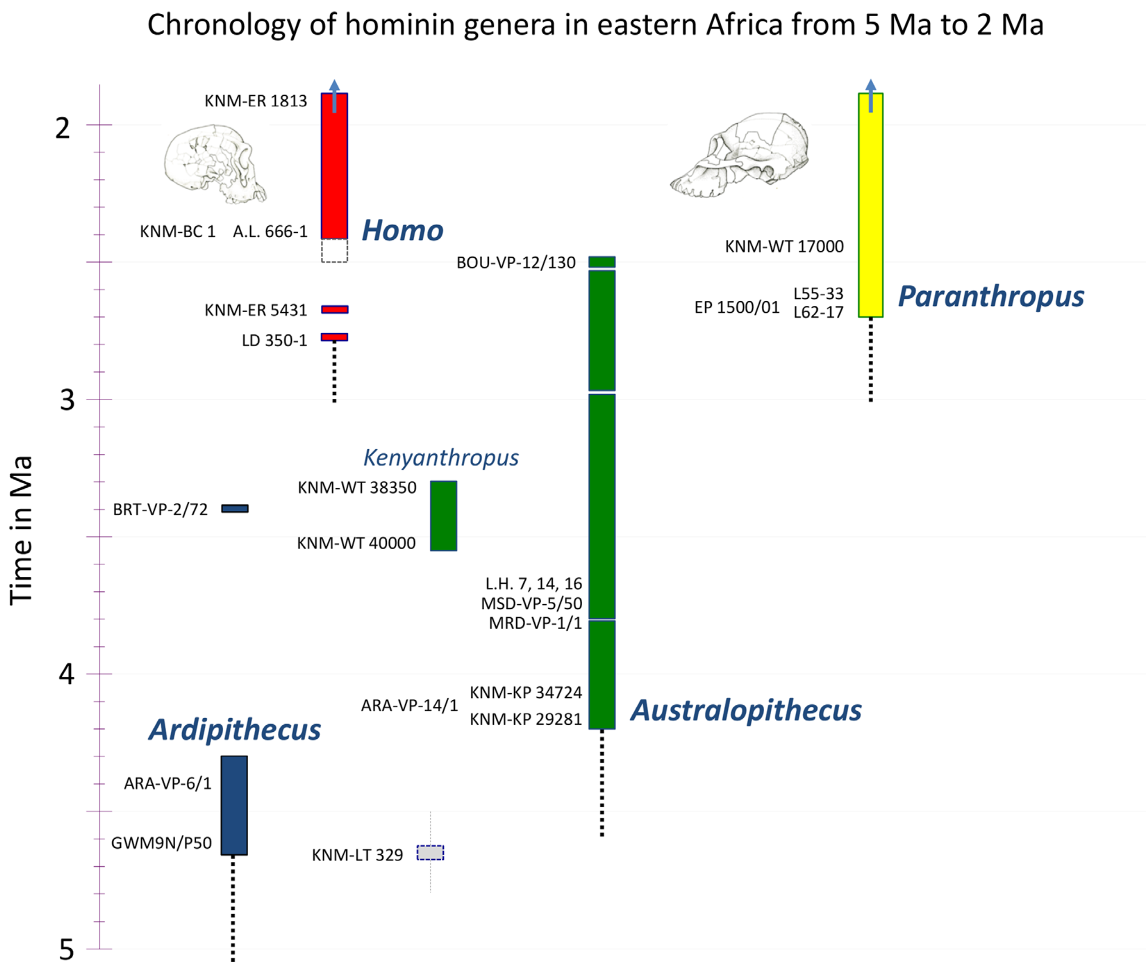

FIGURE 5 Chronology of Pliocene hominins in eastern Africa, with focus on the earliest records of *Australopithecus*, *Homo*, and *Paranthropus*. Some of the key specimens attributed to each taxon are noted on the left of the time-column. Here we consider *Kenyanthropus platyops* as part of the *Australopithecus* radiation. The dashed vertical lines represent confidence intervals on the origin of each genus. Hominin crania artwork by Vanessa Cannon

The largest sample of *Au. anamensis* is from Kanapoi, with 74 specimens assigned to this species.[74,75] Systematic paleontological surveys carried out on the sedimentary exposures of the Kanapoi Formation showed that *Au. anamensis* made up about 1.3% of the fossil mammals.[76] At Asa Issie in the Afar, there are eight hominin individuals (MNI = 8, NISP = 30) in a sample of 540 identifiable vertebrate specimens from an area subject to 100% surface collection, but the published record does not indicate what percentage are mammals.[73] Nevertheless, the relative abundance of *Au. anamensis* at Asa Issie was likely higher than at Kanapoi.

3.1 | How abundant is the relevant african fossil record prior to the first appearance of *Australopithecus*?

