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Systematics of Miocene apes: State of the art of a neverending controversy

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Abstract

Hominoids diverged from cercopithecoids during the Oligocene in Afro-Arabia, initially radiating in that continent and subsequently dispersing into Eurasia. From the Late Miocene onward, the geographic range of hominoids progressively shrank, except for hominins, which dispersed out of Africa during the Pleistocene. Although the overall picture of hominoid evolution is clear based on available fossil evidence, many uncertainties persist regarding the phylogeny and paleobiogeography of Miocene apes (nonhominin hominoids), owing to their sparse record, pervasive homoplasy, and the decimated current diversity of this group. We review Miocene ape systematics and evolution by focusing on the most parsimonious cladograms published during the last decade. First, we provide a historical account of the progress made in Miocene ape phylogeny and paleobiogeography, report an updated classification of Miocene apes, and provide a list of Miocene ape species-locality occurrences together with an analysis of their paleobiodiversity dynamics. Second, we discuss various critical issues of Miocene ape phylogeny and paleobiogeography (hylobatid and crown hominid origins, plus the relationships of *Oreopithecus*) in the light of the highly divergent results obtained from cladistic analyses of craniodental and postcranial characters separately. We conclude that cladistic efforts to disentangle Miocene ape phylogeny are potentially biased by a long-branch attraction problem caused by the numerous postcranial similarities shared between hylobatids and hominids—despite the increasingly held view that they are likely homoplastic to a large extent, as illustrated by *Sivapithecus* and *Pierolapithecus*—and further aggravated by abundant missing data owing to incomplete preservation. Finally, we argue that—besides the recovery of additional fossils, the retrieval of paleoproteomic data, and a better integration between cladistics and geometric morphometrics—Miocene ape phylogenetics should take advantage of total-evidence (tip-dating) Bayesian methods of phylogenetic inference combining morphologic, molecular, and chronostratigraphic data. This would hopefully help ascertain whether hylobatid divergence was more basal than currently supported.

Keywords: Hominoidea; Evolution; Taxonomy; Phylogeny; Cladistics; Homoplasy.

1. Introduction

1.1. What, if anything, is a Miocene ape?

The term ‘ape’ is sometimes used as a synonym of ‘hominoid’—i.e., a member of the superfamily Hominoidea, which includes the families Hylobatidae (gibbons and siamang) and Hominidae (orangutans, gorillas, chimpanzees, and humans; Groves, 2017), plus their extinct relatives. However, following the most common usage of ‘apes’ as opposed to both ‘monkeys’ and ‘humans’ (e.g., Alba, 2012; Tuttle, 2014; Andrews, 2020; Almécija et al., 2021), we restrict the former term to hominoids exclusive of the human lineage (i.e., nonhominin hominoids). Originally, the term ‘ape’ broadly referred to all nonhuman anthropoids, so that nonhuman hominoids were referred to as ‘manlike apes’ (Huxley, 1863) or ‘anthropomorphous apes’ (Darwin, 1871; Huxley, 1872). Huxley (1872) formalized the term ‘anthropomorph’, subsequently used by other authors (e.g., Pocock, 1926; Delson, 1977; Szalay and Delson, 1979), but currently in disuse in the English literature. Hylobatids and nonhominin hominids are customarily referred to as ‘lesser apes’ and ‘great apes’, respectively, in allusion to their size differences (Tuttle, 2014). Extant hylobatids include more than a dozen species classified in four genera, while hominids similarly include four genera but a lower number of species (Groves, 2001, 2017). The restricted diversity of extant hominoids contrasts with that of both extant Old World monkeys and extinct apes. The latter attained a much wider geographic distribution (including Europe and mainland Asia) during the Miocene (e.g., Alba, 2012; Fleagle, 2013; Begun, 2015). As a result of the decimated current genus diversity of hominoids, making sense of their evolutionary history constitutes a monumental challenge from both adaptive and phylogenetic viewpoints (see review in Almécija et al., 2021).

This review focuses on apes recorded from the Miocene—the first geological epoch of the Neogene period, being formally divided into Early (23.04–15.99 Ma), Middle (15.99–11.65 Ma), and Late (11.65–5.33 Ma) Miocene (Raffi et al., 2020). This epoch witnessed important environmental and biotic changes (Zachos et al., 2001; Blois and Hadly, 2009; Raffi et al., 2020). The closure of the Tethys Seaway, due to the collision of the Afro-Arabian and Eurasian plates, enabled intermittent intercontinental dispersals through the Middle East from ~19 Ma onward (Harzhauser et al., 2007), although they were temporarily interrupted during the Langhian transgression at the beginning of the Middle Miocene (~16 Ma; Rögl, 1999). The Mid-Miocene Climatic Optimum, a global warming event that peaked ~17–15 Ma, was followed by the Middle Miocene Climate Transition, a stepwise cooling phase that continued throughout the Late Miocene and had a profound impact on terrestrial ecosystems and mammalian communities (Flower and Kennett, 1994; Zachos et al., 2001; Kürschner et al., 2008; Foster et al., 2012; Pound et al., 2012). The geographic spread of woodland and savanna biomes throughout the Old World, and the associated Pikermian chronofauna adapted to more open and arid environments, started around the Middle to Late Miocene transition and peaked at ~7.5 Ma (Eronen et al., 2009; Kaya et al., 2018). Toward the end of the Miocene, beginning at ~6 Ma, a combination of tectonic and glacioeustatic factors repeatedly isolated the Mediterranean Sea from the Atlantic Ocean during the Messinian Salinity Crisis (Krijgsman et al., 1999), which favored the spread of open landscapes around the Mediterranean and the establishment of additional dispersal routes between Europe and Africa (Gibert et al., 2013).

As for many other groups, the factors outlined above played a major role in shaping hominoid evolution and adaptation (Andrews, 1992, 1996; Andrews and Bernor, 1999; Andrews and Kelley, 2007). Several books (Tuttle, 2014; Andrews, 2015; Begun, 2016) and reviews (Wood and Harrison, 2011; Begun, 2013, 2015; Andrews, 2020; Almécija et al., 2021) have been devoted to Miocene apes during the last decade, and the general picture is quite clear. Hominoids originated in Africa during the late Oligocene, experienced a first radiation in that continent during the Early and Middle Miocene, and later dispersed into Eurasia, where they experienced a second radiation during the Middle to Late Miocene. Subsequently, from the Late Miocene onward, many hominoid genera went extinct and the geographic distribution of hominoids progressively shrank to equatorial Africa and southeastern Asia—with the remarkable exception of members of the human lineage, which radiated during the Plio-Pleistocene and ultimately dispersed throughout the globe. Nevertheless, many uncertainties still persist, particularly regarding the origin of hylobatids and crown hominids (Almécija et al., 2021).

1.2. Taxonomic scope and aims of this review

This review aims to synthesize current knowledge of Miocene ape diversity as well as to critically review their taxonomy, phylogeny, and paleobiogeography in light of the cladistic analyses published during the last decade, with emphasis on hylobatid and hominid origins. A first section with the necessary historical background is followed by an updated classification of Miocene apes and an analysis of their paleobiodiversity dynamics. Various controversial issues (the origin of hylobatids, the relationships of *Oreopithecus*, and the pongine–hominine divergence) are then discussed in the light of phylogenetic uncertainties highlighted by the contradictory cladistic results obtained from craniodental and postcranial data separately. We finally discuss future directions of research with emphasis on phylogenetic inference methods.

Besides Oligocene and Plio-Pleistocene apes, which are excluded from this review by definition, Early and Middle Miocene small-bodied catarrhines from Africa of uncertain affinities have also been left out. These include dendropithecids, which have been variously considered stem catarrhines (Harrison, 2010a, 2013; Nengo et al., 2017; Gilbert et al., 2020a) or stem hominoids (Rae, 1999, 2004; Zalmout et al., 2010; Alba et al., 2015; Begun, 2015; Rossie and Hill, 2018), because we consider that currently available evidence leans against considering them hominoids—albeit recognizing that more complete remains would be required to more conclusively assess their systematic position (see Section 3.5).

Two small-bodied genera from Eurasia of debated affinities have also been excluded. *Kapi ramnagarensis* Gilbert et al., 2020a, based on an isolated M_3 from the Middle Miocene (13.8–12.5 Ma) of India, was originally recovered as a stem hylobatid (Gilbert et al., 2020a), but subsequently reinterpreted as a pliopithecoid (Ji et al., 2022). Similarly, *Pliobates cataloniae* Alba et al., 2015 from the Middle/Late Miocene (11.6 Ma) of Spain, known on the basis of a partial skeleton, was originally considered a stem hominoid (Alba et al., 2015) but alternatively interpreted as a possible pliopithecoid (Benefit and McCrossin, 2015; Nengo et al., 2017; Gilbert et al., 2020a, 2020b). *Pliobates* displays a mosaic of plesiomorphic (stem catarrhine-like) and derived (crown hominoid-like) features (Alba et al., 2015; Bouchet et al., 2021), but work in progress by the authors supports the hypothesis that it is a stem catarrhine postcranially convergent with hominoids.

The hominin status of the Late Miocene genera *Ardipithecus* White et al., 1995 (~5.8–4.4 Ma; White et al., 1994, 2009; Haile-Selassie, 2001; Haile-Selassie et al., 2004, 2009), *Orrorin* Senut et al., 2001 (Pickford et al., 2002; Gommery and Senut, 2006; Almécija et al., 2013), and *Sahelanthropus* Brunet et al., 2002 (~7 Ma; Zollikofer et al., 2005; Guy et al., 2005; Macchiarelli et al., 2020; Daver et al., 2022) has sometimes been questioned (Wolpoff et al., 2002; Macchiarelli et al., 2020; Wood and Harrison, 2011). However, here these genera have been excluded based on the general view (e.g., Harcourt-Smith, 2010; Simpson, 2010, 2013; Pugh, 2022)—further supported by most recent cladistic analyses (Mongle et al., 2019; Pugh, 2020)—that they are early hominins.

