



Opinion

Are Gaps Data? Absence of Evidence in the Interpretation of Miocene Apes and Hominine Origins

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Abstract

The fossil record of Miocene apes is rich, with taxon groups characteristic of each of its major subdivisions, the early, middle, and late Miocene. However, there are gaps among and within these successive radiations, both temporal and geographic, which have contributed to competing hypotheses of ape and human origins. The gaps are sometimes treated as data, informative of patterns of evolution to be discovered once filled. I review the nature of gaps in the fossil record of African apes and humans, their historic and contemporary contexts, and their relevance to the interpretation of the fossil record. I evaluate the premise that gaps in the fossil record represent missing data of in situ evolution in African hominines (African apes and humans), yet to be discovered, in contrast to direct fossil evidence of vicariance.

Keywords: in situ evolution; vicariance; paleobiogeography; hominids; Eurasia

1. Introduction

Charles Darwin was mindful about gaps in the fossil record. He thought that the greatest weakness, the “most obvious and gravest objection”, to his theory of gradual descent with modification, was that it predicted innumerable “intermediate links” that were mostly missing from the known fossil record of the time [1–3]. While Darwin was certain that the absence of intermediates was due to an imperfect fossil record, his contemporaries cited the absence of evidence of transitional fossils as **evidence** that his theory was flawed, as do mostly religious-based skeptics of evolution today. Darwin stressed the extreme imperfection, as he called it, of the fossil record (“For my part, following out Lyell’s metaphor, I look at the natural geological record, as a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines. Each word of the slowly changing language, in which the history is supposed to be written, being more or less different in the interrupted succession of chapters, may represent the apparently abruptly changed forms of life, entombed in our consecutive, but widely separated formations. On this view, the difficulties above discussed are greatly diminished or even disappear.” [1], (pp. 310–311)). Evolutionary biologists today recognize this to be the case, while agreeing that only evolutionary theory explains the abundant patterns of change over time in the fossil record. Paleontologists do not consider gaps in the fossil record to threaten its legitimacy as a source of critical information about evolutionary history. Nevertheless, gaps continue to play a role in interpretations of phylogeny and paleobiogeography.

“The absence of evidence is not evidence of absence” is widely quoted but can be misleading. The implication frequently is not only that the absence of evidence is not



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evidence of absence but that it is in fact evidence of missing links just waiting to be discovered. When does the absence of evidence constitute evidence of absence and when does it imply missing portions of the fossil record? Absence of evidence is regularly treated as data in paleontology.

As an example, the absence of caudal (tail) vertebrae in the large sample of fossils attributed to *Ekembo* (formerly *Proconsul*). This ‘gap’ was used in support of the hypothesis that *Ekembo* was a stem catarrhine, preceding the divergence of Afro-Asian monkeys and apes [4,5]. Stem catarrhines would be expected to have tails, while stem hominoids are hypothesized to have lost them. The absence of caudal vertebrae in the sample of the stem catarrhine *Epipliothecus*, represented by three partial skeletons from Slovakia, has never been used to support the idea that *Epipliothecus* lacked a tail and shared a synapomorphy with hominoids. This is in part because the interpretation of nearly every researcher is that *Epipliothecus* is a stem catarrhine [6], and that the missing caudal vertebrae can be explained taphonomically or perhaps as a hominoid homoplasy. More recent research supports the former hypothesis, as analysis of the well-preserved sacrum strongly suggests that caudal vertebrae were present in this taxon [7].

A taphonomic hypothesis for the absence of caudal vertebrae of *Ekembo* is consistent with the hypothesis that it was a stem catarrhine [4], while the evolutionary loss of caudal vertebrae is consistent with the hypothesis that it was a hominoid [8,9]. Since this debate, more positive evidence has emerged to support the hypothesis that *Ekembo* is a hominoid and that it had a coccyx rather than a tail [8–10]. In this case, continued research resolved a debate in which the proposition of a taphonomic gap in support of one hypothesis was effectively falsified or at least rendered unlikely with new evidence.