To place confidence limits on the origin of *Au. anamensis*, we need to know its relative abundance and the abundance of fossil samples before its first appearance. How likely is it that *Au. anamensis* was present in the Turkana Basin prior to its earliest record? Fossil samples in the Turkana Basin earlier than 4.2 Ma are sparse, until we get to the much earlier record of the Nawata Formation at Lothagam, where most specimens are of late Miocene age (>5 Ma).[77] In the interval from 5 to 4.2 Ma, the main fossil samples come from the Apak Member of the Nachukui Formation.[78] The 166 fossil mammals recovered from the Apak Member is a relatively small sample, with some specimens deriving from the earliest part of the sequence, and others from the later parts (source: PaleoTurkana Database[79]). To assess the probability of *Au. anamensis* occurring in the Apak Member, the entire fossil sample from that member has to be included (see Box 1). Thus, the confidence interval for the origination of *Au. anamensis* in the Turkana Basin stretches back to the earlier part of the Apak Member ~4.6 Ma (Figure 4). In the Afar region of Ethiopia, the situation is different. At Asa Issie *Au. anamensis* is also fairly abundant,[73] as at Kanapoi, but there is a large fossil sample dating to ~4.4 Ma at Aramis, where *Ardipithecus ramidus* is associated with a fossil record of nearly 4000 mammals.[24,80] Since *Ar. ramidus* is the only hominin at Aramis, this would constrain the first appearance of *Australopithecus* in the Afar to after 4.4 Ma.

3.2 | How well constrained is the origin of *Australopithecus*?

If *Australopithecus* originated in the region where we find its earliest record (Kanapoi, Turkana Basin), then the species could have been present in the basin for a few hundred thousand years prior to the existing evidence, but our samples may not be large enough to detect it. Of course, it is also possible, even likely, that *Australopithecus* originated elsewhere in Africa, in regions that lack a currently known fossil record, and then dispersed into the Turkana Basin and the Afar. To summarize, the earliest record of *Australopithecus* in the Turkana Basin is well dated to 4.2 Ma, but the timing of the origination of the *Australopithecus* lineage has significant uncertainties.[76,81]

4 | THE ORIGIN OF *HOMO*

Although defining the genus *Homo* continues to be a problem in paleoanthropology,[82] the current evidence indicates that the earliest records of the genus are the LD 350-1 mandible from Ledi-Geraru in the Afar of Ethiopia dated to almost 2.8 Ma[83] and a specimen from the upper Tulu Bor Member of the Koobi Fora Formation in Kenya, KNM-ER 5431 (a series of associated mandibular teeth) that could be as old as the Ledi-Geraru mandible.[84] After these early records of *Homo*, there is a gap of 400,000 years before the *Homo* sample comes into focus. At about 2.4 Ma, there are records of *Homo* from the Maka'amitalu area of Hadar (Busidima Formation),[85] the Omo (Shungura Formation),[86] West Turkana (Nachukui Formation),[87] the Baringo Basin,[88] and the Malawi Rift.[89] How abundant was earliest *Homo* in the Afar? The Ledi-Geraru mandible and two other *Homo* specimens were part of a sample of 308 fossil mammals from the Gurumaha Fault Block.[90] This indicates that *Homo* constitutes about 0.97% of the mammal fauna at Ledi-Geraru. At Koobi Fora, the upper Tulu Bor Member has a sample of 135 fossil mammals, including KNM-ER 5431 (source: PaleoTurkana Database). Thus, *Homo* would constitute about 0.7% of the fossil mammals in the upper Tulu Bor Member. These rough calculations indicate that earliest *Homo* was rare in both the Afar and the Turkana Basin.

4.1 | How abundant is the relevant african fossil record prior to the first appearance of *Homo*?

How likely is it that *Homo* was present in the Afar region prior to 2.8 Ma? In the Afar, the time from 3.0 to 2.8 Ma is extremely poorly represented in the fossil record: if *Homo* had been present during this interval, the existing site samples of mammals are too small to show it. The sample of 509 fossil mammals, with dates bracketed between 2.96 and 3.11 Ma,[91,92] from the upper part of the Kada Hadar Member (KH-2) in the Hadar Formation, constrains the appearance of *Homo* in the Afar to ~3 Ma (Figure 5). At Koobi Fora, fossil mammal samples between 3.0 and 2.8 Ma are also rare. The sample size in the lower Tulu Bor Member (between 3.4 and 3.0 Ma) consists of 238 fossil mammals. Estimating confidence intervals for the origin of *Homo* at *c*.2.7 Ma in the Koobi Fora Formation would, as in the Afar, extend into the time prior to 3 Ma.

4.2 | How well constrained is the origin of *Homo*?

It is clear from this brief review that specimens of early *Homo* are rare, and that the fossil record preceding the earliest appearance of *Homo* is sparse, both in the Afar and Koobi Fora. The combination of a rare taxon and a poor fossil record preceding its first appearance means that the timing of the origination of *Homo* is poorly constrained by the fossil record.