2. Historical background

For the purposes of the present review, we distinguish three (slightly overlapping) phases of Miocene ape research: (1) from the pioneering works of earliest evolutionists until the 1970s; (2) a turmoil phase characterized by the molecular revolution and the cladistic paradigm shift (1960s–1970s); and (3) a modern phase, characterized by an acceleration of fossil discoveries and the regular application of computer-assisted methods of phylogenetic inference.

2.1. From Darwin to the Ramapithecus *debate*

Ever since Darwin (and *Dryopithecus*) More than a century and a half ago, evidence on extinct apes was very meager. However, largely based on Huxley’s (1863) studies, Darwin (1871) hypothesized an African origin for the human lineage. Given the scarcity of fossil apes known by then, Darwin (1871) recognized that the aforementioned hypothesis was little more than a well-informed guess. Indeed, the discovery of *Dryopithecus fontani* Lartet, 1856 in the Miocene of France already indicated that paleobiogeographic scenarios of ape and human evolution must be more complex than implied by the geographic distribution of extant apes. Darwin's (1871) hypothesis did not gain general acceptance during the following decades, owing to several factors besides the initial dearth of fossil humans in Africa. Even after the discovery of australopiths in South Africa (Dart, 1925), the infamous Piltdown hoax from England (Dawson and Smith Woodward, 1913, 1914) contributed—among other factors—to divert paleoanthropologists' attention from Africa (Tobias, 1985, 1992; Lewin, 1987). The Piltdown Man became eventually sidelined in the 1940s (Harrison and Howells, 2007), before the fraud was uncovered a decade later (Weiner et al., 1953a, 1953b). However, racist prejudices by European researchers arguably played a more important role in the initial dismissal of australopiths as early human ancestors (Lewin, 1987; Bowler, 1992).

<u>A massacre of Miocene apes</u> Fossil evidence from Europe, Asia, and Africa accumulated until Simons and Pilbeam (1965) published a highly influential taxonomic revision of fossil apes. During the 1960s, systematic thinking was dominated by Simpson's evolutionary systematics, which accepted paraphyletic and even polyphyletic taxa and was strongly biased in favor of taxonomic lumping—with the proliferation of genus and species names being debunked as 'typological thinking' (Cartmill, 2018). Following Mayr's (1950) influential contribution, Le Gros Clark (1955: 18) qualified "the somewhat arbitrary multiplication of genera and species" one of "the more vexing taxonomic problems in Primate paleontology". Simons (1963) adhered to such views and put them into practice in Simons and Pilbeam's (1965) revision, which showed a marked lumping tendency—a "massacre of Miocene ape

taxa” (Cartmill, 2018: 680). They shoehorned most fossil large-bodied hominoid remains into just seven species within the genus *Dryopithecus* Lartet, 1856, divided in three subgenera: *Dryopithecus* (*Proconsul*) Hopwood, 1933 from Africa, *Dryopithecus* (*Sivapithecus*) Pilgrim, 1910 from Asia, and *Dryopithecus* s.s. from Europe. Only *Gigantopithecus* von Koenigswald, 1935 (considered an aberrant late offshoot of dryopithecines) and *Ramapithecus* Lewis, 1934 (considered an early member of the human lineage) were spared by Simons and Pilbeam (1965) from being subsumed into *Dryopithecus*.

The rise and fall of *Ramapithecus* The notion that humans and apes (or at least African great apes) diverged from a common stock deep in the Miocene or even earlier was widespread during the 20th century well into the 1960s (e.g., Gregory, 1916, 1927; Keith, 1925; Osborn, 1930; Simpson, 1949; Leakey, 1953; Le Gros Clark, 1955, 1959)—albeit with widely divergent viewpoints between Gregory and Osborn (see review in Lewin, 1987). Following Lewis's (1934) original suggestion, Simons (1961, 1964) resurrected *Ramapithecus* as an early representative of the human lineage, contrasting to the previously prevailing view that it was a dryopithecine (Simpson, 1963). By that time, Leakey (1961) made a similar proposal for *Kenyapithecus wickeri* Leakey, 1961 from Africa, subsequently criticizing Simons and Pilbeam's (1965) proposed synonymy with *Ramapithecus punjabicus* (Pilgrim, 1910) as an "extreme example of taxonomic lumping” (Leakey, 1967: 155).

As characterized in the 1960s, *Ramapithecus* fulfilled the expectations for a fossil human relative (parabolic dental arcade, small upper incisors and canines, and orthognathous face; Simons, 1961, 1964). This contention led to the so-called “*Ramapithecus* debate,” which “had a profound and lasting effect on paleoanthropology” (Ward, 1997a: 270). According to Simons and Pilbeam (1965), *Ramapithecus* might have evolved from an early species of *Dryopithecus* and bounded the divergence between humans and apes to not later than 14

Ma, while extant African apes might have originated from later species of *Dryopithecus*, and orangutans from an even older dryopithecine ancestor back in the Oligocene. Pilbeam (1966, 1969) even hypothesized ancestor–descendant relationships between extant great ape genera and different Miocene ape species. As epitomized by the same author three decades later (Pilbeam, 1997: 13–14): “When the number of taxa was limited, the number of morphological characters small, phylogenetic analysis not rigorous, and when molecular clocks could safely be ignored, there were few impediments to tracing extant lineages well back into the Neogene, or even earlier.”

The status quo set forth by Simons and Pilbeam’s (1965), particularly regarding *Ramapithecus* (see also Pilbeam and Simons, 1965; Pilbeam, 1966), was contested by other paleontologists during the following decade (see below) but temporarily led to a mainstream consensus that drastically differs from current views on hominin origins. This is illustrated by Campbell and Bernor’s (1976) review of ape evolution, explicitly aimed to evaluate the place of origin of the human lineage. The views summarized by these authors still hold nowadays regarding hominoid origins in Africa and their subsequent dispersal into Eurasia ~16 Ma. However, their discussion about hominin origins was colored by the wide geographic range still attributed by then to *Ramapithecus*, concluding that “Dryopithecines in either Africa or Eurasia could have given rise to early Hominidae [currently Hominini]”, such that “neither continent can be precluded as the place of origin” (Campbell and Bernor, 1976: 441). Toward the end of the 1970s, Simons (1977) maintained unaltered his opinion about *Ramapithecus*. Pilbeam and colleagues (Pilbeam et al., 1977, 1980; Pilbeam, 1979) were more amenable to different interpretations—he subsequently admitted having doubts since the mid 1970s (Pilbeam, 1983)—but still highlighted the distinctiveness of *Ramapithecus*.

In contrast, other authors voiced multiple criticisms against the interpretation of *Ramapithecus* as an early member of the human lineage. *Ramapithecus wickeri* was resurrected for the African remains (Andrews, 1971) and it was shown that this species lacked a rounded, human-like dental arcade (Walker and Andrews, 1973; Frayer, 1976; Greenfield, 1978). Von Koenigswald (1973) resurrected *Kenyapithecus* Leakey, 1961 for this species and considered it an ape, while Greenfield (1974) argued that some remains from Asia also belonged to dryopithecines and criticized the purported status of *Ramapithecus* as a human ancestor. A more thorough rebuttal was provided by Frayer (1976), then Pilbeam (1978) acknowledged that *Ramapithecus* lacked a parabolic arcade, and finally Greenfield (1979) concluded that *Ramapithecus* is a junior subjective synonym of *Sivapithecus*—leading him to favor a late divergence for the human lineage (Greenfield, 1980). During the 1980s, only a few researchers (e.g., Kay, 1982; Kay and Simons, 1983) still supported 'hominid' status of these taxa despite accepting their synonymy.

2.2. The molecular revolution and the paradigm shift of cladistics

The molecular revolution Early studies of hominoid phylogeny based on serological data indicated that humans are more closely related to African apes than to orangutans (Zuckerkandl et al., 1960; Goodman, 1962a, 1962b, 1963). Although this was recognized by Simons and Pilbeam (1965), they did not see it as a challenge for an early divergence of the human lineage. Studies based on protein data subsequently supported a much more recent divergence between humans and African apes (Sarich and Wilson, 1967; Wilson and Sarich, 1969; Goodman et al., 1971; Goodman, 1974). However, paleoanthropologists were unwilling to accept such a late divergence (e.g., Simons, 1969; Leakey, 1970; Uzzell and Pilbeam, 1971) with just few exceptions (Washburn, 1967). Only the end of the

Ramapithecus debate enabled them to more widely reject the long held assumption that apes were closely related and the human lineage divergent (Pilbeam, 1983).

In the following decade, molecular studies conclusively settled the identity of humans' closest relatives. Initial results based on mitochondrial DNA (Ferris et al., 1981) were ambiguous, but further analyses based on proteins (Goodman et al., 1983) and DNA hybridization (Sibley and Ahlquist, 1984; Caccone and Powell, 1989; Sibley et al., 1990) strongly supported a sister-taxon relationship between humans and chimpanzees. This was confirmed by mitochondrial and nuclear DNA data during the late 1980s and 1990s (Miyamoto et al., 1987, 1988; Williams and Goodman, 1989; Goodman et al., 1990, 1994; Ruvolo 1994, 1997; Ruvolo et al. 1994; Arnason et al. 1996; Goodman, 1996). Current estimates based on molecular data indicate that humans and chimpanzees diverged sometime during the Late Miocene (~9–7 Ma; Perelman et al., 2011; Springer et al., 2012; Moorjani et al., 2016).

