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Origins of the African hominoids: an assessment of the palaeobiogeographical evidence

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Abstract

The origin of the African hominoid clade is a matter of current debate, with one hypothesis proposing that chimpanzees, humans, and gorillas originated in tropical Africa, while another suggests they originated in Eurasia. Support for the latter hypothesis includes biogeographical patterns inferred from the fossil record and proposed Miocene hominoid phylogenetic relationships. The absence of fossil apes from the African Late Miocene has been used as evidence that crown hominoids were not present in Africa during this period. An alternative explanation for the paucity of these hominoids is that biases in collection and preservation have affected the African Miocene fossil record. A survey of currently known African Later Miocene sites and their faunas shows that these sites generally do not contain hominoids because of small sample sizes, poor preservation, or inappropriate habitat sampling. These preservation biases have important implications for evaluating the origins of the Homininae. ***To cite this article: S.M. Cote, C. R. Palevol 3 (2004).***

Résumé

Les origines des hominoïdes africains : évaluation des faits paléobiogéographiques. L'origine géographique du clade des hominoïdes africains est couramment débattue, les hypothèses suggérant d'une part l'Afrique tropicale, d'autre part l'Eurasie, pour l'origine des gorilles, des chimpanzés et des humains. Les arguments en faveur de la seconde hypothèse se basent sur les schémas biogéographiques obtenus à partir de l'enregistrement fossile et les reconstitutions phylogénétiques des hominoïdes miocènes. L'absence de fossiles de grands singes dans le Miocène africain récent indiquerait que les hominoïdes n'étaient pas présents en Afrique à cette période. Des biais dans les collections et la préservation du registre fossile du Miocène africain pourraient toutefois constituer une hypothèse alternative expliquant la rareté de ces hominoïdes. Une étude des sites actuellement connus dans le Miocène africain et de leur faune montre que l'absence de restes d'hominoïde est la conséquence de la petite taille des échantillons, de la faible qualité de préservation et d'un d'échantillonnage inapproprié (lacune des milieux forestiers). Ces biais de préservation ont des implications importantes dans la résolution de l'origine du clade des hominoïdes africains. ***Pour citer cet article : S.M. Cote, C. R. Palevol 3 (2004).***

Keywords: Hominoids; Africa; Late Miocene; Chimpanzee fossils; Taphonomy

Mots clés : Hominoïdes ; Afrique ; Miocène récent ; Fossiles de chimpanzés ; Taphonomie

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Deux hypothèses différentes ont été proposées pour rendre compte de l'origine du clade des hominoïdes africains. La première suppose que les gorilles, les chimpanzés et les hommes sont originaires d'Afrique tropicale (Fig. 1b), tandis que la seconde suggère une origine eurasiatique et une migration vers l'Afrique durant le Miocène récent (Fig. 1a). Les arguments en faveur de la seconde hypothèse reposent sur des reconstitutions phylogénétiques qui suggèrent une étroite relation de parenté entre les hominoïdes africains modernes et les hominoïdes miocènes eurasiatiques [12]. Toutefois, ces relations de parenté ne sont pas toujours corroborées par d'autres analyses phylogénétiques (e.g., [56]). Les relations phylogénétiques des hominoïdes miocènes sont actuellement mal comprises et il est difficile d'interpréter ces données avec confiance pour reconstituer l'histoire évolutive des grands singes africains modernes.

En raison de l'incertitude sur les relations au sein du groupe des hominoïdes miocènes, de nombreux spécialistes se sont tournés vers l'examen d'autres types d'indices confortant l'hypothèse d'une origine eurasiatique des grands singes africains modernes. Le problème fondamental dans l'étude de l'origine du clade africain est de savoir s'il existe, en Afrique, des candidats ancestraux potentiels. Bien sûr, le meilleur moyen de tester ceci est de rechercher davantage d'hominoïdes fossiles dans le Miocène africain moyen et récent. De tels fossiles n'ont encore pas été découverts, ce qui a conduit Begun [9–11] à suggérer qu'en fait, ils n'existaient pas. Spécifiquement, Begun [9] suggère que l'absence notable de fossiles de grands singes au Miocène récent infirme l'hypothèse d'une origine africaine à cette période. Alternativement, il propose que les ancêtres des hominoïdes aient migré vers l'Eurasie il y a 17 Ma, le rameau africain revenant en Afrique entre 6 et 9 Ma (Fig. 1A). Begun [9] dénombre, en Afrique, 26 localités fossiles datées du Miocène récent, pour lesquelles les grands singes ne sont pas représentés. Selon cet auteur, ceci constitue une démonstration suffisante pour conclure que les hominoïdes sont absents en Afrique à cette période. Le principal objectif de cette étude est d'évaluer ces assertions en examinant les données relatives à ces localités fossiles.

Les données ont été établies à partir de 25 localités africaines datées entre 12 et 5 Ma ; elles incluent les taxons mammaliens présents, le nombre de fossiles collectés, le contexte écologique supposé, les biais (taphonomie, préservation) pouvant affecter ces sites. Les résultats de cette étude montrent que les localités miocènes connues en Afrique sont inégalement distribuées dans l'espace (Fig. 2). Sur 25 localités fossiles africaines étudiées, presque toutes sont orientales ($n = 11$) ou septentrionales ($n = 13$). Seul un site représente l'Afrique du Sud, tandis qu'il n'existe aucune occurrence pour les régions centrales et occidentales du continent dans la liste de Begun. De même, les localités fossiles africaines sont irrégulièrement distribuées temporellement durant le Miocène (Fig. 3). La plupart des sites correspondent à la tranche d'âge 5 à 7 Ma, tandis que la période située entre 7 et 9 Ma est particulièrement peu représentée. En fait, des hominoïdes sont présents dans quelques unes des localités étudiées (Tableau 1) ; leur représentation est toutefois peu envisageable dans les sites restants, principalement en raison du peu d'échantillons collectés, de la mauvaise qualité de préservation, etc. Un nombre extrêmement faible de sites miocènes africains connus semblent enregistrer des communautés écologiques similaires à celles des grands singes actuels.