5 | THE ORIGIN OF *PARANTHROPUS*

The genus *Paranthropus* was proposed by Robert Broom in 1938 to accommodate the newly recognized species *Paranthropus robustus* from Kromdraai, South Africa.[93] If this genus is interpreted to include *Paranthropus boisei*[94] and *Paranthropus aethiopicus*[95] as well as *P. robustus*, then its range included the Transvaal region of southern Africa, Malawi, Olduvai Gorge and Peninj, the Turkana Basin, and the Konso region of southern Ethiopia.

The earliest record of the genus *Paranthropus* is from Omo Shungura Member C, with specimens L62-17 and L55-33, dating to about 2.7 Ma (source: Omo Paleontology Database[79]). Specimens of *Paranthropus* dating to between 2.7 and 2.3 Ma are typically attributed to the species *P. aethiopicus*.[95] The holotype is the edentulous mandible Omo 18-1967-18, but the best-known specimen is the "Black Skull", KNM-WT 17000, from the Lokalalei Member of the Nachukui Formation, dating to *c*.2.5 Ma. Almost the entire record of *P. aethiopicus* comes from the Omo-Turkana Basin,[96] and the only other place where it has been suggested that the species has been sampled is Laetoli, where two specimens from the Upper Ndolanya Beds (an edentulous maxilla, EP 1500/1 and a proximal tibia, EP 1000/98) dated to 2.66 Ma have been assigned to *P. aethiopicus*.[97]

The species *P. aethiopicus* is rare in the Omo Shungura Formation, never exceeding 0.5% of the fossil mammal fauna in Shungura Members C through F (i.e., from its FAD of 2.7 to 2.3 Ma). There are 51 specimens of *P. aethiopicus* in the Omo Shungura Formation between 2.7 and 2.3 Ma, in a total sample of 18,335 fossil mammals.[79] Thus, the species has a relative abundance of ~0.3% of the mammalian fauna. In the upper Lomekwi and Lokalalei Members of the Nachukui Formation (West Turkana), *P. aethiopicus* was more abundant, but samples from West Turkana are generally much smaller than those of equivalent time periods in the Omo.

5.1 | How abundant is the relevant African fossil record prior to the first appearance of *Paranthropus*?

The time interval preceding the first appearance of *Paranthropus*, 2.9–2.7 Ma, has an extremely sparse fossil record in eastern Africa. Further back in time, the sample from Shungura upper Member B (*c*.3 Ma) is much larger, with 2754 mammals. Given the low relative abundance of *Paranthropus* in the Omo-Turkana region, if it was present in the interval 2.9–2.7 Ma, our samples are likely too small to detect it. Furthermore, although the sample of upper Member B at *c*.3 Ma is better, most specimens consist of isolated teeth, and it may be difficult to differentiate isolated teeth of earliest *Paranthropus* from those of late *Australopithecus*. Thus, much larger samples are needed to establish if the first appearance datum of *Paranthropus* in the Omo-Turkana Basin at 2.7 Ma corresponds to a true origination event.

6 | CONCLUSIONS

Understanding the timing of origin and extinction of species in the fossil record is fundamental for our assessment of species longevity, taxonomic diversity, patterns of turnover, geographic distributions, and correlations between origination/extinction events and climate or environmental changes. To place confidence intervals on the first appearance datum (FAD) and last appearance datum (LAD) of a given taxon, depending on the method used it is necessary to measure the abundance of the taxon in question as well as to evaluate the fossil record before the FAD and after LAD.[5] Here we review the fossil record associated with the FAD of the potential earliest hominins between 6 and 7 Ma, the FAD of *Australopithecus* *c*.4.2 Ma, the FAD of *Homo* *c*.2.8 Ma, and the FAD of *Paranthropus* *c*.2.7 Ma.

Candidates for the earliest hominin have an estimated relative abundance ranging from *c*.0.2% to ~1% of the mammalian fauna. Earliest *Australopithecus* has a relative abundance of *c*.1.3% of the mammalian fauna at Kanapoi, earliest *Homo* *c*.0.9% of the mammalian fauna in the Afar (or *c*.0.7% of the mammalian fauna at Koobi Fora), and early *Paranthropus* *c*.0.3% of the mammalian fauna in the Omo-Turkana Basin. These estimates indicate that early hominin fossils are relatively rare in relation to the assemblages of non-hominin mammals, which means that large samples are needed to detect the presence, or infer the absence, of these taxa. But sites or fossiliferous sediments providing samples of fossil mammals immediately preceding the FAD of each taxon evaluated here are sparse and geographically highly restricted. This means that for each group evaluated here, the confidence interval on the origination of the focal taxon is large, and it would be unwise to consider its FAD as equivalent to a real origination, dispersal, or speciation event. This reality has implications for efforts to assess taxic hominin diversity,[25,98] as well as for those who interpret temporal coincidence between hominin taxon FADs and LADs and biotic and abiotic phenomena.

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DATA AVAILABILITY STATEMENT

The data derive from the published record.

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