The paradigm shift of cladistics Besides the paleoanthropologist's reluctance to accept the conclusions of 'outsiders' from another discipline in front of the 'hard evidence' provided by fossils (see Lewin, 1987), several reasons explain the former's adherence to an early divergence of humans until the 1970s. First, the molecular revolution took several decades to complete, such that the closer relationship between humans and chimpanzees did not became firmly established until the 1980s (see above). Second, during the 1960s and early 1970s, paleoanthropologists lacked the necessary analytical methods to rigorously infer phylogenetic relationships. In the 1960s and 1970s, most paleoanthropologists were still anchored to the Simpsonian systematic paradigm, which allowed for paraphyletic taxa as long as they were based on structural grades (e.g., Simpson, 1945). For this reason, Simons and Pilbeam (1965) favored the traditional division between pongids and hominids

(Simpson, 1945, 1963) despite recognizing that humans were more closely related to African apes than orangutans.

The conceptual cladistic toolkit was available since the publication of Hennig's (1966) book in English and molecular biologists pioneered the introduction of cladistic ideas in anthropology (Goodman, 1996), as illustrated by their tendency to redefine the content of the Hominidae (e.g., Goodman, 1963). However, it was not until the early 1970s that cladistics started to gain ground in vertebrate paleontology, largely thanks to the work of paleontologists from the American Museum of Natural History (AMNH) in New York (e.g., Nelson, 1972; see review in Cartmill, 2018). In turn, the somewhat slower diffusion of the cladistic paradigm in paleoanthropology during the late 1970s was promoted by Eric Delson, by then already affiliated to the AMNH, and some of his colleagues there (Delson, 1977; Delson et al., 1977).

In retrospect, the paradigm shift from Simpsonian to Hennigian systematics throughout the 1970s and 1980s was relatively rapid, according to Cartmill (2018) because the cladistic revolution was mostly 'esthetic' (sensu Kuhn, 1970)—i.e., not dictated by new facts or data but by disagreements as to how phylogeny should be reflected in the classifications. Certainly, unlike the molecular revolution in phylogenetic inference, the cladistic paradigm shift was not driven by wealth of new data. Nevertheless, Cartmill's (2018) account downplays the profound influence that the cladistic paradigm had in the methods and practice of morphology-based phylogenetic inference. Although many aspects of cladistic classification are debatable (e.g., Mayr, 1974), the spread of cladistic analysis had much deeper implications by prompting an explicit recognition that phylogenetic relationships must be determined on the basis of shared-derived features (synapomorphies) as opposed to shared-primitive characters (symplesiomorphies).

Cartmill (2018) argued that many previous systematists implicitly accepted that only synapomorphies should be considered for assessing phylogeny. However, this was not the case for most paleoanthropologists during the 1960s and early 1970s—as explicitly admitted by Pilbeam (1986). This is also evident from the pioneering work of Delson and Andrews (1975: 405), which aimed to assess the "phyletic relationships among Old World higher primates in the light of the "cladistic" methodology." These authors had to explain that "only those linkages based on shared derived ("advanced," apomorphous) characters reflect true phyletic relationships" (Delson and Andrews, 1975: 406), which denotes that this was not yet clearly perceived by then. This is even more clear-cut from Delson's (1977) didactic effort to explain to the paleoanthropological community the concepts, methods, merits, and pitfalls of cladistics. In turn, Delson et al. (1977) put theory into practice by applying the cladistic methodology to apes and humans. These contributions by Delson and colleagues played a key role in promoting the application of cladistic principles and methods to paleoanthropology despite being still influenced by the then prevailing paradigm that considered *Ramapithecus* an early member of the human lineage. For example, Delson (1977) adopted a very wide definition of the Hominidae (including apes and humans) but still classified humans and African apes in different subfamilies (Ponginae and Homininae; see also Szalay and Delson, 1979). In any event, the spread of cladistics promoted a more thorough evaluation of morphological evidence (both craniodental and postcranial) in the following decades.

2.3. The modern phase: Cladistics at its peak and the Sivapithecus *dilemma*

<u>*Sivapithecus* and the beginning of the modern phase</u> The mid-1970s and 1980s witnessed the description of much more complete cranial remains of Miocene apes (Tekkaya, 1974;

Kretzoi, 1975; de Bonis and Melentis, 1978; Andrews and Tekkaya, 1980; Wu et al., 1981, 1982, 1983, 1984; Pilbeam, 1982; Ishida et al., 1984; Leakey and Walker, 1985; Leakey and Leakey, 1986a, 1986b; Teaford et al., 1988; Zhang et al., 1988) than in the preceding decades—leading to the appreciation that Miocene apes were far more diverse than previously considered (Pilbeam, 1986). Campbell and Bernor's (1976) attempt of paleobiogeographic synthesis soon became outdated but was followed by Bernor's (1983) renewed efforts, which could not yet include the determinant discovery of a partial cranium of *Sivapithecus* that showed many orangutan-like features (Pilbeam, 1982; see also Andrews, 1982). By then, persuaded by similarities between material from Turkey (now in *Ankarapithecus* Ozansoy, 1957) and *Sivapithecus* (Andrews and Tekkaya, 1980), Andrews had also independently arrived to the conclusion that the latter was an orangutan relative and that the molecular divergence times were correct (Andrews and Cronin, 1982).

The discovery of the *Sivapithecus* cranium led to many new lines of research (Ward, 1997a), such as a detailed anatomical analysis of hominoid subnasal morphology (Ward and Kimbel, 1983; Ward and Pilbeam, 1983; McCollum et al., 1993; McCollum and Ward, 1997). These and other analyses led to the recognition of *Sivapithecus* as the Miocene ape most clearly related to orangutans (Preuss, 1982; Ward and Kimbel, 1983; Ward and Pilbeam, 1983; Pilbeam and Smith, 1984; Pilbeam, 1985; Shea, 1985; Ward and Brown, 1986; Brown and Ward, 1988). By this time, the synonymy between *Ramapithecus* and *Sivapithecus* became widely accepted (Andrews, 1982; Andrews and Cronin, 1982; Kay, 1982; Lipson and Pilbeam, 1982) and paleoanthropologists finally embraced the molecular-based late divergence between humans and chimpanzees. As noted by Lewin (1987) and Pilbeam (1997), besides the fossil evidence itself this shift in opinion about *Ramapithecus* was deeply influenced by the molecular data, even if this was not widely acknowledged at the time (but see Greenfield, 1980).

The establishment of a late-diverging chimpanzee–human clade thus prompted a critical rethinking of the available morphological evidence, while *Sivapithecus* served to calibrate the hominoid molecular clock. The confluence of these factors with the spread of cladistics gave rise to a new consensus in hominoid phylogenetics during the 1980s (Andrews and Cronin, 1982; Pilbeam, 1984) and a brand-new phase of interpretation of Miocene ape evolution. Thus, since the mid-1980s, most researchers (e.g., Andrews, 1985, 1992; Alba, 2012; Fleagle, 2013; Groves, 2017; Almécija et al., 2021), only with few exceptions (e.g., White, 2002; Tuttle, 2014), have distinguished only two extant hominoid families: Hylobatidae and Hominidae, with the latter subdivided into Ponginae and Homininae. The former distinction (e.g., Simpson, 1945) between Pongidae (for apes or great apes) and Hominidae (for humans) became untenable because, from a cladistic viewpoint, paraphyletic groups are unnatural.

Nevertheless, as researchers struggled to make compatible the molecular data with the morphological evidence of extant hominoids, this consensus temporarily led to a plethora of widely divergent morphology-based cladistic hypotheses supporting the monophyly of either all great apes (Kluge, 1983), African apes (Andrews, 1987; Andrews and Martin, 1987a), humans and chimpanzees (Groves, 1986), or even humans and orangutans (Schwartz, 1984a, 1984b). This is attributable to several factors: (1) some paleoanthropologists had yet to embrace the view that molecular phylogenies were more reliable than morphology-based ones; (2) the implementation of maximum-parsimony computer algorithms for cladistic analysis was still underway; (3) there is an inherent arbitrariness in the selection of characters and the definition of character states (Pilbeam and Young, 2001; Cartmill, 2018);

and (4) there is a lot of ‘phylogenetic noise’ caused by homoplasy (false homology; e.g., Larson, 1998). While the two first problems were solved during the next decade, the latter two issues have proven more enduring and difficult to resolve.

The *Sivapithecus* dilemma Despite difficulties in retrieving the molecular phylogeny of hominoids based on morphological data, the resolution of the *Ramapithecus* debate and the discovery of the *Sivapithecus* cranium soon led to renewed optimism. During the 1980s, it seemed as if a new synthesis of Miocene ape evolution based on the “judicious use of paleontological and neontological data sets” (Pilbeam, 1985: 51) was going to emerge as new fossils were discovered and carefully analyzed. Then, in the blink of an eye, the view that *Sivapithecus* is a member of the orangutan clade was questioned owing to the discovery of new postcranial remains of this taxon. In particular, two humeri of *Sivapithecus* indicated that it displayed pronograde locomotor behaviors unlike those of modern hominoids (Pilbeam et al., 1990)—as was further corroborated by additional postcranials during the following decades (Madar et al., 2002; Morgan et al., 2015). More complete postcranial material of other Miocene apes was also discovered throughout the 1980s and 1990s (Walker and Pickford, 1983; Ward et al., 1993; Moyà-Solà and Köhler, 1996), indicating that Early Miocene apes (with some possible exceptions; Gebo et al., 1997) were predominantly pronograde (Ward, 1993; Ward et al., 1993), whereas at least some Late Miocene apes appeared suspensory (Moyà-Solà and Köhler, 1996).