L'hypothèse selon laquelle les hominoïdes fossiles ont pu être présents en Afrique mais n'ont pas été échantillonnés dans l'enregistrement fossile, est confortée par l'extrême rareté des fossiles de chimpanzé et de gorille dans le registre fossile. Les lignées conduisant aux chimpanzés et aux gorilles étaient vraisemblablement déjà présentes en Afrique au moment de leur divergence à partir de leur ancêtre commun, il y a environ 8 Ma. Malgré tout, leurs restes fossiles sont encore très rares avec un seul fossile probablement apparenté au gorille [55,60]. Ceci suggère que l'enregistrement fossile représentant le Miocène africain est incorrectement échantillonné, ceci étant d'autant plus vrai dans le cas des taxons décrivant un milieu forestier. Finalement, le seul moyen de préciser l'origine géographique du rameau africain des hominoïdes est de rechercher de nouveaux sites à hominoïdes sur le terrain, particulièrement dans les régions actuellement non prospectées. En identifiant de nouvelles régions d'exploration paléontologique, plus en adéquation avec les milieux de vie habituels des grands singes, nous pourrons trouver les nouveaux fossiles essentiels à la résolution du débat actuel sur la phylogénie et la paléobiologie des hominoïdes.

1. Introduction

The African hominoid clade consists of humans, chimpanzees, gorillas, and extinct forms more closely related to them than orangutans. This group is also often referred to as the Homininae or hominines (Fig 1C and D). The terms hominines and African hominoid clade will be used interchangeably in this paper. Two different hypotheses have been proposed to explain the geographic origins of this group. These hypotheses can be summarized as follows:

H_1: *Modern African hominoids arose in Africa.*

This hypothesis proposes that stem catarrhines and hominoids arose in Africa. Some lineages then migrated into Asia giving rise to modern gibbons, orangutans, and Eurasian Miocene apes. The stem African hominine lineage remained in Africa, eventually diversifying into gorillas and the chimpanzee-human lineage, which in turn diverged into the chimpanzee and human lineages. Thus, some crown hominoids persisted in Africa throughout the Miocene, and all modern hominoids have an ultimate African origin.

H_2: *Modern African hominoids arose in Eurasia.*

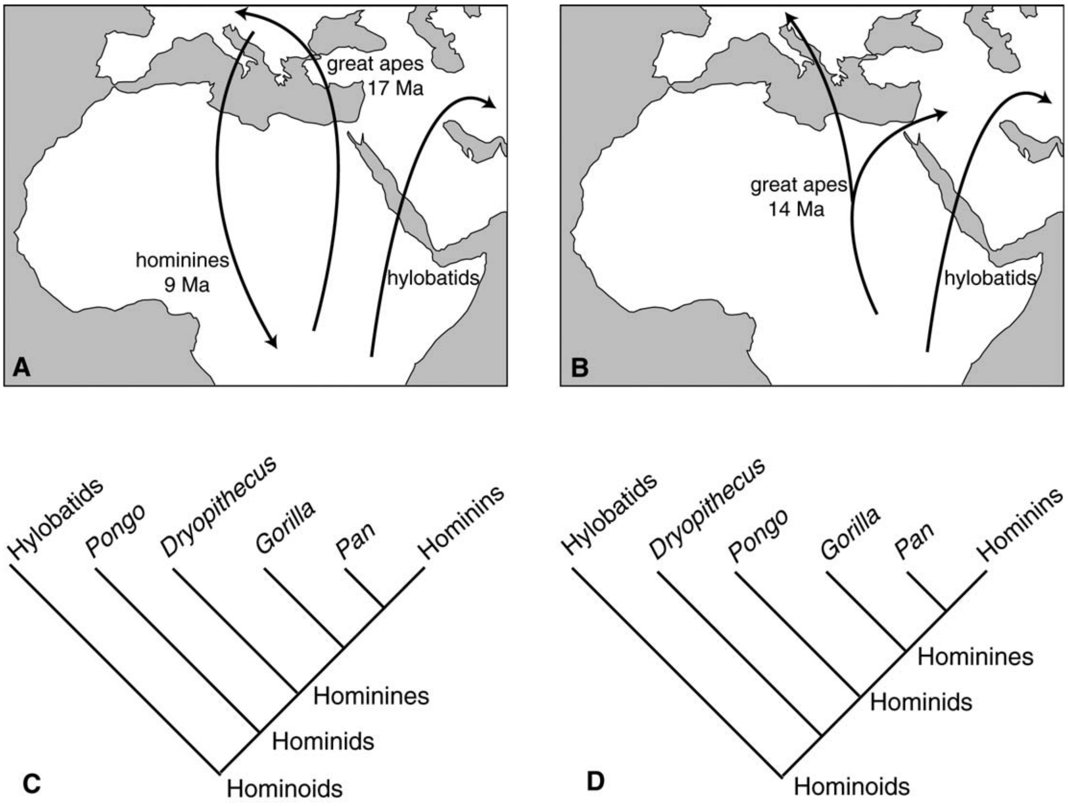

Fig. 1. **A**. Outline of the Eurasian hominine origin hypothesis as suggested by Begun [9,11] and Stewart and Disotell [76] in which hominoids migrate out of Africa approximately 17 Ma and hominines re-enter Africa at 9 Ma. **B**. Outline of the African hominine origin hypothesis in which only the lineages giving rise to modern gibbons, orangutans, and Eurasian Miocene apes migrating to Eurasia, while some crown hominoids remain in Africa, eventually giving rise to the hominines. **C**. Simplified cladogram of hominoid relationships that fits with the Eurasian hominine origin hypothesis [12]. **D**. Simplified cladogram showing hominoid relationships that fit with an African origin of the Homininae.

Fig. 1. **A**. Schéma de l'hypothèse d'une origine eurasiatique des hominoïdes selon laquelle il y a eu migration de ce groupe vers l'Eurasie il y a 17 Ma, puis migration des hominines vers l'Afrique il y a environ 9 Ma [9,11,76]. **B**. Schéma de l'hypothèse d'une origine africaine des hominoïdes où seuls les ancêtres du groupe gibbons, orang-outans et grands singes eurasiatiques du Miocène ont migré en Eurasie, tandis que quelques hominoïdes restaient en Afrique, conduisant éventuellement aux hominines. **C**. Cladogramme simplifié des relations entre les hominoïdes selon l'hypothèse d'une origine eurasiatique [12]. **D**. Cladogramme simplifié des relations entre les hominoïdes selon l'hypothèse d'une origine africaine des hominines.

This hypothesis also suggests that the stem catarrhines originated in Africa. The common ancestor of the extant large hominoids migrated to Eurasia approximately 17 Ma. This lineage then diversified into the modern and fossil Eurasian apes, and all remaining African Miocene hominoids went extinct. The common ancestor of the Homininae arose in Eurasia in the earliest Late Miocene and migrated back to Africa between 6 and 9 Ma ago, diversifying rapidly into the modern African forms including hominins. Thus, in this hypothesis, hominines have a Eurasian origin.