The absence of a tail, or more accurately the transformation of a tail into a coccyx, is a hominoid synapomorphy of *Ekembo*. In paleontology the absence of certain taxa in specific sites has been used to support the hypothesis of a position in geologic time. During the record of Miocene apes, the absence of *Hippotherium* (*Hipparion*) denotes time before the Vallesian [11]. Another example is the absence of the murine (rats and mice) rodent *Progonomys* before the middle Vallesian (MN 10) [11]. Regarding *Hippotherium*, the three-toed horse and a precursor to modern equids, the negative evidence of its absence and the positive evidence of the presence of *Anchitherium*, its putative ancestor, is widely held to be evidence of a pre-late Miocene assemblage [11]. While paleontologists are well aware that missing taxa may turn up with more sampling, requiring a biochronological revision, it is common practice to cite the absence of important marker taxa in support of a particular chronological hypothesis.

In the case of the absence of hominines in Africa before 6–7 Ma, the presence of hominines in Europe/Western Asia and their absence in Africa from the many sampled late Miocene sites between 13.5 and 6 Ma, together supports the biogeographic hypothesis that hominines were not present in Africa until they dispersed there from Eurasia [8,10–14]. Other research [15–24] rejects this hypothesis with alternative interpretations of the fossil evidence. These are nearly always supported by the premise that further sampling in Africa will reveal the presence of hominines on that continent, thus falsifying the hypothesis that hominines originated in Eurasia. I explore the concept of the hominine “gap” in Africa in the context of this debate.

2. The Hominine “Gap”

In the fossil record of the Catarrhini (stem catarrhines, Afro-Asian monkeys, apes, humans) (Table 1) there are many gaps. There is essentially no fossil record of the individual crown lineages of African apes (*Pan* and *Gorilla*), nor is there much of a record of hylobatid evolution (gibbons and siamangs) [25]. The stem catarrhine superfamily Pliopithecoidea

appears in Asia around 18 Ma from a presumed African origin as a branch of the Eocene-Oligocene Propliopithecoida, with a 12+ Ma gap between them. There is also an impressive gap between the first pliopithecoids of Asia and the flourishing of the clade in Europe after about 13 Ma [6]. Clearly, there are big gaps in the fossil evidence of catarrhine evolution. However, in all these cases there are no fossils, anywhere, that might represent candidates to fill these gaps. Yet, we know from well-resolved phylogenetic studies that there must have been intermediates in these gaps. These are clear examples of missing data, recalling Darwin's famous metaphor.

Table 1. Classification of catarrhines discussed in this study.

Catarrhini
Propliopithecoids (<i>Aegyptopithecus</i>)
Pliopithecoids (<i>Pliopithecus</i>)
Eucatarrhines (Afro-Asian monkeys, apes and humans)
Cercopithecoids (Afro-Asian monkeys)
Hominoids (Apes and humans)
Stem hominoids (<i>Proconsul</i> , <i>Ekembo</i> , <i>Nyanzapithecus</i> , <i>Samburupithecus</i> , <i>Oreopithecus</i>)
Hylobatids (Gibbons and siamangs)
Hominids (Great apes and humans)
Stem hominids (<i>Equatorius</i> , <i>Nakalipithecus</i> , <i>Kenyaipithecus</i>)
Pongines (<i>Pongo</i> and its fossil relatives)
Hominines (African apes and humans)
Dryopithecins (<i>Dryopithecus</i> , <i>Pierolapithecus</i> , <i>Anoiapithecus</i> , <i>Danuvius</i> , <i>Hispanopithecus</i> , <i>Rudapithecus</i>)
Graecopithecins (<i>Ouranopithecus</i> , <i>Anadolovius</i> , <i>Graecopithecus</i>)

Notes: This classification is consistent with most phylogenetic analyses [10,12–14,16,17]. Pugh [17] prefers an alternative in which dryopithecins are stem hominids, but at least one of the author's most parsimonious cladograms is consistent with this classification.

There is a long history to the argument that the absence of hominines in Africa before 6–7 Ma is an artefact of sampling bias. It originates with Darwin's prediction that the common ancestor of African apes and humans is most likely to be found in Africa [26]. Hill et al. [27], (p. 760) state "These various kinds of data can be synthesized into a generally consistent scheme for hominoid radiation, suggesting significant stages of hominoid evolution so far unrepresented as fossils (Figure 1). They are *predicted to occur* (emphasis mine) in the time period between 14 and 4 million years ago (m.y.a.)." Their Figure 1 is reproduced here (Figure 1).

While hominoids were indeed absent in many periods from the African fossil record, even when [27] was published there was no systematic temporal gap in the African vertebrate fossil record between 13.5 and 4 Ma, any more than the various gaps during that time period in Western Europe, Western Asia, South Asia, and East Asia (see below). Figure 1 depicts the state of the fossil record in Africa in 1985 (left) and today (right). Hill et al. [27] includes several sites in that time period. Many more are known today (Figure 2). Many of these localities include rare taxa or taxa represented by relatively fragile elements. It is also unclear why there would be a systematic bias against the recovery of apes in Africa but not in Eurasia, where gaps exist as well.