In the early 1990s, the consensus emerging from the previous decade was probably too immature to readily comprehend the implications of a Miocene ape combining an orangutan-like cranium with primitive postcranials closely resembling those of the Early Miocene taxa. No matter how *Sivapithecus* was interpreted from a phylogenetic viewpoint, it was evident there must be a considerable amount of homoplasy involved—implying an independent evolution of its orangutan-like cranial morphology, an evolutionary reversal of its postcranium, or the independent acquisition of postcranial similarities by crown hominoids. This conundrum was dubbed the '*Sivapithecus* dilemma' (Pilbeam and Young, 2001; Young, 2003), and has ever since permeated debates about Miocene ape phylogeny.

Andrews (1992) reviewed the Miocene apes known by then from a cladistic perspective and favored the view that *Sivapithecus* was closely related to *Pongo* Lacépède, 1799, which is the interpretation favored by most subsequent authors until the present (e.g., Ward, 1997a, 2015; Larson, 1998; Kelley, 2002; Alba, 2012; Begun, 2015; Pugh, 2022). However, during the 1990s an alternative interpretation was championed by Pilbeam (1996, 1997), who reacted to the *Sivapithecus* dilemma by closely adhering to the postcranial evidence—incidentally qualifying the profession as "craniophilic" (Pilbeam, 1996: 162). On this basis, he concluded that most Miocene apes—including Middle and Late Miocene ones, such as *Sivapithecus*, and with only the exception of *Oreopithecus* Gervais, 1872 and maybe some dryopithecines—were most likely 'archaic' hominoids that diverged before the radiation of hominoids of 'modern aspect'.

Pilbeam's (1996) interpretation of the postcranial similarities between hylobatids and hominids as synapomorphic was a logical consequence of accepting the cladistic paradigm established during the 1980s—contrasting with the prevailing view during the 1950s–1970s, according to which such features would have been developed independently a number of times in different lineages (see discussion in Harrison and Rook, 1997). Similar views were expressed by the latter authors, who referred to previous papers by Harrison (1986, 1987a, 1987b, 1991) when concluding that "the postcranial features and character complexes shared by extant hominoids are so detailed and so pervasive that they are extremely unlikely to be the product of convergent evolution" (Harrison and Rook, 1997: 331). This quotation illustrates that that adoption of the cladistic paradigm in paleoanthropology during the 1980s implied an increased reliance on postcranial features, which some researchers were reluctant to abandon in favor of the old-fashioned greater reliance on craniodental remains.

The *Sivapithecus* dilemma was eventually solved in favor of postcranial homoplasy following a highly influential paper by Larson (1998), who advocated the plausibility of many purported postcranial synapomorphies of hominoids having evolved in parallel multiple times along the various extant lineages. This claim was still a matter of intense debate during the 2000s, including various attempts to measure whether the craniodental or the postcranial data displayed a greater degree of homoplasy (Finarelli and Clyde, 2004; Young, 2005). In any event, the discoveries made during the last two decades (e.g., Moyà-Solà et al., 2004) have failed to support Pilbeam’s (1996, 1997) prediction that the discovery of additional skeletons would strengthen the view that most Miocene apes are unrelated to the modern radiation. Rather the contrary, Larson’s (1998) views have been vindicated further, supporting the contention that many postcranial similarities among extant ape lineages are indeed homoplastic and that reconstructing last common ancestors based on extant apes alone is totally unreliable (Alba, 2012; Ward, 2015; Almécija et al., 2021).

Cladistics in the Computer Age Despite having the problem of postcranial homoplasy in mind, since the 1990s paleoanthropologists have increasingly performed morphology-based cladistic analyses based on both craniodental and postcranial characters to decipher the phylogenetic relationships among the ever-increasing list of Miocene ape taxa. These analyses have been prompted by the important discoveries and reanalyses of Miocene ape crania and postcrania that have taken place during the last three decades (e.g., de Bonis et al., 1990; de Bonis and Koufos, 1993; Moyà-Solà and Köhler, 1993, 1996; Gebo et al., 1997; Nakatsukasa et al., 1998; Ward et al., 1999; Kordos and Begun, 2001; Moyà-Solà et al., 2004, 2009a, 2009b; Kunimatsu et al., 2007; Suwa et al., 2007; Böhme et al., 2019). The more or less informal cladistic attempts of the early 1990s (Begun, 1992a; Moyà-Solà and Köhler, 1995) were soon replaced by formal analyses based on larger taxon-character matrices and performed with the aid of computer algorithms (Begun, 1994, 1995; Shoshani et al., 1996; Begun et al., 1997, 2012; Cameron, 1997a; Finarelli and Clyde, 2004; Rossie and MacLatchy, 2005; Zalmout et al., 2010; Stevens et al., 2013; Alba et al., 2015; Nengo et al., 2017; Rossie and Hill, 2018; Gilbert et al., 2020a; Pugh, 2022; Ji et al., 2022).

The cladistic analyses performed during the 1990s started to find support for the chimpanzee–human clade on morphological grounds (e.g., Begun, 1992a; Shoshani et al., 1996; Begun et al., 1997) and the debate about human origins switched toward the reconstruction of the chimpanzee–human last common ancestor (for recent reviews, see Andrews, 2020 and Almécija et al., 2021). However, it soon became obvious that uncertainties about Miocene ape phylogeny hindered the resolution of this question, as determining the ancestral hominin morphotype cannot be properly done without the aid of the Miocene ape fossil record (e.g., Andrews and Harrison, 2005; Andrews, 2020; Almécija et al., 2021).

The changing views on Miocene ape phylogenetic relationships have also given rise to new paleobiogeographic scenarios. In the late 1990s, paleobiogeographic discussion was focused on vicariance, either by assessing alternative phylogenetic hypotheses or by explicitly favoring one of these hypotheses (Begun, 1994, 1995; Agustí et al., 1996; Andrews and Bernor, 1999; Begun et al., 1997). In the 2000s, the recognition that *Kenyapithecus* was recorded both in Africa and Turkey during the Middle Miocene (Kelley et al., 2008) deserves particular mention, as it has interesting paleobiogeographic implications for hominoid dispersal events (Andrews and Kelley, 2007; Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2011; Alba, 2012). In any case, given the diverging opinions on Miocene ape phylogeny, several competing paleobiogeographic scenarios are still subject to ongoing debates (Almécija et al., 2021).

3. Systematics of Miocene apes

Systematics classifies organisms based on evolutionary relationships but has also a utilitarian function so that there is no single true classification to be discovered (Benton, 2000)—see Supplementary Online Material (SOM) S1.1 for further details. The classification of Miocene apes presented in this article (Tables 1 and 2) relies on the use of Linnean ranks and other the provisions of the International Code of Zoological Nomenclature; ICZN, 1999). Unless we abandon Linnean nomenclature (see SOM S1.2 for further discussion), paraphyly is ultimately inescapable at the species and genus ranks (Sarmiento et al., 2002), but our systematic scheme assumes that the distinguished family-group taxa are monophyletic (i.e., clades). If the paraphyletic status suspected for some of these taxa was more conclusively supported in the future, our classification should be changed accordingly. Even within the framework of phylogenetic systematics (which aims to faithfully reflect phylogeny and avoid paraphyletic taxa), constructing a classification is a subjective exercise that depends on the taxonomist’s decisions about what phylogenetic hypotheses are best supported, as well as which clades must be denoted as taxa and what ranks should be attributed to each. Therefore, we do not expect our systematic proposal to be uncritically adopted by other scholars. We rather conceive it as a utilitarian construct to transmit our interpretation of current knowledge about Miocene ape evolution.

Given that the true phylogeny of any group is scientifically unknowable, phylogenetic inference plays a central role in systematics. In the case of Miocene apes, most studies have used cladistic analysis of morphological data based on maximum parsimony to test competing phylogenetic hypotheses (for the epistemological basis of cladistics, see SOM S1.3). Only a few studies have relied on other methods, including Finarelli and Clyde's (2004) analysis based on stratocladistics—an alternative method of phylogenetic inference that combines morphological and chronostratigraphic data (Fisher, 2008; see SOM S1.4)—and the most recent exploration of Bayesian analyses (see SOM S1.5) by Pugh (2022). We mostly relied on the results of recent cladistic analyses (Nengo et al., 2017: Fig. 5; Gilbert et al., 2020a: Fig. 4; Pugh, 2022: Fig. 5), coupled with the synthetic cladogram hypothesized by Gilbert et al. (2020b: Fig. 17.1) and the cladistic results by other authors (Begun et al., 1997: Fig. 1, 2012: Fig. 9; Alba et al., 2015: Fig. 8; Rossie and Hill, 2018: Fig. 5; Ji et al., 2022: Fig. 11). The first three recent cladistic analyses mentioned above were performed by the same authors, and hence do not represent independent attempts at Miocene ape phylogenetic reconstruction. However, Pugh's (2022) analyses were more focused on hominids and hence are more comprehensive regarding the phylogenetic relationships inferred for this group. The phylogenetic and nomenclatural rationale underpinning our classification of Miocene apes, together with taxonomic remarks for particular taxa, are provided below (see SOM S2 for nomenclatural remarks).