The first hypothesis (H_1) has been the traditional view for many years (e.g., [4]). Once it was known that the earliest catarrhines and hominoids were found in Africa, it seemed logical that the modern African apes also originated there, and that only the lineages leading to Eurasian hominoids migrated out of Africa (Fig. 1B). Currently accepted molecular divergence dates for the apes suggest that the *Pongo*-hominine split is at 14 Ma, while gorillas diverge at approximately 8 Ma, and hominins and chimpanzees diverge at around 6.5 Ma [65]. Thus according to the African origin hypothesis, we should expect to find the stem hominine ancestor living in Africa between 14 and 8 Ma. It has been proposed that this ancestor would likely be chimpanzee or gorilla like, in that it would have eaten ripe fruits and lived in tropical forests [85]. Since tropical forests in Africa during this period would have largely been restricted to Central and Western Africa, we might predict that it is most likely that hominine ancestors would have inhabited these areas.

New hominoid discoveries in Eurasia have caused some researchers to support the second hypothesis – that the ancestor of all living hominoids migrated out of Africa into Eurasia, and that the common ancestor of the African apes migrated back into Africa in the Late Miocene. Begun [8–12] has been the major advocate of a Eurasian origin for the Homininae. He hypothesizes that Miocene hominoids originated from a thick-enameled common ancestor, such as *Afropithecus* (17–18 Ma in Kenya) or *Heliopithecus* (Early Middle Miocene, Saudi Arabia). This lineage migrated to Eurasia, its oldest representative being a molar fragment from Engelswiess Germany, currently dated to 16.5 Ma [11,31]. A radiation of Eurasian Middle Miocene hominoids followed, with the ancestor of the hominines eventually migrating back into Africa (Fig. 1A). The implications of this hypothesis are that hominine ancestors should not be found in Africa between 14 and 8 Ma, but only after they return from Eurasia and diverge into gorillas and the hominin-chimpanzee lineage. Under this hypothesis, hominines could not be completely restricted to tropical forest, since they would have needed to expand their range in the early Late Miocene between Eurasia and Africa through non-tropical forest habitats [11]. Consequently, we might expect that they would have a more widespread distribution in Africa than extant apes.

Begun's reasons for suggesting a Eurasian origin for the Homininae stem mostly from the fact that he, like many researchers, does not recognize any of the few known African Miocene hominoids as good ancestral candidates for modern African apes and humans. Instead, based on cladistic analyses, he believes that *Dryopithecus* and *Ouranopithecus* from Europe are most closely related to the ancestor of the hominines [10,12,46] (Fig. 1C). Further, he argues that the absence of fossil remains of likely hominine ancestors in Africa suggests that they were not present in Africa during this period.

Stewart and Disotell [76] have examined the role of intercontinental population range extensions in hominoid evolution as a way of evaluating the Eurasian hypothesis for the origin of hominines. They propose that the most likely scenario for the origin of the Homininae is one that requires the fewest migration events. Their analysis supports Begun's hypothesis [11,12] since they conclude that an Asian origin is more likely because it requires fewer migration events and is therefore more parsimonious. Stewart and Disotell's conclusion concerning hominoid migrations is based on presumed relationships between fossil hominoid taxa taken directly from Begun's work [10,12] and as such is not an independent test of his hypothesis. In addition, they assume that many Eurasian fossil hominoids have separate African origins, requiring several migrations of hominoids into Eurasia, but it is unclear why this must be the case. As suggested by Moya-Sola et al. [57], it is plausible that the distribution of Eurasian hominoids can be explained by two extensions into Eurasia – one for the lesser apes, and one for the modern and fossil Asian great apes (Fig. 1B).

1.1. Evaluating the evidence

There are many issues to consider in evaluating the two models for the origin of the Homininae. First, they are effectively mutually exclusive hypotheses – either hominines arose in Africa or they arose in Eurasia. These hypotheses have been supported using both phylogenetic and biogeographic evidence. Only by locating new hominoid fossils can these alternative hypotheses be adequately tested. For the present time, we must be content to evaluate these hypotheses based on the evidence at hand – the currently known fossil evidence on which they are based.

1.1.1. Miocene hominoid phylogeny

In general, the phylogenetic relationships of Miocene hominoids are poorly understood [64,65] and hominoids are so poorly sampled, that it is difficult to know how to use the data to reconstruct the evolutionary history of modern African apes. Begun's [10–12] hypothesis concerning hominine origins is largely driven by his phylogenetic reconstructions of hominoid relationships (Figs. 1A and B) and, while Begun argues for a link between *Dryopithecus* and the hominines to the exclusion of modern Asian apes, others (e.g., [56]) make an equally strong case for the affinities of *Dryopithecus* and Asian apes. Other phylogenies (e.g., [3,29,56,72]) that do not propose close links between *Dryopithecus* and the African apes support an African origin for the hominines (Figs 1B and D).

It is important to note that the probability of recognizing a Eurasian fossil taxon as a likely ancestor for the Homininae is higher simply because there are more taxa known. In other words, the fact that there seem to be better modern hominoid ancestors in Eurasia could be an artifact of there being more candidates to choose from. Uncertainty in Miocene hominoid relationships has led many researchers to examine other types of evidence to strengthen the assertion that modern African apes arose in Eurasia.

1.1.2. Distribution of Miocene hominoid fossils

It is generally recognized that there is a gap in the fossil record of African hominoids between 13 and 6 Ma ago. Traditionally, this gap has been viewed as a period of 'missing evidence' when hominoids are not found due to a lack of collections from suitably aged and located deposits (e.g., [64]). In contrast, Begun [9] has suggested that this gap is real and represents the period before Africa was repopulated by Eurasian-derived hominoids. Recent fossil finds have closed this gap significantly (e.g., [20]), but the African hominoid record is still extremely sparse between 12 and 7 Ma with the notable exception of *Samburupithecus*, a Kenyan hominoid dated to 9.5 Ma [37]. Conversely, hominoid fossils are abundant throughout much of Eurasia during this period. Begun [9] concludes that this difference indicates that hominines and their ancestors were absent from Africa during the early part of the Late Miocene.

Some authors have commented that Begun's assertion that hominoids were absent from Africa is premature because the fossil record from this period is extremely poor [57,64,81]. Is the African Miocene fossil record good enough to test hypotheses concerning hominoid distributions and origins? And how can we account for differences in hominoid abundances between Eurasia and Africa if it is not due to the actual absence of hominoids in Africa?

One approach to this question is to look at the distribution and characteristics of currently known African Late Miocene sites in order to determine if they provide adequate evidence to conclusively determine the presence or absence of fossil apes in the early Late Miocene of Africa. Begun [9 (p. 244)] lists twenty-six fossil localities dating to the Late Miocene of Africa (between 5–12 Ma). He notes that only three of these localities have yielded hominoids, and that they sample the habitats in which hominoids would be expected to live. He further suggests that these localities provide sufficient evidence to conclude that hominoids are absent from Africa during this period. The main goal of this paper is to evaluate these statements by examining the data from these fossil localities.