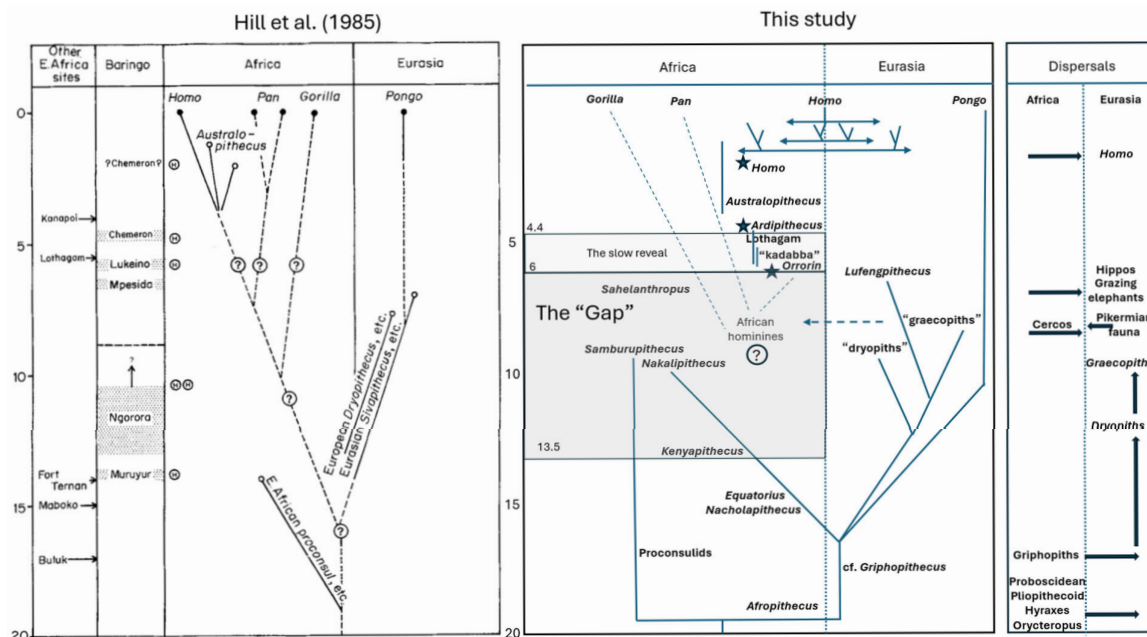


Figure 1. A comparison of phylogenetic and paleobiogeographic hypotheses of ape and human evolution. On the left is a figure reproduced from [27]. It shows the then and current consensus of evolutionary relations among great apes and humans, with *Pan* as the sister clade to *Australopithecus* and *Homo*, *Gorilla* the next outgroup, and *Pongo* the next. Their recognition that the traditional hominid/pongid dichotomy (humans as the only hominid and all great apes united under the Pongidae) was no longer tenable was still controversial at the time but universally accepted today. Since 1985 more information on the phylogenetic positions of Eurasian fossil great apes (dryopithecus, graecopithecus, pongines) has emerged, requiring a revision of the proposed evolutionary relations (right; see [10]). The expanse of time represented by a poor fossil record in 1985 in Africa (“The Gap”, darker grey square), emphasized by some authors (see text) is occupied by the stem hominoids or stem hominids *Nakalipithecus*, *Samburupithecus*, and *Sahelanthropus*. The slow reveal represents the gradual increase in hominins after 6 Ma until they become more firmly established after 4.4 Ma. In Eurasia, a diverse radiation of stem hominines and pongines thrives. It is from within this radiation, ranging from Spain to China, that the ancestors of the crown hominines evolve and disperse into Africa [10,12]. The branches for *Homo* are not meant to depict specific events or patterns but to convey the diversity of *Homo* taxa in both Eurasia and Africa after 2 Ma, and their probable frequent intercontinental dispersals. The dotted lines leading to *Pan*, *Gorilla*, and the hominins represent the unknown histories of these clades at those times in their evolution. See text.