3.1. A stem-based definition of the Hominoidea

Since Simpson's (1945) seminal paper, most authors have classified apes and humans within a single superfamily Hominoidea (e.g., Szalay and Delson, 1979; Groves, 1986), with only a few exceptions (e.g., Delson and Andrews, 1975; Thenius, 1981). Simpson (1945) distinguished two families (Pongidae for apes and Hominidae for humans) but other authors restricted pongids to the great apes and distinguished the Hylobatidae for lesser apes (e.g., Fiedler, 1956). The latter scheme was widely used until the molecular revolution led to an expanded concept of the Hominidae including the African apes (Goodman, 1974; Andrews and Cronin, 1982), all the great apes (Goodman, 1974; Schwartz et al., 1978; Andrews, 1985; Groves, 1986), or even both lesser and great apes (Delson and Andrews, 1975; Delson 1977; Szalay and Delson, 1979; Goodman et al., 1990, 1998; Goodman, 1996). Groves' (1986) classification of extant hominoids in two families (Hylobatidae and Hominidae) and hominids in two subfamilies (Ponginae and Homininae) has been very influential, being subsequently adopted by most paleoanthropologists (Andrews, 1992; Andrews et al., 1996; Shoshani et al., 1996; Delson, 2000; Wood and Richmond, 2000; Begun, 2002a, 2010; Kelley, 2002; Ward and Duren, 2002; Wood and Harrison, 2011; Alba, 2012; Fleagle, 2013; Almécija et al., 2021). The traditional restricted usage of the Hominidae has been favored recently by several researchers (e.g., White, 2002; White et al., 2009; Tuttle, 2014; Schwartz, 2015). However, such an arrangement can only prevent paraphyly by distinguishing gorillas and chimpanzees at the family rank (i.e., Gorillidae Frechkop, 1943 and Panidae Delson, 1977, respectively; e.g., Schwartz, 1986), which is not favored here.

In accordance with many previous contributions (e.g., Andrews, 1992; Alba, 2012; Nengo et al., 2017; Gilbert et al., 2020a; Almécija et al., 2021), here we adopt a stem-based definition of the Hominoidea (Fig. 1) and other included family-group taxa (families, subfamilies, and tribes; see SOM S1.6 for further details). This implies that taxa are defined as putatively monophyletic groups on the basis of the subtaxa included within them, with extant taxa defining the crown group and the extinct members equally related to all of them constituting the stem lineage—for the concepts of 'total group,' 'crown group,' and 'stem lineage', see Figure 1 and SOM S1.7. Thus, crown hominoids are defined as the clade composed by hylobatids and hominids, whereas stem hominoids constitute a paraphyletic assemblage of extinct taxa more closely related to both hylobatids and hominids than to the extant sister taxon of hominoids (i.e., cercopithecoids). In turn, crown hominids include pongines and hominines, whereas stem hominids include crown hominoids more closely related to both pongines and hominines than to hylobatids.

The theoretical distinction between hominoids and stem catarrhines is straightforward but determining the systematic status of many extinct catarrhines is complicated by uncertainties regarding their branching order relative to cercopithecoids (see Section 1.2). The same applies to the distinction between stem and crown hominoids. Begun et al. (1997) and Begun (2001) informally employed the terms 'eohominoids' and 'euhominoids' to distinguish what Pilbeam (1996, 1997) termed hominoids of 'archaic aspect' and 'modern aspect,' respectively. This distinction was subsequently formalized by Begun (2009, 2015) by distinguishing the superfamilies Proconsuloidea and Hominoidea within a magnafamily Hominidea. Indeed, these terms are equivalent to stem and crown hominoids, respectively, and hence unnecessary (Alba, 2012). A distinction of a superfamily Proconsuloidea would only make sense if the included taxa are considered stem catarrhines preceding the cercopithecoid-hominoid split (Harrison, 2002, 2010a). However, the latter view is at odds with the results of formal cladistic analyses (e.g., Begun et al., 1997, 2012; Zalmout et al., 2010; Stevens et al., 2013; Alba et al., 2015; Nengo et al., 2017; Rossie and Hill, 2018; Gilbert et al., 2020a) and not followed here.

Several family-group taxa (of questionable monophyly) have been recently distinguished within the Hominoidea at the family and/or subfamily rank (Alba, 2012; Fleagle, 2013; Nengo et al., 2017; Gilbert et al., 2020b). Here we follow Gilbert et al. (2020b) in distinguishing three families of putative stem hominoids (Proconsulidae Leakey, 1963, Afropithecidae Andrews, 1992, and Nyanzapithecidae Harrison, 2002), which correspond to the three subfamilies formerly distinguished by Harrison (2002, 2010a) within the Proconsuloidea. Some cladistic results (Nengo et al., 2017, Gilbert et al., 2020a) support a basalmost divergence of proconsulids within the hominoid stem lineage, followed by a clade including the paraphyletic Afropithecidae and the Nyanzapithecidae, sister to crown hominoids (Fig. 2a). On this basis, Gilbert et al. (2020b) depicted afropithecids and nyanzapithecids in a trichotomy with crown hominoids. In contrast, Rossie and Hill (2018) recovered a basalmost divergence of nyanzapithecids (together with dendropithecids), followed by the paraphyletic proconsulids and finally afropithecids as the sister-taxon of crown hominoids (Fig. 2b). Most recently, Pugh (2022) supported the more basal status of equatorine afropithecids compared with hylobatids. However, the fact that proconsulids were employed as an outgroup (i.e., assumed a priori to be more basal than afropithecids) and that neither afropithecines nor nyanzapithecids were included in Pugh's (2022) analyses makes it uncertain the early branching topology and putative monophyly of stem hominoid families.

Both proconsulids and nyanzapithecids are represented among the earliest known hominoids from the Oligocene of Africa. Proconsulids are recorded by *Kamoyapithecus hamiltoni* Leakey et al., 1995 from Kenya, ~28–24 Ma, formerly interpreted as a stem catarrhine (Harrison, 2010a, 2013; Zalmout et al., 2010; Stevens et al., 2013) but already showing the distinctive canine morphology of *Proconsul* (Hammond et al., 2019). Nyanzapithecids are first recorded by *Rukwapithecus fleaglei* Stevens et al., 2013 from Tanzania at 25.2 Ma and an indeterminate species that co-occurs with *Ka. hamiltoni* (Hammond et al., 2019). Although these Oligocene hominoids are only recorded from scarce dentognathic material, recent cladistic analyses supported the nyanzapithecid affinities of *Rukwapithecus* (Nengo et al., 2017; Gilbert et al., 2020a). Together with the fact that afropithecids are not recorded until several million years later, from the Early Miocene, these results support an early diversification of stem hominoids well within the Oligocene—in rough agreement with average estimates of the cercopithecoid–hominoid divergence between 32 Ma (Perelman et al., 2011) and 25 Ma (Springer et al., 2012)—as well as a less basal status for afropithecids. Thus, although Nengo et al. (2017) and Gilbert et al. (2020a) recovered afropithecids as paraphyletic, we prefer to keep them as a distinct family until their phylogenetic relationships are clarified further.

3.2. Proconsulidae

Proconsulids include multiple species from the Early Miocene of Kenya and Uganda (~21–16 Ma; Tables 2 and 3). The members of this family show a remarkable body mass disparity (from ~5 to 50 kg; Ruff et al., 1989; Rafferty et al., 1995; Harrison, 2010a) and retain multiple plesiomorphic features compared with crown hominoids (Harrison, 2010a; Begun, 2015), such as well-developed molar cingula, an open palatine fenestra, a short tubular ectotympanic with a deep V-shaped notch in the external margin, and a deep subarcuate fossa. Postcranially, they display a mosaic of primitive (mostly platyrrhine-like) and derived (hominoid-like) postcranial features, overall indicative of a pronograde body plan suggestive of generalized arboreal quadrupedalism and powerful-grasping cautious climbing (Rose, 1983, 1997; Ward, 1993, 1997b, 2015; Ward et al., 1993; Kelley, 1997; Walker, 1997; Harrison, 2010a; Daver and Nakatsukasa, 2015). The hominoid status of proconsulids is highlighted by the lack of an external tail (Ward et al., 1991; Kelley, 1997; Nakatsukasa et al., 2003), although they display other more subtle features derived toward the hominoid condition, such as an incipient distal radioulnar diarthrosis (Daver and Nakatsukasa, 2015). Proconsulids display a lower degree of encephalization than great apes (being more comparable in this regard to extant hylobatids; Walker et al., 1983; Alba, 2010) but perhaps—based on crown formation time—already possessed a somewhat slower life history than cercopithecoids (Kelley, 1997, 2004; Kelley and Smith, 2003).

We recognize the genus *Ekembo* McNulty et al., 2015 for two species—*Ekembo nyanzae* (Le Gros Clark and Leakey, 1950) and *Ekembo heseloni* (Walker et al., 1993)—formerly included in *Proconsul* (e.g., Harrison, 2010a). According to McNulty et al. (2015), *Ekembo* displays some derived features relative to *Proconsul*, but thus far cladistic analyses have not recovered the two genera as distinct subclades (Nengo et al., 2017; Rossie and Hill, 2018; Gilbert et al., 2020a). However, it is noteworthy that Pugh (2022) refrained from analyzing the two *Ekembo* species separately because of the difficulties to delimit their respective hypodigms. We also follow most previous authors (MacLatchy and Rossie, 2005; Harrison and Andrews, 2009; Harrison, 2010a, McNulty et al., 2015) in considering that *Ugandapithecus* Senut et al., 2000, originally erected for *Proconsul major* Le Gros Clark and Leakey, 1950 and subsequently expanded by some authors (Pickford and Kunimatsu, 2005; Pickford et al., 2009a) to include *Proconsul meswae* Harrison and Andrews, 2009, *Proconsul gitongai* (Pickford and Kunimatsu, 2005), and *Proconsul legetetensis* (Pickford et al., 2009a), is a junior subjective synonym of *Proconsul*. However, *Ugandapithecus* remains potentially available for *P. major* if other species are eventually shown to be more closely related to it than to *Proconsul africanus* Hopwood, 1933. Moreover, following Pickford et al. (2020, 2021) we find the synonymy favored by McNulty et al. (2015) between *P. legetetensis* (originally described in *Ugandapithecus*) and *P. major* unconvincing (as they remarked the distinctiveness of the holotype mandible) and tentatively prefer to keep the species distinct.