2. Materials and methods

Many different factors affect the composition of a fossil assemblage, in addition to the composition of the biota from which the fossil assemblage derives. Factors that can affect the probability of finding hominoids at a given site include:

1. *Habitat sampling*. Although Miocene hominoids are generally no longer thought to be suspensory arborealists like modern apes, they are still interpreted as maintaining an arboreal lifestyle throughout the Middle and Late Miocene [70]. Some Miocene hominoids such as *Griphopith-*

   ecus and *Kenyapithecus* have been interpreted as inhabiting non-tropical woodland habitats [2,86]. These forms are not closely related to the modern African apes and consequently should not be used to reconstruct the chimpanzee and gorilla ancestral morphotype. Modern hominoids are restricted to tropical forests, and it is likely that this is the case for the last common ancestor of chimpanzees and gorillas as well.

   Chimpanzees and gorillas have extremely similar morphologies, and have been suggested to be roughly scaled versions of the same animal [30]. If this is the case, then it seems likely that the common ancestor of chimpanzees and gorillas would have been very similar to the modern forms and, as such, would have inhabited an analogous tropical forest environment and relied heavily on ripe fruits. The location and extent of tropical forest in Africa has varied through time, however there has always been tropical forest habitat in Africa that would be suitable for large bodied apes. Consequently, only fossil localities which sample forested environments are expected to yield hominoid remains.

2. *Sample size*. The total number of fossils collected from a site (both total number of fossils, and total number of identifiable specimens) has important implications for how the site can be interpreted. It is well known that the diversity of species sampled at a fossil locality increases with the number of specimens recovered [6,24]. Thus, rare taxa have a higher probability of being found when sample sizes are large. Hominoids are expected to be rare in the fossil record because they have low population densities and slow rates of turnover [42]. Thus, to have a high probability of finding fossil hominoids, sample sizes must be relatively large.
3. *Preservational biases*. Many different taphonomic factors affect the types of fossils that are found at a locality. For example, differential weathering of bone, different burial rates, size of bone fragments and other factors can generate biased samples that represent only part of the ecological community that existed. In general, preservation of fossil remains in forested environments is thought to be rarer than preservation in dry or lacustrine environments. However, recent archaeological investigations in Central Africa have clearly demonstrated that preservation of vertebrate fossils does occur in forests [54].

With these factors in mind, a literature review was conducted for the African localities listed by Begun [9]. For each locality, data was collected for the following parameters:

1. Species diversity – the faunal list of all mammalian taxa reported at the locality.
2. Sample size – the total number of fossils removed from the locality.
3. Ecological context – as reported in the literature, or inferred from faunal lists and/or geology.
4. Taphonomy – information on potential biases in preservation.

Once data was collected for these parameters, sites were evaluated to determine whether it is likely that hominoids would be found at the fossil site if they had been present in the living community. The prediction is that sites that contain fossil hominoids should have relatively large sample sizes and should represent forested environments. Fossil sites that do not have these characteristics should not be expected to contain fossil hominoids. If there are several sites that meet these criteria, but do not contain fossil hominoids, then this might be good evidence that hominoids were absent from Africa during this period. On the other hand, if none of the surveyed sites meet these criteria, then it is premature to assume that hominoids are indeed absent.

Often, complete information was not available for all the data categories for a given site. In particular, information on total sample sizes and the abundance of each fossil taxon at a locality are often not reported in the literature. Also, many research reports do not include the numbers of unidentifiable specimens that were recovered from the site. The total number of specimens is reported whenever it is known, but in many cases I have estimated the total sample size, dividing sites into categories of small ($n < 100$), medium ($100 < n < 1000$), and large ($n > 1000$). Abundance data for specific taxa and for unidentifiable material were not estimated, and are often missing from the data set. In addition, some fossil sites examined consist of a number of separate fossil localities that often sample different time periods or environments. Reported sample sizes are for the entire site because it was generally difficult to get abundance and species data for individual localities.

An additional issue is that taxonomic identifications for many of the localities excavated in the earlier part of the twentieth century are often out of date. This was not a major problem because identifications to the genus level were adequate for the purposes of this project. Faunal lists are as thorough as possible, but it seems likely that at many sites there are additional taxa not described in the literature – particularly micromammals.

3. Results

After reviewing the available information for the African localities between 5 and 12 Ma old listed by Begun [9], it is apparent that the African Late Miocene fossil record is indeed rather poor (Table 1). First, known fossil localities are unevenly distributed in space (Fig. 2). Of the 25 fossil sites surveyed, most sites are from East ($n = 11$) and North ($n = 13$) Africa, with only one site from Southern Africa, and none from Central or Western Africa. Late Miocene deposits in these regions are probably rare, but until more palaeontological exploration is done in these under-sampled areas the African Late Miocene fossil record will be poorly sampled geographically. Most of the known Late Miocene localities in Africa fall outside of the likely distribution of tropical rainforest during the Miocene.

The temporal distribution of African Miocene fossil localities is also uneven (Fig. 3). Most sites date to between 5 and 7 Ma, with the period between 7 and 9 Ma being particularly poorly sampled. This trend is even more exaggerated when one looks at sample sizes of sites through time. The sites with the largest sample sizes are almost always in the 5 to 7 Ma range, such as Lothagam, the Lukeino Formation, and Sahabi. Newly reported fossil finds from the Late Miocene of Chad also fall in this interval [20]. Conversely, only a few hundred specimens are reported for the entire two million year period between 7 and 9 Ma ago. Uneven sampling suggests that much taxonomic diversity is being missed, particularly in poorly sampled time periods. Given such small sample sizes, it is not surprising that fossil apes have not been found in this critical period.

Although hominoid remains are extremely rare in Africa between 5 and 12 Ma ago, they are present. Three of the fossil sites have hominin remains – Lothagam, the Lukeino Formation, and the Middle Awash deposits [47,73,74], in addition to recently reported hominin finds from Chad [20]. An additional three localities have ape remains – the Ngorora Formation in the Tugen Hills (3 specimens), Nkondo, and Samburu [34,37,60]. Fossil hominins and apes are never found at the same locality, reinforcing the hypothesis that apes would have remained in closed forest, while early hominins would have moved into woodland environments.