Cote [28] examines the evidence for habitat suitability and taphonomic bias at African Miocene sites listed in [29], many of which appear in Figure 2 here. The author makes a reasonable case that a number of these sites have small samples, poor preservation, or habitats that the author concludes were unsuitable for apes. However, small samples and poor preservation also characterize sites in Eurasia with apes, including Valentine and La Grive St. Alban (*Dryopithecus fontaini*), Devínska Nová Ves (*Griphopithecus*), Klagenfurt (*D. carinthiacus*), Udabno (*Udabnopithecus*), and Klein Hadersdorf (*Austriacopithecus*) [10]. Regarding habitat suitability, ref. [28] states that many African localities were likely too dry or open (savanna) for apes. However, recent studies suggest that even in the early and middle Miocene apes many have lived in relatively drier ecological contexts, and certainly by the late Miocene, after 10 Ma, many apes lived in more open settings [30–37].

There is in fact a patchy but continuous record of fossiliferous sediments in Africa throughout the Miocene. Ngorora is particularly extensive and rich [38], but other formations such as Chorora, Mamurungule, and Aka Aiteputh in East Africa and Beglia in North Africa also contain multiple fossiliferous horizons. Yet they contain very few and highly

fragmentary hominoids, none of which are convincingly hominine. Since more primitive hominoids are found in some of these sites, why would there be a bias only to prevent the recovery of more advanced, i.e., hominine, apes?

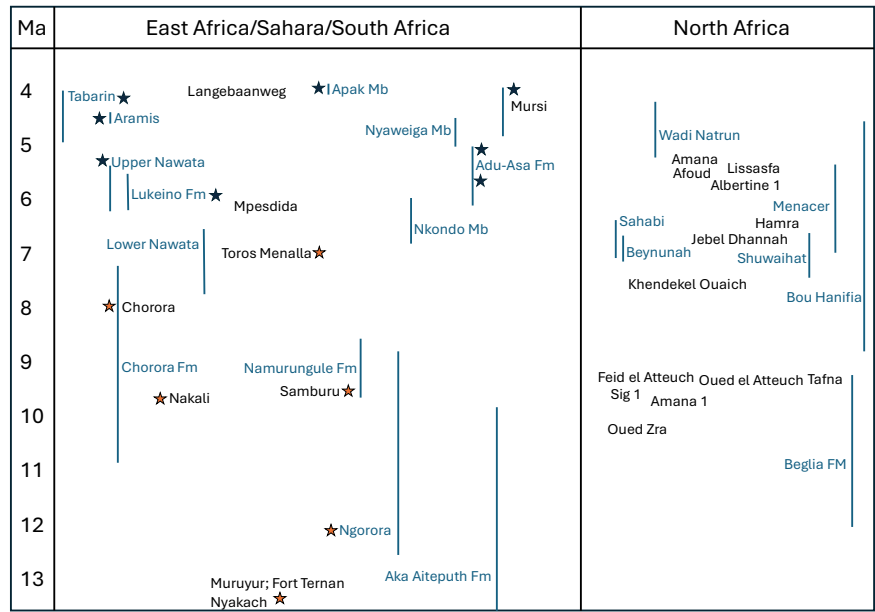


Figure 2. Fossil localities between 13.5 and 4 Ma in Africa, illustrating the quasi-continuous nature of the record during this time. Before 7 Ma there is a continuous record with scattered rare occurrences of apes, (red stars), all of which are stem hominids or hominoids [10,12]. After 7–6 Ma rare hominines appear, becoming progressively more abundant in the fossil record (blue stars; the slow reveal, Figure 1). The waning terminal lineages of early and middle Miocene apes before 7 Ma disappear before the dispersal into Africa and subsequent radiation of hominins after 6 Ma. After about 4.4 Ma their abundance begins to increase, between *Ardipithecus ramidus* and *Australopithecus afarensis*. It is also only after this noticeable increase in abundance that the record begins to show an expanding diversity of hominin taxa. Such a delay, despite a rich fossil record, is unexpected in a scenario of in situ evolution over millions of years but is consistent with the recent arrival of this clade. No mammals with African affinities disperse into Eurasia between 16 and 8 Ma, which is counter to the hypothesis of multiple dispersals of stem apes into Eurasia from Africa [19,21,39,40], while many mammals from Eurasia are documented to have entered Africa at this time ([39]. Geochronology and localities from [27,28,38–40]). See Appendix A for additional details.