We also include in this family the genus *Kalepithecus* Harrison, 1988—whose type species, *Kalepithecus songhorensis* (Andrews, 1979), was left as incertae sedis by Harrison (2010a)—because most recent analyses (Nengo et al., 2017; Gilbert et al., 2020a) have supported the proconsulid affinities previously noted for this species (Rae, 1997). *Kalepithecus* differs from small-bodied stem catarrhines in the inferiorly broader nasal aperture and relatively deep clivus (Harrison, 1988, 2002, 2010a; Rae, 1997), supporting its hominoid status. Proconsulids may be thus more diverse than currently recognized, as it seems plausible that other small-bodied catarrhines from Africa, mostly known from dentognathic material, might ultimately be shown to belong to this family when more complete cranial material becomes available.

3.3. Nyanzapithecidae and Oreopithecini

<u>Nyanzapithecidae</u> The Miocene species and genera included here in the Nyanzapithecidae follow Harrison's (2010a) concept of Nyanzapithecinae with the addition of *Nyanzapithecus alesi* Nengo et al., 2017 and *Samburupithecus kiptalami* Ishida and Pickford, 1997. The latter species, known from the Late Miocene (~8.5 Ma) of Kenya on the basis of a maxillary fragment, only slightly postdates the otherwise last occurrence of the group at ~10 Ma (Kunimatsu et al., 2007) but is much larger than other nyanzapithecid described genera (~10–15 kg for males; Harrison, 2010a; Fleagle, 2013). *Samburupithecus* Ishida and Pickford, 1997 was originally considered a stem hominine (Ishida et al., 1984; Andrews, 1992; Ishida and Pickford, 1997; Pickford and Ishida, 1998) but subsequently interpreted by as a late surviving stem hominoid by other authors (Begun, 2001, 2013, 2015; Olejniczak et al., 2009; Almécija et al., 2012; Begun et al., 2012)—see discussion in Harrison (2010a). Pugh's (2022) analyses linked *Samburupithecus* with *Oreopithecus* based on dental similarities shared with nyanzapithecids. The nyanzapithecid-like dental features of *Samburupithecus* had been already noted by Harrison (2010a), who nevertheless left the genus as incertae sedis. Based on the meager evidence available, we consider that an inclusion of *Samburupithecus* within the Nyanzapithecidae is warranted. Other large nyanzapithecids are recorded in Africa but remain

indeterminate due to the scarcity of material. They include Early/Late Miocene (~16 Ma) remains from South Africa that represent the southernmost record of Miocene apes (Senut et al., 1997; Harrison, 2010a). This species might be related to the younger and somewhat smaller nyanzapithecid from the Middle Miocene of Kenya (Fort Ternan and Kapsibor, 13.7 Ma; Leakey, 1968; Harrison, 1986, 1992), which likely represents a new genus and species (Harrison, 2010a).

Nyanzapithecids possess a distinctive dental morphology (Harrison, 2013; Nengo et al., 2017; Rossie and Cote, 2002) and, based on *Nyanzapithecus* Harrison, 1986 and *Turkanapithecus* Leakey and Leakey, 1986b, also cranial similarities with hylobatids, which are generally interpreted as homoplastic (Nengo et al., 2017). *Nyanzapithecus* displays a fully ossified external acoustic meatus (Nengo et al., 2017), which appears more extant-catarrhine-like than in *Ekembo* and stem cercopithecoids—despite being fully ossified, in the latter taxa the ectotympanic is shorter and lacks a completely closed ventral tip (Alba et al., 2015), implying some degree of independent evolution of ectotympanic ossification, as previously suggested (Begun, 2002b). The postcranial morphology of nyanzapithecids suggests that they were above-branch, pronograde quadrupeds broadly similar to proconsulids, but perhaps with enhanced climbing abilities (Harrison, 2010a).

Recent cladistic analyses have supported nyanzapithecids as more basal than proconsulids (Rossie and Hill, 2018) or as less basal than both proconsulids and afropithecids (Nengo et al., 2017; Gilbert et al., 2020a)—see Figure 2. We follow Harrison (2010a) in considering that *Xenopithecus* Hopwood, 1933 is distinct from *Proconsul* (see also Pickford and Kunimatsu, 2005) and shows nyanzapithecid affinities based on dental morphology. *Mabokopithecus* von Koenigswald, 1969 shows more unambiguous nyanzapithecid affinities, and while some authors have favored a generic distinction from *Nyanzapithecus* (Benefit et al., 1998), Harrison

(2002, 2010a) tentatively supported their synonymy—although he did not formalize it, pending the description of unpublished material. As remarked by Harrison (2002, 2010a), *Mabokopithecus* has priority over *Nyanzapithecus*, so the species currently included in the latter genus might have to be eventually transferred to the former. In any event, this would not affect the validity of family-group taxa based on *Nyanzapithecus*. Pending further clarification of the internal phylogenetic relationships of the Nyanzapithecidae and their possible link with *Oreopithecus* (see below), we refrain from distinguishing nyanzapithecid subfamilies.

Oreopithecini *Oreopithecus*, from the Late Miocene of Europe (~8–7 Ma; Rook et al., 2011), is the most completely preserved Miocene ape, being known from dental, cranial, and postcranial remains. However, due to a unique combination of features, the phylogenetic relationships of *Oreopithecus* have been controversial for a century and a half (see review in Delson, 1986). *Oreopithecus* has been recognized as a hominoid mostly based on its derived postcranium (Harrison, 1987a, 1991; Sarmiento, 1987; Harrison and Rook, 1997), being considered a close relative of nyanzapithecids from Africa (Harrison, 1986, 1987a; Benefit et al., 1998; Benefit and McCrossin, 2001; Rossie and Cote, 2022) or a descendent of dryopithecines from Europe (Harrison and Rook, 1997; Moyà-Solà and Köhler, 1997).

Former cladistic analyses recovered a basalmost stem hominid position for *Oreopithecus* (Begun et al., 1997, 2012), but more recent ones supported its nyanzapithecid affinities (Nengo et al., 2007; Gilbert et al., 2020a) and hinted at a possible relationship with *Samburupithecus* (Pugh, 2022). The combined results of these cladistic analyses, largely driven by dental similarities, could justify the inclusion of *Oreopithecus* in the Nyanzapithecidae—which, as noted by Gilbert et al. (2020b), would imply that the correct name for the family is Oreopithecidae Schwalbe, 1915, as already used for these taxa in previous decades (e.g., Harrison, 1986, 1987a; Benefit et al., 1998; Benefit and McCrossin, 2001). Here we take a conservative approach and refrain from formalizing the inclusion of *Oreopithecus* in the Nyanzapithecidae, classifying it instead in a tribe of its own, which is left as incertae sedis within the Hominoidea (Gilbert et al., 2020b).

Oreopithecus is larger-bodied (>30 kg in males; Jungers, 1987) than most nyanzapithecids except Nyanzapithecidae nov. from Fort Ternan and Kapsibor as well as *Samburupithecus*. The postcranial material of *Oreopithecus* further differs from the scarce postcranials available for nyanzapithecids by possessing multiple adaptations for antipronograde positional behaviors (Harrison, 1987a, 1991; Jungers, 1987; Sarmiento, 1987), which have been subject to different interpretations. Some features have been interpreted as indicative of terrestrial bipedalism (Straus, 1963; Köhler and Moyà-Solà, 1997; Rook et al., 1999; Moyà-Solà et al., 2005a), in agreement with the possession of human-like hand proportions suitable for refined manipulation (Moyà-Solà et al., 1999a, 2005a; Almécija et al., 2014). In contrast, other authors have emphasized the possession of adaptations for vertical climbing (Sarmiento, 1987; Sarmiento and Marcus, 2000; Hammond et al., 2020) and suspensory behaviors (Jungers, 1987; Harrison, 1991; Harrison and Rook, 1997; Susman, 2004; Begun, 2007; Deane and Begun, 2008; Russo and Shapiro, 2013). Part of the debate around the locomotion of *Oreopithecus* stems from focusing on artificial locomotor categories instead of positional repertoires with different behaviors displayed at varying frequencies. The lower torso of *Oreopithecus* lacks features related to stabilization during bipedalism as well as the stiffness characteristic of extant great apes, being rather reminiscent of hylobatids (Hammond et al., 2020). Coupled with its manual proportions and large body mass, this evidence suggests that *Oreopithecus* might have been an orthograde arboreal ape that specialized in slow climbing but was committed neither to bipedalism or suspension, even if these behaviors might have been part of its positional repertoire.

3.4. Afropithecidae

As noted above, the monophyly of afropithecids as conceived here (Tables 1 and 2) remains to be better ascertained, even if most analyses concur that they are less basal than proconsulids (Nengo et al., 2017; Rossie and Hill, 2018; Gilbert et al., 2020a; Pugh, 2022), in agreement with their younger chronostratigraphic range. Afropithecids include medium- to large-bodied species recorded from the Early to Middle Miocene (from~21–20 to ~12 Ma) of Kenya, Uganda, Namibia, and Saudi Arabia (Table 3). Two afropithecid subfamilies are recognized here (Afropithecinae Andrews, 1992 and Equatorinae Cameron, 2004), which are separately discussed below. The phylogenetic relationships of some Miocene apes generally considered to be more or less closely related to *Afropithecus* Leakey and Leakey, 1986a—namely *Heliopithecus* Andrews and Martin, 1987b and *Otavipithecus* Conroy et al., 1992 (Andrews, 1992; Andrews and Kelley, 2007; Harrison, 2010a; Alba, 2012; Begun, 2013, 2015)—is particularly uncertain because they have not been included in recent cladistic analyses. *Heliopithecus*, from the Early Miocene (16 Ma) of Saudi Arabia, has been tentatively included in the Afropithecinae based on dental similarities (Andrews and Martin, 1987b; Harrison, 2010a). In turn, the medium-sized (14–20 kg) *Otavipithecus*, from the Middle Miocene (12 Ma) of Namibia, has been included in the Afropithecidae given the affinities with *Afropithecus* suggested by several authors (e.g., Andrews, 1992; Harrison, 2010a) and further supported by a cladistic analysis of mandibular characters (Singleton, 2000). However, *Otavipithecus* has been left as subfamily incertae sedis given the lack of cladistic studies evaluating its relationships with other afropithecids. *Otavipithecus* is recorded by craniodental and some postcranial remains (the latter being indicative of arboreal locomotion) and represents one of the southernmost occurrences of Miocene apes (Conroy et al., 1992; Mocke et al., 2022).