Sites that contain either apes or hominins have larger than average sample sizes. The site with the smallest sample size that contains a hominoid is Nkondo in Uganda with a total of 832 fossils collected [62,63]. Of the nineteen sites that contain neither hominins nor apes, twelve have significantly fewer than 500 collected specimens (Table 1), and therefore have a very low probability of sampling fossil hominoids even if they had been present in the biotic community because the sample size is too small to sample rare taxa. This leaves seven Late Miocene African sites that are large enough to sample rare taxa, and would be the best candidates for containing hominoid fossils. These seven sites are Sahabi, Bled Douarah, Nchorora, the Mpesida Beds in the Baringo Basin, the Sinda Basin localities, Manonga Valley, and Langebaanweg.

Sahabi in Libya and Bled Douarah in Tunisia are both large North African fossil sites. Sahabi has an extremely diverse fauna that contains several species of carnivores and Old World Monkeys [17]. Mammalian species of a wide range of body sizes are represented. The environment of Sahabi is reconstructed as representing a mosaic of mixed-woodland and open-country habitats [15]. Thus, the absence of fossil apes in the Sahabi localities is likely due to the fact that this site samples a non-forested environment unsuitable for apes. Bled Douarah is significantly older than Sahabi (9.5–12.5 Ma), but in other respects is quite similar. Several thousand specimens have been collected and there is a relatively diverse fauna [51,68]. This fauna includes early equids and hypsodont bovids [67], suggesting that the environment is relatively open and again is unsuitable for hominoids ancestral to chimpanzees and gorillas.

The Nchorora Formation in Ethiopia is dated to 10.7–10.5 Ma [79]. There is no published information on the number of fossils collected from the site. How-

Table 1

Results of the survey of Late Miocene fossil localities. The sample-size column contains known numbers of specimens when possible. Estimated sample sizes have been divided into small (< 100), medium (< 1000), and large (> 1000) categories. Faunal diversity column refers to the taxonomic diversity of mammalian faunas found at the site. Environment column refers to published environmental interpretations. The inferred environment column contains personal inferences on the environment based on information from published sources. Superscript numbers refer to primary sources for the data, and are listed in the references for the paper.

Résultats de l'étude des localités fossiles du Miocène récent. La taille de l'échantillon correspond au nombre de spécimens lorsqu'il est connu. Les tailles estimées ont été divisées selon trois catégories : petit (< 100), moyen (< 1000), et grand (> 1000). La diversité faunique réfère à la diversité taxonomique des faunes mammaliennes récoltées dans un site donné. La colonne environnement représente les inférences établies à partir des informations fournies dans la littérature, mais l'information dans la colonne sur l'environnement inféré correspond à des inférences personnelles.

	Site	Country	Age	Sample size	Faunal diversity	Fauna notes	Environment (published)	Inferred environment	Taphonomy
1	Sahabi	Libya	4.2–7.1 Ma	Large–over 2000	Diverse [15]	Carnivores and primates well represented [17]	Savannah mosaic [17]	Relatively open with some woodland areas	Suggested bias against open country forms
2	Wadi Natrun	Egypt	5–6 Ma	No data (medium?)	Moderately diverse	Cercopithecines present	Open country near lake with wooded shoreline [59]	Relatively open	
3	Oued Zra	Morocco	10.5–10.7 Ma	Small	Rodents and insectivores only	Some fish, bird, and amphibian remains	Relatively open [38]	Relatively open	
4	Ait Kandoula	Morocco	10–6 Ma	Small	Diverse	Rodents only [13]	Dry and relatively open [38]	Probably relatively open	
5	Khendek el Ouaich	Morocco	7.4 Ma [77]	Small	Low diversity	Rodents and insectivores only [38]	Dry and relatively open [38]	Probably relatively open	
6	Bou Hanifia	Algeria	12 Ma (Vallesian) [1]	No data (small?)	Moderately diverse (12 species)	Some primates, large mammals [1,5]	None published	Uncertain. Early equids, colobines suggest mix of habitats	
7	Menacer	Algeria	5.3–7.1 Ma [77]	Small (~75)	Moderately diverse	Dominated by primate remains [5,78]	None published	Relatively open with some woodland areas	Poor preservation and fragmentary remains
8	Oued el Atteuch	Algeria	9.7–10.0 Ma [77]	Small	Low diversity	Rodents, Hipparion, and two bovid species [5,22]	None published	Equids suggest some open environments	
9	Amama 1 and 2	Algeria	1: 10 Ma 2: 7–8Ma [77]	Small	1: Rodents and insectivores only [38]	2: Three Hipparion teeth and proboscidean fragments [77]	None published	Probably relatively open	

(continued on next page)

Table 1
(continued)

	Site	Country	Age	Sample size	Faunal diversity	Fauna notes	Environment (published)	Inferred environment	Taphonomy
10	Bled Douarah	Tunisia	9.5–12.5 Ma[a]	Large >1000 [68]	Diverse [16,66–68]	Small and large species	Older level–river and savannah. Younger level–river and forest [68]	Hypsodont bovids and horses indicate some open environments	
11	Douaria	Tunisia	5.3–7.1 Ma[a]	Small (~ 20)	Large mammal fauna only [77]	Giraffids, rhinocerotids, and one bovid [69]	None published	Probably relatively open	
12	El Hamma du Djerid	Tunisia	~ 10 Ma	Small (< 30)	Large mammal fauna only [5,18,51,75]	Artiodactyls, equids, and one proboscidean	None published	Probably relatively open–equids	Poor preservation
13	M'Dilla	Tunisia	Late Miocene [77]	Small	Large mammal fauna only	Hipparion, proboscideans, bovids [5,77]	None published	Probably relatively open	
14	Nchorora (Chorora)	Ethiopia	10.5–10.7 Ma [79]	No data (medium)	Moderately diverse [39,40]	Some carnivores	Lakeside setting [41]	Probably wooded with more open habitats surrounding	Remains heavily fragmented
15	Middle Awash	Ethiopia	5.3–6.2 Ma [41,84]	Large ~2000	Moderately diverse	Primates and carnivores well represented. Hominins present [40,84]	Mosaic of woodland and more open habitats. Becomes more open in younger times [41,84]	Contains hominids, probably wrong environment for apes	
16	Samburu	Kenya	8–10 Ma (9.5 Ma)	Large >1500	Diverse [58]	Hominoids represented	Mosaic of dry and forested habitats. Represents transition to savannah biome [58]		
17	Lothagam	Kenya	5–7 Ma [53]	Large – over 2200	Diverse [47,48]	Carnivores, monkeys, several hominin specimens	Mixed woodland/ open country [47]	Contains hominids, probably wrong environment for apes	Good preservation
18	Baringo Basin (Mpesida Beds)	Kenya	6.2–7 Ma [34]	No data (medium?)	Moderately diverse– mostly large bodied	Colobines, chalicotheres, little equid material, modern rhinocerotids [35,44]	Strong evidence of tropical forest. Also C4 signal from tooth enamel [44,45]	Different environments sampled. Some tropical forest, seasonal forest, and open country	