Since Hill and Ward [38] several studies have purported to provide evidence that fills this perceived gap in the hominine fossil record, but unfortunately none are convincing, mainly due to the poor preservation of the samples involved. Hill and colleagues [27,38,40] describe some isolated hominoid teeth from about 12.5 Ma in the Ngorora Fm that they attribute to a proconsulid and a hominoid of unknown affinities (Table 1). Another more complete specimen from a different locality was the first to be interpreted as hominine and cited as evidence of in situ evolution in Africa of hominines from African stem hominid ancestors. *Samburupithecus*, known from a maxillary fragment from Samburu Hills in Kenya dated to between 9.5 and 10 Ma (Figure 1), was originally interpreted as a hominine [15], but this view is rejected by most researchers in favor of the interpretation that it represents a surviving member of earlier hominoid radiations [10,12,13,18,41].

Pugh et al. [18] in their reanalysis of *Samburupithecus* suggest that it is a member of the clade that includes *Oreopithecus* and *Nyanzapithecus*. Because there are no intermediates between *Nyanzapithecus* (13–16 Ma) and *Samburupithecus* (9.5–10 Ma), both from Kenya, these authors conclude that there must be a gap in the fossil record of that lineage. The theoretical intermediates between *Samburupithecus* and *Oreopithecus*, known mainly from

~7 Ma sites in Tuscany, are also missing, suggestive of another gap. They state, “Africa between ~13 and 10 Ma provides additional evidence that a real sampling bias exists during this crucial time period, perhaps obscuring our understanding of hominine evolutionary history” [18], (pp. 12–13). How a bias affecting the distribution, frequency, and preservation of one taxon (oreopithecids) can be used to explain the absence of a different taxon (hominines), with different adaptations, ecological preferences, and geographic distributions is unclear, especially when there is evidence of hominines elsewhere (The hominine status of dryopithecins is debated. While many opinions are expressed, all the formal numerical phylogenetic (cladistic) analyses recover dryopithecins are hominines, as one or all most parsimonious hypotheses [10,12,14,16,17]).

The existence of this “gap” of course requires that [18] are correct in assigning *Samurupithecus* and the nyanzapithecines to the clade that includes *Oreopithecus*, which is contested [41–43]. It also requires the assumption that lineages are more likely to evolve in situ than by vicariance and dispersal. In Pugh et al. [18] the conclusion that data are systematically missing and will be recovered with more exploration is based on proposed evolutionary relations and assumed most likely modes of evolution. The relevance of this theoretical gap to hominine evolution, which is not analyzed in [18], is paramount to their thesis, based on repeated references to hominine origins, including confident conclusions at the end of both the abstract and the concluding paragraph. Pugh et al. [18], (p. 12) state that “**unambiguous evidence** (emphasis mine) of this temporal gap within a single, long lived, and highly successful ape lineage such as the Oreopithecidae provides additional support for the hypothesis that the absence of hominines in Africa during this period may be an artifact of a fragmentary fossil record”. These authors are proposing that a perceived “gap”, based on phylogenetic and evolutionary hypotheses that are contested [41–43], extends to other taxa. They continue “Put another way, the recognition of oreopithecoid taxa on either side of this temporal gap makes it more difficult to argue that only hominines are missing from the African fossil record during this time period. Instead, it is clear that the fossil record also fails to record other successful (**and almost certainly present**, emphasis mine) African hominoid groups, such as oreopithecids, between ~13 and 10 Ma.” [18], (p. 12). The confidence that these authors have that the “gaps” are in fact data, providing evidence of incompleteness, is clear. They may well be correct. My point here is that in effect, the gap is a datum in their analysis. Furthermore, they state, “Thus, future fieldwork targeted at African deposits between ~13 and 10 million years of age **is likely to result** (emphasis mine) in the recovery of additional cercopithecoid, oreopithecoid, and hominine fossils that will help to further diminish this gap.” [18], (p. 12).

Pugh et al. [18], (p. 12) recognize, as do I, that “future support or rejection of the ‘back-into-Africa’ hypothesis for hominine origins will ultimately rest on morphological analyses demonstrating the clear phylogenetic affinities of European apes and/or future African fieldwork targeted at exploring Late Miocene deposits”. Yet this is at odds with their repeated observation that the gap is real evidence, and that hominines will be found in Africa. They state in their abstract “Finally, the presence of oreopithecids in Africa on either side of a notable gap in the Late Miocene African fossil record of apes (from ~13 to 10 Ma) demonstrates that the rarity of fossil African apes (i.e., nonhominin hominines) during this period **is likely due to sampling biases** (emphasis mine) rather than a recent immigration back into Africa from Eurasia”. How the probabilities are assessed between these two alternative interpretations is not provided. As noted, oreopithecids are not hominines, so it is not clear how the theoretical absence of intermediates, if their evolutionary reconstruction is correct, is relevant to an assessment of the completeness of the hominine fossil record in Africa. Why gaps should be interpreted as missing fossils to be inevitably recovered, as opposed to evidence of vicariance and dispersal or uncertainty in their evolutionary scenario is