Afropithecinae Afropithecids are first recorded by afropithecines, which display a primitive nasoalveolar morphology (Begun and Gülec, 1998; Brown et al., 2005; Nakatsukasa and Kunimatsu, 2009; Begun, 2015) and differ from proconsulids in craniodental features probably related to sclerocarpic feeding (Leakey and Walker, 1997; Begun, 2015; Deane, 2017). The postcranial morphology of afropithecines is less thoroughly known than that of proconsulids, but similarly indicative of a pronograde body plan (Ward, 2015), except for some postcranial remains attributed to *Morotopithecus bishopi* Gebo et al., 1997, which are suggestive of orthograde behaviors (Sanders and Bodenbender, 1994; Gebo et al., 1997; MacLatchy et al., 2000, 2019; MacLatchy, 2004; Nakatsukasa, 2008). This species has sometimes been recovered as a stem hominid by cladistic analyses (Young and MacLatchy, 2004), but the most recent ones recovered it as a stem hominoid more basal than (Nengo et al., 2017; Gilbert et al., 2020a) or as basal as (Rossie and Hill, 2018) *Afropithecus*.

The distinctiveness of the genus *Morotopithecus* Gebo et al., 1997 has been disputed by several authors, who considered its type and only species (*M. bishopi*) a junior synonym of *Afropithecus turkanensis* Leakey and Leakey, 1986a (Pickford, 2002, 2021; Pickford et al., 2003, 2017; Patel and Grossman, 2006; Harrison, 2010a; Pickford et al., 2017; Van Couvering and Delson, 2020). Under this view, the cranial differences between the two genera (Gebo et al., 1997; MacLatchy et al., 2000; Begun, 2015; Deane, 2017) might be attributable to pathological remodeling in the holotype of *M. bishopi* and diagenetic deformation in that of *A. turkanensis* (Pickford, 2002; Pickford et al., 2017), which other authors also consider to be badly distorted (Begun, 2015). Based on the dental differences between *M. bishopi* and *A.*

turkanensis pointed out by MacLatchy et al. (2019), we tentatively favor the distinction of these taxa at least to the species rank, but remain skeptical about the generic distinction for several reasons. First, the putative differences in facial morphology—including the seemingly more restricted palatine fenestra of *Afropithecus* (Gebo et al., 1997; Brown et al., 2005; MacLatchy et al., 2019)—are uncertain in the light of the aforementioned arguments about remodeling and distortion. Second, MacLatchy et al.'s (2019) contention that the age difference between the two taxa (>3 Myr, assuming a dating of 21 Ma is correct, see footnote in Table 2) supports their distinction is not particularly relevant from a taxonomic viewpoint and applies to Miocene ape species but not genera.

The original diagnosis of *Morotopithecus* was partly based on its purported derived (crown hominoid-like) postcranial features (Gebo et al., 1997). Nevertheless, it has subsequently been argued that more than a single hominoid is present at Moroto. MacLatchy et al. (2019) recognized *M. bishopi* and a smaller proconsulid, while Jansma and MacLatchy (2015) further reported a nyanzapithecid. In contrast, Pickford et al. (2017) and Pickford (2021) recognized *A. turkanensis*, *P. gitongai*, and *Nacholapithecus kerioi* Ishida et al., 1999. Pickford (2021) even discussed the possibility that the Moroto vertebrae assigned to *M. bishopi* (Walker and Rose, 1968; Sanders and Bodenbender, 1994; Gebo et al., 1997; Nakatsukasa, 2008) might date to the Plio-Pleistocene. Such a claim would have important implications for the earliest evidence of orthograde in the hominoid fossil record (Gebo et al., 1997; MacLatchy, 2004; Young and MacLatchy, 2004). However, it is based on very circumstantial evidence—basically, that the fossils were surface-collected from sediments that have also yielded some Plio-Pleistocene fossils and that differences in preservation hint at a different taphonomic history for the vertebrae. Therefore, unless geochemical analyses eventually prove the contrary, a Miocene age seems much more likely. Nevertheless, the impossibility to demonstrate a close spatial association between the holotype and the postcranial remains casts some doubts on their attribution to the same taxon (MacLatchy et al., 2019; Pickford, 2021). Pending future analyses that might clarify the number and identity of large hominoid taxa present at Moroto and the composition of the *M. bishopi* hypodigm, we consider it prudent to keep the genus distinct.

Equatorinae Equatorines have been inferred to display, like afropithecines, adaptations to hard-object feeding (McCrossin and Benefit, 1993, 1997; Nakatsukasa and Kunimatsu, 2009). *Nacholapithecus* Ishida et al., 1999 differs from afropithecines by possessing slight premaxillary-maxillary overlap (Ishida et al., 2004) as well as an obliterated subarcuate fossa (Kunitmatsu et al., 2019). These features, which cannot be ascertained in *Equatorius* Ward et al., 1999, have given rise to different phylogenetic interpretations for *Nacholapithecus* (Alba, 2012; Kunimatsu et al., 2019; Pugh, 2022). The postcranial morphology of equatorines is better known than that of afropithecines and similar to that of proconsulids, being indicative of a pronograde body plan without external tail (as in *Nacholapithecus*; Nakatsukasa et al., 2003). However, *Nacholapithecus* possesses some features indicative of increased forelimb-dominated arboreal behaviors (climbing and clambering; Ishida et al., 2004; Nakatsukasa and Kunimatsu, 2009), while *Equatorius* shows evidence of semiterrestriality (McCrossin and Benefit, 1997; Patel et al., 2009).

Following the description of *Equatorius*, this genus has been considered distinct from both *Kenyapithecus* and *Griphopithecus* Abel, 1902 (here included in the Hominidae, see below) by most (e.g., Alba, 2012; Begun, 2015) but not all (Begun, 2000, 2001, 2002a; Benefit and McCrossin, 2000; Güleç and Begun, 2003; Kunimatsu et al., 2004; Mocke et al., 2022) researchers. Begun (2002a) even formally proposed to synonymize the genus *Equatorius* with *Griphopithecus*, but subsequently abandoned this view (e.g., Begun et al., 2012; Begun, 2015). We concur with most authors (e.g., Kelley et al., 2000, 2002; Ward and

Duren, 2002; Andrews and Kelley, 2007; Kelley et al., 2008; Harrison, 2010a; Alba, 2012; Begun, 2015) that *Equatorius* is sufficiently distinct from *Kenyapithecus*, with the latter differing, among other features, by possessing derived hominid synapomorphies such as a higher zygomatic root (Pickford, 1985; Harrison, 1992).

The systematic position of *Equatorius* and *Nacholapithecus* has been subject to different interpretations. Ward et al. (1999) considered *Equatorius* to be a stem hominoid less derived than *Kenyapithecus* and more closely related to *Afropithecus*, but Ward and Duren (2002) included them all within the Hominidae (albeit in different subfamilies). Alba (2012), in contrast, considered only *Afropithecus* to be a stem hominoid and included the other genera within the Hominidae, distinguishing two tribes within the Kenyapithecinae Andrews, 1992. Following the recent cladistic results indicating that *Equatorius* is a stem hominoid, perhaps even more basal than *Afropithecus* (Nengo et al., 2017; Gilbert et al., 2020a), Gilbert et al. (2020b) left *Equatorius* and *Nacholapithecus* as family incertae sedis—even though *Nacholapithecus* was not included in these analyses. Pugh's (2022) results recovered *Equatorius* and *Nacholapithecus* as a clade of stem hominoids, but her analyses did not include *Afropithecus*, thereby leaving unresolved the relationships between afropithecines and equatorines. Based on current knowledge, we prefer to group *Equatorius* and *Nacholapithecus* in a single subfamily (Equatorinae) within the Afropithecidae, while recognizing that the latter family might ultimately prove to be paraphyletic.

3.5. Hylobatidae

The origin of hylobatids is one of the most enduring problems in hominoid phylogenetics. As noted in Section 1.2, the Middle Miocene small catarrhine *Kapi* Gilbert et al., 2020a from India was originally interpreted as a stem hylobatid (see also Gilbert et al., 2020b) but has more recently been considered a pliopithecoid (Ji et al., 2022). This conclusion partly relies on the interpretation that *Kapi* possesses an incipiently developed mesial arm of the pliopithecine triangle, coupled with other dental similarities (Ji et al., 2022). The homology of the weakly developed crest displayed by *Kapi* with the pliopithecine triangle is debatable, but in the lack of additional material we concur that the stem hylobatid status of *Kapi* is insufficiently supported at present. In contrast, *Yuanmoupithecus xiaoyuan* Pan, 2006, from the Late Miocene (~8.0–7.0 Ma) of China, is known from multiple teeth and a partial lower face (Pan, 2006; Harrison et al., 2008; Harrison, 2016; Ji et al., 2022) and more unambiguously supported as a stem hylobatid by cladistic analyses (Gilbert et al., 2020a; Ji et al., 2022). For this reason, we classify this genus in a monotypic subfamily within the Hylobatidae, Yuanmoupithecinae subfam. nov. (type genus: *Yuanmoupithecus*), so as to reserve the Hylobatinae for crown hylobatids. Ji et al. (2022) also recovered the dendropithecid *Micropithecus* Fleagle and Simons, 1978 as a stem hylobatid but they interpreted this result as an artifact caused by functional dental convergence. This interpretation is also favored here but, given that some cladistic analyses have supported a stem hominoid status for dendropithecids (see Section 1.2) and that the Early Miocene forerunners of hylobatids are unknown, the possibility that *Micropithecus* is more closely related to hylobatids than to other dendropithecids from Africa (see also Section 4.3) should be investigated further.