(continued on next page)

Table 1
(continued)

	Site	Country	Age	Sample size	Faunal diversity	Fauna notes	Environment (published)	Inferred environment	Taphonomy
19	Lukeino	Kenya	5.6–6.2 Ma [34]	Large	Diverse [35,82]	Hominins represented. Fauna dominated by colobines and bovids [35,61]	Most fauna suggests a mix of woodlands and more open habitat. Rodents suggest a savannah habitat [83].	Mosaic of open and closed habitats. Probably a woodland–savanna mosaic	
20	Ngorora	Kenya	8.5–13 Ma [36]	Large > 1000?	Diverse	Hominoids represented, other primates, carnivores [14,36,58]	Botanical remains suggest tropical lowland rainforest early in sequence, replaced by arid open woodland after 10 Ma [34,44]	Good habitat for hominoids early in sequence, probably not later.	Often isolated teeth
21	Nakali	Kenya	8.5–9 Ma [36]	Small– unknown	Limited diversity	One colobine, large mammals, few rodents [14,58]	None published	Equids, colobines etc–probably a mosaic of open and closed environments with dry woodlands	
22	Sinda Basin	Zaire	Late Miocene	Medium (report 579 not all identified) [87]	Large mammal fauna only	Perrisodactyls, proboscideans, bovids etc. [87]	Suggest mosaic of environments sampled, including tropical rain forest [52]	May represent forested habitat	Very poor preservation–all tooth fragments of large mammals
23	Nkondo	Uganda	5–6 Ma [63]	Medium (832)	Moderately diverse	Hominoids, cercopithecoids represented [60,62,63]	Humid environment with mosaic of forest and savannah. Also supported by fossil woods and fruits [23]	Gorilla suggests well-forested environment	
24	Manonga Valley	Tanzania	5.0–5.5 Ma	Medium (852)	Moderately diverse [27]	No primates	Mosaic of more open and more bushy habitats near lake [28]	Lack of arboreal taxa suggests no closed forest	One fossiliferous horizon with no transport of fossils
25	Langa-baanweg	South Africa	5 Ma [33]	Large > 1000	Diverse	Includes carnivores, few primates [21,32,33,82]	Seasonal rainfall with woodland giving way to fynbos (open vegetation) [26,33]	Mixed fauna with many grazers. Temperate climate – too seasonal for hominoids	Good preservation

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[a] Data from NOW – Neogene of the Old World Database of fossil mammals http://www.helsinki.fi/science/now.

Fig. 2. Map of Africa showing the spatial distribution of 25 fossil localities listed by Begun [9] dated to between 12–5 Ma. Shaded gray area shows the likely distribution of gorillas and chimpanzees. **1**, Sahabi, Libya **2**, Wadi Natrun, Egypt **3**, Oued Zra, Morocco **4**, Aït Kandoula, Morocco **5**, Khendek el Ouaich, Morocco **6**, Bou Hanifia, Algeria **7**, Menacer, Algeria **8**, Oued el Atteuch, Algeria **9**, Amama 1 and 2, Algeria **10**, Bled Douarah, Tunisia **11**, Douaria, Tunisia **12**, El Hamma du Djerid, Tunisia **13**, M'Dilla, Tunisia **14**, Nchoroa, Ethiopia **15**, Middle Awash, Ethiopia **16**, Samburu, Kenya **17**, Lothagam, Kenya **18**, Mpesida Beds, Baringo Basin, Kenya **19**, Lukeino Formation, Kenya **20**, Ngorora Formation, Kenya **21**, Nakali, Kenya **22**, Sinda Basin, Zaire **23**, Nkondo, Uganda **24**, Manonga Valley, Tanzania **25**, Langebaanweg, South Africa. The 26th localitiy listed by Begun (Abu Dhabi, Saudi Arabia) was omitted from analysis.

Fig. 2. Carte de l'Afrique, montrant la distribution géographique des 25 localités datées entre 5 et 12 Ma et examinées par Begun [9]. **1**, Sahabi, Libye **2**, Wadi Natrun, Egypte **3**, Oued Zra, Maroc **4**, Aït Kandoula, Maroc **5**, Khendek el Ouaich, Maroc **6**, Bou Hanifia, Algérie **7**, Menacer, Algérie **8**, Oued el Atteuch, Algérie **9**, Amama 1 et 2, Algérie **10**, Bled Douarah, Tunisie **11**, Douaria, Tunisie **12**, El Hamma du Djerid, Tunisie **13**, M'Dilla, Tunisie **14**, Nchorora, Ethiopie **15**, Middle Awash, Ethiopie **16**, Samburu, Kenya **17**, Lothagam, Kenya **18**, Mpesida, bassin de Baringo, Kenya **19**, formation de Lukeino, Kenya **20**, formation de Ngorora, Kenya **21**, Nakali, Kenya **22**, Sinda Basin, République Démocratique du Congo **23**, Nkondo, Ouganda **24**, Manonga Valley, Tanzanie **25**, Langebaanweg, Afrique du Sud.

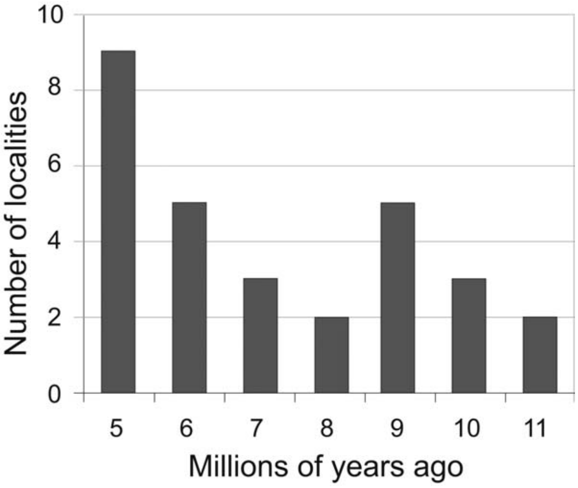

Fig. 3. Temporal distribution of the 25 fossil localities dated to between 12–5 Ma.

Fig. 3. Distribution en fonction du temps des 25 localités fossiles datées entre 5 et 12 Ma.

ever, the fauna is only moderately diverse, and fossil remains are heavily fragmented [79]. The faunal list includes rodents, a felid, early equids, suids, and bovids. The environment is reconstructed as representing a lakeside setting, with wooded and more open country environments nearby [39,40]. This environment is probably not suitable for hominoids during this period.