not addressed. To quote Darwin, “there has been ample time for migration on the largest scale” [26], (p. 199). The importance of the “gap” as evidence and the maintenance of its significance, for whatever reason, does appear to supersede evidence of alternative scenarios, despite the presence of fossil localities in the “gap” time (see above).

It should be noted that I am not criticizing the logic, rationale, or legitimacy of the hypotheses presented in [18], as this is not a review of fossil ape evolutionary relationships. I am simply pointing to the use of the idea of a gap in support of a particular biogeographic hypothesis. While I disagree that their phylogenetic hypothesis regarding the Oreopithecidae constitutes evidence of a gap in the hominine fossil record, I recognize that it is a possibility.

Chororapithecus, from 8 Ma sediments at Chorora in Ethiopia, is said to be a member of the gorilla clade [19,44]. The evidence for a link with gorillas is weak, as evidenced initially by the tentative proposal in [19] and subsequent research, generally concluding that the sample is too poorly preserved to support any phylogenetic interpretation [10,12,13,17,20]. Aside from the inadequacy of the sample of *Chororapithecus*, the conclusions of the authors reveal a persistent embracing of “gap” philosophy. “The Chorora evidence effectively refutes a 9–10 Ma Eurasian origin of the African ape and human clade, and highlights the need of more fossils, especially those of large-bodied apes from the 12 to 7 Ma time interval of sub-Saharan Africa.” [19], (p. 218). Since *Chororapithecus* is 8 Ma it is unclear how that refutes a Eurasian origin of the hominines that is hypothesized to have occurred around 12.5 Ma [10]. Nevertheless, I concur with the authors that more fossils are needed in Africa to test this hypothesis, though, as noted, multiple basins with lengthy fossiliferous sequences exist in Africa with no evidence of hominines.

Some researchers consider *Nakalipithecus*, from the 9.8 Ma sediments at Nakali in Kenya, to represent more convincing evidence of a hominine in the late Miocene of Africa before 7 Ma [17,21]. The sample consists of a handful of isolated teeth and a jaw fragment with extremely worn teeth. These authors argue that a few attributes of the dentition of *Nakalipithecus* link it with *Ouranopithecus*. *Ouranopithecus* is a well-known late Miocene ape from northern Greece widely recognized as one of the oldest known hominines [10,12–14,16,17,29,36,45]. Other analyses find the affinities of *Nakalipithecus* to be close to *Equatorius*, a middle Miocene stem hominid from Kenya [10,12].

Pugh [17] and Kunimatsu et al. [21] propose that *Nakalipithecus* fills a gap between middle Miocene stem hominids and crown hominines. The hypothesized affinities with *Ouranopithecus* suggests to these authors that a descendant of *Nakalipithecus* dispersed into Europe after 9.8 Ma and evolved into *Ouranopithecus*, only to subsequently go extinct. The true intermediates between *Nakalipithecus* and crown hominines remain to be found in Africa. Emphasis is again on the hypothesis of a gap in the fossil record in East Africa obscuring the “true” link between *Nakalipithecus* and crown hominines. This contrasts with the hypothesis that *Ouranopithecus* is part of an in situ radiation of hominines in Europe starting with the dryopithecins (*Pierolapithecus*, *Anoiapithecus*, *Dryopithecus*, *Danuvius*, *Hispanopithecus*, *Rudapithecus*) that gives rise to African hominines via vicariance and dispersal (Table 1). Sevim-Erol et al. [12], following [10], conclude that *Ouranopithecus* is a member of a clade that includes *Anadoluvius* from Anatolia and *Graecopithecus* from Attica (southern Greece). In their cladograms this clade is the sister to the dryopithecins, thus representing a lengthy in situ evolution of hominines in Europe from about 12.5 to 7.2 Ma ([12], Figures 4 and 5).