The Mpesida Beds in the Tugen Hills of Kenya are dated to 7–6.2 Ma. Outcrops of these beds occur in distinct, unconnected lenses of different ages [35] that probably sample different environments. The number of fossils collected from the Mpesida Beds is not published, but the sample size is likely to be relatively small as the mammalian fauna recovered from the site is not very diverse. The fauna includes colobines, proboscideans, equids, suids, giraffids, and bovids, and is mostly large-bodied. Fossil plants have been recovered from several localities. One locality contains fossil wood indicating the presence of tropical lowland rain forest at 6.3 Ma, while another suggests more seasonal woodlands [44]. The tropical lowland forest habitat could be good ape habitat, but the number of fossils that actually come from this habitat is probably quite small, suggesting that apes would not be sampled even if they were present in the living community.

The Sinda Basin localities are found in the Western Rift Valley in Eastern Uganda [52,87]. The localities are not well dated, but biostratigraphy indicates the fossils are Late Miocene in age. Over 500 fossils have been collected, of which only 52 could be identified as mammalian, and only 27 were assigned a more specific taxonomic designation. The fossil assemblage appears to have been subject to a rather rigorous set of taphonomic processes, with only tooth fragments of very large taxa preserved. The Sinda Basin fossiliferous localities have been interpreted as representing a humid tropical forest fauna [87], likely suitable for apes. But since preservation at these localities is biased in favor of large taxa, and the number of fossils collected is relatively small, we would not expect to find hominoid remains at this site.

The Ibole member of the Wembere–Manonga Formation in the Manonga Valley, Tanzania is dated to 5.0–5.5 Ma by biostratigraphic correlation with other East African sites [27]. The Ibole Member faunas are not very diverse and are dominated by large bodied animals, so there may be a size bias in preservation. Fossil and sedimentological evidence suggests that the Ibole deposits represent a lakeside setting. Proboscideans and suids dominate the fauna and suggest that closed habitats surrounded the lake [28]. On the other hand, bovids are also relatively common, representing 25% of the total fauna, and suggest the presence of more open habitats in the area. The four species of rodents present are considered to be characteristic of open or semi-aquatic environments [27]. In addition, the Ibole Member fauna contains no primates and no arboreal taxa. The lack of small arboreal taxa suggests that the Ibole faunas may not represent a closed forest habitat and would therefore not be suitable ape habitat, although it may be suitable for hominins [20].

Most fossils from Langebaanweg in South Africa have come from the ‘E’ quarry locality and the fauna has been roughly dated to 5 Ma by biostratigraphy. Thousands of specimens have been removed from this locality from several fossil horizons in the Varswater Formation [33]. The fauna is extremely diverse with a large range of body sizes represented and many carnivore species. The only primate remains known are two cercopithecid teeth. The presence of rhinocerotids, equids, and several species of hypsodont bovids suggest a relatively open environment [26]. Hendy [33] concludes that the Langebaanweg fauna represents a temperate environment in transition from woodland vegetation into a more open grassland environment with strong seasonal rainfall – a habitat unsuitable for Late Miocene apes ancestral to chimpanzees and gorillas.

Thus none of the Late Miocene African sites surveyed would necessarily be expected to contain hominoids ancestral to modern African apes. Sites that do contain fossil apes share the following features: (1) they sample forested environments, (2) have large sample sizes with at least 500 specimens, and often considerably more, (3) have a high taxonomic diversity, (4) and a high quality of preservation. Few sites combine all of these characteristics, and those that do contain ape remains (Ngorora, Samburu, and Nkondo). None of the other fossil sites examined have all these features (Table 1).

In summary, many Late Miocene African sites have extremely small sample sizes, indicating that rare faunal elements would not be preserved. Others have obvious sampling biases, containing only fragments of very large mammals, or consisting solely of micromammal teeth, and others probably did not sample suitable habitat for apes. Thus it is not unexpected that they do not contain fossil apes and these sites should not be used as evidence to suggest that hominoids were not present in Africa at this time. I conclude therefore that biases in preservation and inadequate exploration of the African continent lead to the poor Middle and Late Miocene hominoid record in Africa, not an actual absence of crown hominoids.

4. Discussion

Because the question of where hominines originated is a controversial one, temporal gaps in the record and fragmentary fossils allow much room for interpretation, and result in alternative hypotheses concerning the evolutionary history of Miocene hominoids. I have reviewed some of the evidence associated with Begun’s [9] hypothesis that the Homininae have a Eurasian origin, most particularly the claim that the fossil record is sufficient to conclude that hominoids do not exist in Africa throughout much of the Miocene.

Results of my analysis show that the Late Miocene fossil record in Africa is relatively poor, particularly when compared with the Eurasian fossil record from this period. There are numerous palaeontological sites, but many of these sites contain few fossils and are biased towards either only very large or very small taxa. Four of the twenty-five sites examined contained only micromammals (rodents and insectivores), while five contained only large mammals (Table 1). It is unlikely that hominoids would be found in sites with such preservation patterns.

Sample sizes at most of these African Miocene sites tend to be quite small. Specific data on the number of specimens recovered from a site is frequently not available, but approximate estimates of sample size can be made for most localities. Forty-four percent of the 25 localities examined had fewer than 100 specimens, and none of these contained hominoids. At the three sites in which ape fossils were recovered, sample sizes tend to be significantly larger, with at least 500 specimens recovered (Table 1). Hominoid remains formed less than 0.5% of the total fossil assemblage at each of these sites. This figure is similar to hominoid sites in Eurasia. For example, even though over 300 *Sivapithecus* fossils have been found in the Siwaliks of Pakistan, they represent only 0.75% of the fossil assemblage collected [7,43]. This is presumably due to the fact that hominoids are relatively rare components of a living faunal assemblage because of their low population densities and long life histories [42]. Consequently, a site with less than a hundred fossils has a very low probability of containing a hominoid fossil – even if hominoids were present in the living community. One good indicator that sample size and diversity are high enough to sample rare taxa is when the faunal list also contains several species of other rare taxa such as carnivores.

Some sites do have large sample sizes but still do not contain fossil apes. This can be explained as the result of unsuitable environmental sampling, as these sites typically represent more open country or savannah environments. As discussed previously, it is unlikely that the immediate ancestors of chimpanzees, humans, and gorillas would have lived in such open environments. There is evidence to suggest that Miocene hominoids occupied a broader ecological niche than modern apes, however still lived in largely forested environments [2,3,80]. In general, it would seem that although some Miocene hominoids did move into ‘more open’ environments, these habitats were still forested, but were more seasonally variable than the rainforest habitats favored by modern apes [2,3].