It is beyond the scope of this study to explore the relative merits of each of these hypotheses. However, in terms of continuities and discontinuities, the African origins hypothesis, with its hypothetical gaps, requires multiple dispersals of apes into Europe from Africa between 13 and 9.5 Ma. This would have involved the ancestors of the dryopithecins (hypothesized by some to represent multiple clades [22], thus several independent

dispersals), the ancestors of *Ouranopithecus*, and the ancestors of *Oreopithecus*. However, there is no evidence of the dispersal of any mammals from Africa to Eurasia at these times (Figure 1), making the hypothesis of multiple dispersals only involving hominids unlikely [39]. In contrast, the hypothesis of an in situ radiation of hominines in Europe and western Asia between 12.5 and 7.2 Ma requires one dispersal from Africa in the late early to early middle Miocene, which is documented for several lineages, and one back to Africa, for which there is also abundant evidence in many mammalian lineages [39] (Figure 1).

The use of the idea of a gap to justify a specific biogeographic or evolutionary hypothesis needs to be judicious and based on direct taphonomic, geologic, phylogenetic, and paleontological evidence. As specifically applied to hominine origins, a “gap” hypothesis needs to account for challenges that arise in explaining the presence of hominine attributes where they should not occur (e.g., Western Europe) and the implications for dispersals not found in any other lineages.

3. Other “Gaps” in the Miocene Ape Fossil Record

The absence of hominines in the fossil record of Africa until about 6 Ma has been interpreted in different ways, as noted above. There are similar “gaps” in the early and middle Miocene of Africa and in the European and Asian records as well, though they do not figure as prominently in discussions of phylogeny and biogeography. These are in addition to the gaps previously noted in the pliopithecoid, hylobatid, and African ape lineages.

There is a significant gap between the earliest purported hominoids or eucatarrhines from the Oligocene of Kenya and Tanzania (ca. 26 Ma) and the oldest Miocene apes from Kenya and Uganda (ca. 22 Ma) [5,10,14,20,46,47]. The Oligocene taxa appear to provide a link between primitive catarrhines from the Fayum deposits of Egypt and East African early hominoids. Despite this gap and the recent discovery of a 17 Ma stem ape in Egypt [14] it has not been suggested that perhaps the ape record from East Africa is a side-branch and that the in situ evolution of hominoids occurred in North Africa. This may present itself as a viable hypothesis in the future with more fossils but for now it seems unlikely, especially in light of the many hominoid attributes found in the samples from East Africa.

Another important gap is the absence of fossil apes between the latest early Miocene apes (ca. 17.5 Ma) and earliest middle Miocene apes (ca. 15.5 Ma) in Africa, around the time that apes first appear in Europe [10,48–50]. It is possible that apes from Europe or Western Asia dispersed into Africa around 15–16 Ma but the prevailing hypothesis is that middle Miocene apes evolved in situ from early Miocene ape ancestors, and subsequently dispersed into Eurasia [10,49].

There are other gaps as well. There is very little known between the middle (ca. 12.5 Ma) and late (post-10 Ma) Miocene apes from the Siwaliks, all generally attributed to *Sivapithecus* [51]. It is possible that late Miocene *Sivapithecus* is descendant from *Ankarpithecus*, a 10 Ma pongine from Türkiye [52], though the prevailing hypothesis favors an in situ evolution in South Asia with the Anatolian taxon as a side-branch that dispersed westward. The gaps between middle and late Miocene European apes [10] may suggest separate dispersals from Africa (e.g., [10,22–24,40]), though again the hypothesis of in situ evolution prevails.

Finally, important gaps exist between Western/Central European apes, the *Dryopithecus* and the Balkan hominines *Ouranopithecus*, *Anadoluvius*, and *Graecopithecus* [10,31,36,39,45,49]. Among the Balkan apes there is also a 1.5 Ma gap between *Anadoluvius* and *Graecopithecus* [12,31,36]. In this case, as noted above, opinions are divided as to whether these gaps are simply missing data in an in situ fossil history (e.g., [10,12]) or represent separate dispersal events (e.g., [17,21]). Following precedent in interpretations

of gaps in the hominoid fossil record, an in situ hypothesis might seem to be the default, but this is not the case in this instance, for reasons discussed above. While these gaps do indeed introduce uncertainty in our understanding of fossil hominoid paleobiogeography, the gaps themselves are not data in support of one hypothesis or another.

4. Conclusions

The oldest hominids (great apes and humans), by most phylogenies are the dentally thickly enameled apes of the middle Miocene of Africa, Europe, and Anatolia [10,12,14,16,17,30,48–50]. The oldest of these are from Europe [30,48]. While there is a near continuous chronological record of hominids since the middle Miocene, there are many temporal and geographic gaps, and perceived “gaps”. The mere absence of fossils in a place and time can neither support nor falsify phylogenetic hypotheses. In the end, only comprehensive and well executed phylogenetic analyses can directly address competing hypotheses. In the case of African ape and human evolution, the absence of fossil hominines in Africa between 13.5 and 6–7 Ma is consistent with the hypothesis that hominines originate in Eurasia and disperse into Africa after 7 Ma, but it is not “evidence” of such a dispersal. As more sites are described in Africa from this time the persistent absence of hominines strengthens confidence in the conclusion that they were not present. The presence of hominines in Eurasia in this time interval is also consistent but does not prove that hominines originated there. However, at some point, if this pattern persists, it would be reasonable to abandon Darwin’s preferred hypothesis of hominine origins in favor of the alternative he also embraced [26], which is consistent with most research on European Miocene apes.

The suggestion that evidence needed to falsify a hypothesis is currently missing but will surely be found with more exploration, is difficult to address as are ad hoc explanations generally. In paleontology other similar special pleading examples are arguments without phylogenetic analysis of parallelism to explain away certain evolutionary hypotheses. It is an easy argument to make, but a difficult one to test. However, theoretically missing data are especially weak in defense of an argument when evidence supporting an alternative hypothesis exists. Like the tail of *Ekembo*, despite no unequivocal evidence of caudal (tail) vertebrae among the hundreds of fossils from some of the richest hominoid localities in the world, it is theoretically possible that *Ekembo* had a tail, supporting the hypothesis that it was a stem catarrhine. However, using the absence of definitive caudal or coccygeal vertebrae as positive data favoring a stem catarrhine hypothesis is unconvincing. Similarly, the presence of hominines in Europe and Western Asia in the late Miocene and their absence in Africa until 6–7 Ma, though also dependent on a phylogenetic hypothesis, is more convincing evidence of a dispersal of hominines into Africa than is their absence in support of theoretically missing evidence of in situ evolution.

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Conflicts of Interest: The author declares no conflicts of interest.

Appendix A. Dispersals

Taxon ¹	Departure ²	Arrival ³
<i>Stegodon</i>	9 Ma (Asia)	7 Ma (Mpesida)
<i>Anancus</i>	8.6 (Dhok Pathan)	7.3 (Toros Menalla)
<i>Hystrix</i>	8.7 (Europe)	7.3 (Toros Menalla), Lower Nawata
<i>Leporids</i>	8.7 (Europe)	7.3 (Toros Menalla, Chorora)
<i>Indarctos</i>	11–10 (Europe/Anatolia)	7.3 (Menacer)
<i>Agriotherium</i>	9.8 (Dhok Pathan)	5.8 Middle Awash, Sahabi
<i>Vulpes</i>	8.2 (North America)	7.3 (Toros Menalla)
<i>Plesiogulo</i>	13.5 (Anatolia)	7 (Baynunah)
<i>Chasmaporthetes</i>	8 (China)	7.3 (Toros Menalla)
<i>Adcrocuta</i>	10 (Europe)	5.8 (Sahabi)
<i>Propotamochoerus</i>	10 (Eurasia)	5.8 (Sahabi)
<i>Bohlinia/Paleotragus</i>	7–8 (Europe)	7 (Toros); Giraffa (Pliocene)
<i>Helladotherium/Sivatherium</i>	7–8 (Europe)	7 (Toros Menalla)
<i>Tragoportax</i>	10 (Europe)	7.3 (Baynunah)
<i>Pachyportax</i>	10 (Dhok Pathan)	7.3 (Baynunah)
<i>Prostrepsiceros</i>	10 (Dhok Pathan)	7.3 (Baynunah)
<i>Dorcadoxa</i>	10 (Dhok Pathan)	7 Ma (Mpesida)
<i>Bovini</i>	10 (Dhok Pathan)	7 (Toros Menalla)

Species dispersals from Eurasia to Africa between about 7.5 and 6 Ma. See Figure 2 and references. ¹. See [39] for discussion of taxonomic attributions. ². Refers to the likely FAD (first appearance datum) at the source of dispersal, not necessarily the geographic origin or FAD of the taxon. Age in Ma and locations (Regions and/or locality complexes) in parentheses. ³. FAD in Africa.

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