There is limited evidence to suggest that some African hominoids, such as *Kenyapithecus* may have moved into savannah-like environments at sites such as Fort Ternan and Kaimogool (e.g., [86]), however this evidence is controversial, and most environmental reconstructions and the available morphological evidence suggest forested environments [3]. Even if *Kenyapithecus* had occupied non-forested environments, this should not be used as evidence to reconstruct the environment of the immediate common ancestor of the modern African ape clade because *Kenyapithecus* is not closely related to this group. The principle of parsimony suggests that if gorillas, bonobos, and chimpanzees all inhabit tropical forest environments, then most likely their common ancestor did as well – accepting that hominins clearly represent a derived condition [64,65,85].

4.1. Other approaches

This paper has considered one approach to examining the question of where hominines originated. A future step in this research would be to attempt to ‘quantify’ the type of palaeontological site that is likely to contain hominoids. It is generally thought that apes are expected to be relatively rare components of a fossil assemblage [42]. However, the degree to which this is true is currently unknown. Models that can predict the proportion of hominoids a fossil assemblage should contain are required to further address this question. Surveying modern ape biocommunities and forming accurate estimates of the biomass of great apes relative to their forest community will be needed in order to incorporate information about turnover rates and ape biomass into models. Data on probable hominoid abundance is necessary for paleontologists to know how large a fossil sample from a site must be before one can conclude that hominoids are actually absent from that palaeocommunity.

There has been little palaeontological research done in central and western Africa (Fig. 2). Since this area includes the range of modern chimpanzees and gorillas, it is likely that apes would have lived there in the past. Most palaeoanthropological fieldwork in Africa has focused on East and South Africa, with very little attention given to the interior of the continent. This bias is partly due to the fact that sedimentary deposits in East and South Africa are abundant and easily accessible to researchers. Some palaeontological exploration has taken place in Cameroon, with the goal of discovering fossil deposits outside of traditionally researched areas. This research uncovered Cretaceous aged vertebrates [19,25]. Miocene deposits were also located, but thus far have yielded only plant and insect fossils [71]. Further research in these areas may yield

Miocene vertebrate remains. These and other areas should be explored before concluding that hominoids were not present in Africa during the early Late Miocene.

4.1.1. Fossils of the living African apes

Another approach to assessing the quality of the African record is to look at the distribution of fossils of the modern African apes. It is reasonable to hypothesize that chimpanzees and gorillas would have diverged in Africa, even if their common ancestor had migrated to Africa from Eurasia. The recent discovery of the hominin species *Sahelanthropus tchadensis* dated to 6–7 Ma [20] suggests that the chimpanzee-hominin split is older than previously thought, indicating that the last common ancestor of chimpanzees and gorillas would have lived between eight and eleven million years ago [65]. This suggests that the chimpanzee and gorilla lineages would have been living in Africa for at least the last eight million years.

It can also be hypothesized that throughout this period the chimpanzee and gorilla lineages were similar in their ecology and morphology to their descendants, being large bodied, rare, forest dwelling frugivores [64,85]. It is reasonable to assume that other African crown hominoids, prior to the appearance of hominins, would have been similarly adapted. If we have truly sampled the African fossil record in such a way as to find these rare, forest dwelling taxa, then fossil remains of the chimpanzee and gorilla lineages should have been found.

There are in fact very few known chimpanzee or gorilla fossils. Reported chimpanzee fossils include associated dental remains from near Lake Naivasha, Kenya [50], an isolated canine from the Serengeti region of East Africa (unpublished data), and postcranial remains of two different individuals from the Pleistocene site of Mumba, Tanzania [49]. The only reported gorilla fossil is a canine from Nkondo, Uganda dated to 5–6 Ma [60].

Following restudy, none of the purported chimpanzee fossils actually is a chimpanzee. The Lake Naivasha dental remains, thought to represent a canine and two premolars, are carnivore incisors, most likely a hyaenid (L. Werdlin, J. Barry, personal communication). The Serengeti chimpanzee canine is not fossilized, but modern, is of uncertain provenience having been moved around in museum collections, and is unlikely to be from the Serengeti region (W.D. Heinrich, personal communication). The Mumba material has been restudied and represents *Homo sapiens* (T. Harrison, personal communication). However, the gorilla canine from Nkondo probably does represent the first fossil gorilla [55,60], and the only fossil of a modern African ape.

This reanalysis shows that fossil remains of chimpanzees and gorillas are extremely rare in the African fossil record, indeed effectively absent. This could mean that chimpanzee and gorilla remains are not frequently fossilized due to biases in preservation in heavily forested environments. However, numerous Pleistocene and Holocene archaeological sites containing faunal remains indicative of forested settings have been reported throughout Central Africa [54], suggesting that fossil preservation does occur in these habitats. If we have not been successful in locating fossil remains of modern African apes, then it is clearly unsound to assume that we have adequately sampled the African Late Miocene fossil record in such a way as to uncover other fossil hominoid species. Possible reasons why chimpanzee and gorilla fossils have not been recovered are (a) that they are very rare and (b) that paleontologists have not been successful in locating extensive fossil deposits in Western and Central Africa – the areas in which the ancestors of chimpanzees and gorillas are most likely to have lived.

5. Conclusions

The suggestion that hominoids ancestral to hominines lived in Eurasia and not Africa during the Late Miocene is based on the fact that appropriate ancestral candidates have not been found in Africa [9]. Several authors have commented that this assertion is premature because the fossil record in Africa from this period is poor [57,64,81]. The goal of this paper was to examine whether or not the quality of the African Late Miocene record is sufficient to conclude that hominoids were indeed absent during this period.

A literature review of known African early Late Miocene sites demonstrates that these sites are unevenly distributed in space and time (Figs. 2 and 3), with little information available from Central and Western Africa – the geographical areas most likely to have been home to apes. Even with this large gap in our knowledge, fossil ape remains are present at three different localities in East Africa, demonstrating that they were present in Africa during this time period. This suggests that further palaeontological exploration could uncover new fossil taxa, perhaps including the ancestors of the Homininae.

Many currently known Miocene fossil localities do not contain hominoids. This can be interpreted to mean either that hominoids were not present in these areas [9,76], or that hominoid remains have not been preserved at these sites due to small sample sizes, sampling of non-forested environments, or biased preservation. The fact that fossil chimpanzees and gorillas have not been found in later periods when it is certain that they were present should make us skeptical that we have adequately sampled the fossil faunas of the African Miocene.

Ultimately, the only way to know where the ancestor of the Homininae resided is to look for new hominoid sites, particularly in currently unsampled areas. Large portions of Eurasia as well as Africa are unstudied, leading to serious gaps in our knowledge of hominoid history. By identifying new areas for palaeontological exploration, particularly in areas where modern apes live, we may find new fossils that will help resolve current disputes in hominoid phylogeny and palaeobiology.

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