3.6. Stem Hominidae

Kenyapithecinae We distinguish a hominid subfamily (Kenyapithecinae) for *Kenyapithecus* and *Griphopithecus*, which is equivalent to Alba’s (2012) tribe Kenyapithecini and Gilbert et al.’s (2020b) family Kenyapithecidae. The latter authors considered unresolved the systematic position of this taxon (stem vs. crown hominoid) but, based on Pugh's (2022) results, a stem hominid status seems more likely. Although there has been some confusion about the taxon name for the clade including both *Kenyapithecus* and *Griphopithecus*, Kenyapithecinae is to be preferred over Griphopithecinae (Casanovas-Vilar et al., 2011; see SOM S2.1 for further details).

Kenyapithecines are medium to large-bodied apes (~27–48 kg; Fleagle, 2013) known from isolated teeth, dentognathic fragments, and a few postcranial remains, the latter consistent with a pronograde body plan adapted to semiterrestrial quadrupedalism (Begun, 1992c, 2002a, 2015; Ersoy et al., 2008; Harrison, 2010a; Alba, 2012). The two kenyapithecid genera are distinguished mostly on the basis of dentognathic features (Kelley et al., 2008). *Kenyapithecus* is here considered the oldest known hominid from Africa (13.7 Ma) and also the only one recorded both in Africa and Eurasia, where it is represented by a slightly older species from Turkey (~14.5–14.0 Ma). *Griphopithecus* also comprises two species from the Middle Miocene, one from Turkey (~14.5–13.4 Ma) that co-occurs with *Kenyapithecus*, and another from Central Europe (Germany and Slovakia) that is probably younger (~13.8–12.7 Ma). There are two species names available for the latter species, but *Griphopithecus suessi* Abel, 1902, as the type species of the genus, is to be preferred for the reasons explained in SOM S2.2. Middle Miocene kenyapithecines, given their African and Eurasian geographic distribution, play a key role for understanding the dispersal and subsequent radiation of Miocene apes in Eurasia. Their oldest representatives predate the appearance of both dryopithecines and pongines in Eurasia ~13.0–12.5 Ma (Alba, 2012; Alba et al., 2017, 2022; Gilbert et al., 2020b), and thus represent plausible potential ancestors for these groups in chronological terms.

In the past, some cladistic analyses indicated a stem hominoid status for *Kenyapithecus* s.l. (before *Equatorius* was distinguished; Begun et al., 1997) or *Kenyapithecus* s.s. (Finarelli and Clyde, 2004), although the alternative stratocladistic analysis by the latter authors supported *Kenyapithecus* as the last common ancestor of crown hominids (see SOM S1.4 regarding stratocladistics). Indeed, there is a broad (even if not universal) consensus that *Kenyapithecus* is likely a stem hominid (Harrison, 1992, 2010a; Ward et al., 1999; Kelley et al., 2002, 2008; Ward and Duren, 2002; Andrews and Kelley, 2007; Alba, 2012), as further supported by recent cladistic analyses (Begun et al., 2012; Pugh, 2022). *Kenyapithecus* already displays a clear hominid synapomorphy in the possession of a high zygomatic root (Pickford, 1986; Harrison, 1992, 2010a; Kelley et al., 2008; Alba, 2012; Begun, 2015). Other features that generally distinguish *Kenyapithecus* from *Equatorius* (such as the configuration of the maxillary sinus) are found in pongines but not hominines (Harrison, 1992, 2010a), and indeed some recent analyses recovered *Kenyapithecus* as crown hominid more closely related to pongines (Nengo et al., 2017; Gilbert et al., 2020a). Nevertheless, Pugh's (2022) cladistic analyses—specifically focused on great apes—supported instead the stem hominid status of *Kenyapithecus*, in agreement with Harrison's (1992, 2010a) interpretation that the features shared with pongines are symplesiomorphic.

The hominid status of *Griphopithecus* is less clear-cut, as it has not been frequently included in cladistic analyses. Begun et al. (2012) recovered it as a stem hominoid but Pugh's (2022) analyses supported its stem hominid status as well as its inclusion within the same clade as *Kenyapithecus*—albeit only in some cases as sister taxa and in most other instances together with the dryopithecines *Pierolapithecus* Moyà-Solà et al., 2004 and *Anoiapithecus* Moyà-Solà et al., 2009b, thereby only tentatively justifying the inclusion of *Griphopithecus* in the Kenyapithecinae. The oldest record of hominoids in Eurasia consists of an upper molar fragment from Engelswies (~16.5–16.0 Ma; Casanovas-Vilar et al., 2011) that has been variously attributed to cf. *Griphopithecus* sp. (Heizman and Begun, 2001; Begun, 2015), ?*Griphopithecus* sp. (Andrews et al., 1996), and aff. *Griphopithecus* (Begun, 2002a). However, Casanovas-Vilar et al. (2011) questioned the possibility to reach an assignment (even if tentative) at the genus rank, and we concur it is best attributed to cf. Kenyapithecinae.

<u>Dryopithecinae</u> We follow Alba (2012) and other recent authors (e.g., Andrews, 2020; Gilbert et al., 2020b) in classifying many European Middle to Late Miocene apes in a distinct subfamily of putative stem hominids (Dryopithecinae Gregory and Hellman, 1939), rather than a tribe (Dryopithecini) of stem hominines (Begun, 2009, 2010, 2013, 2015). We also follow Alba (2012) in distinguishing the dryopithecine tribes Dryopithecini and Hispanopithecini Cameron, 1997a, respectively for Middle Miocene (12.4–11.6 Ma) and early Late Miocene (11.6–9.5 Ma) genera. However, we exclude the graecopithecin *Ouranopithecus* de Bonis and Melentis, 1977 (9.7–7.6 Ma) from this subfamily (see next subsection). Dryopithecines are mostly recorded from western and central Europe (Casanovas-Vilar et al., 2011), but persisted until ~8 Ma in Georgia as recorded by ?*Udabnopithecus* Burchak-Abramovich and Gabashvili, 1945 (Agustí et al., 2020), of uncertain taxonomic validity, thus overlapping by more than 1 Myr with the chronostratigraphic range of graecopithecins.

Dryopithecines are large-bodied apes that display multiple crown-hominid cranial synapomorphies, such as a high zygomatic root, deep palate, and wide nasal aperture (Moyà-Solà and Köhler, 1993, 1995; Begun, 1994; Moyà-Solà et al., 2004; 2009a, 2009b; Alba, 2012; Gunz et al., 2020). *Pierolapithecus*, *Hispanopithecus* Villalta Comella and Crusafont Pairó, 1944, and *Rudapithecus* Kretzoi, 1969 are the best known dryopithecine genera, both cranially and postcranially, although some cranial remains are also available for *Dryopithecus* and *Anoiapithecus*. *Hispanopithecus* and *Rudapithecus* further lack a subarcuate fossa (Moyà-Solà and Köhler, 1993, 1995; Kordos and Begun, 1997, 2001; Begun, 2015) but the importance of this feature as a hominid synapomorphy is currently uncertain (Pugh, 2022; see Subsection 4.5). Postcranial remains are known for all dryopithecine genera except *Anoiapithecus* and ?*Udabnopithecus*. *Dryopithecus* is not very well-known postcranially, but available specimens (Pilbeam and Simons, 1971; Moyà-Solà et al., 2009b; Alba et al., 2011; Almécija et al., 2012) are suggestive of powerful grasping above-branch quadrupedalism and cautious climbing without evidence of an orthograde body plan (Pina et al., 2019). In contrast, the roughly coeval *Pierolapithecus* represents the oldest unambiguous evidence of an orthograde body plan in the fossil hominoid record (Moyà-Solà et al., 2004; Alba, 2012), despite the lack of specific adaptations to suspensory behaviors (Moyà-Solà et al., 2004, 2005b; Almécija et al., 2009; Alba et al., 2010; contra Begun and Ward, 2005; Deane and Begun, 2008, 2010; Begun et al., 2012). Overall, the postcranial evidence for *Pierolapithecus* indicates a forelimb-dominated locomotor repertoire with a significant component of vertical climbing despite retaining adaptations for above-branch powerful-grasping quadrupedalism (Moyà-Solà et al., 2004, 2005b; Almécija et al., 2009; Alba et al., 2010; Alba, 2012; Hammond et al., 2013). *Danuvius* Böhme et al., 2019 similarly displays an orthograde body plan but already shows suspensory adaptations (Böhme et al., 2019; Williams et al., 2020; Almécija et al., 2021), which are even more clearly expressed in *Hispanopithecus* (Moyà-Solà and Köhler, 1996; Almécija et al., 2007; Alba et al., 2010, 2012b; Alba, 2012; Susanna et al., 2014; Pina et al., 2012) and *Rudapithecus* (Morbeck, 1983; Begun, 1988, 1992c, 1993, 1995). Nevertheless, at least *Hispanopithecus* still retains some features functionally related to above-branch quadrupedalism (Almécija et al., 2007; Alba et al., 2010, 2012b).

It is generally considered that dryopithecines are less basal hominids than kenyapithecines (e.g., Moyà-Solà and Köhler, 1993, 1995, 1996; Moyà-Solà et al., 2004, 2009a, 2009b; Begun, 2009, 2010, 2015; Alba et al., 2010; Casanovas-Vilar et al., 2011; Alba, 2012; Gilbert et al., 2020b), as supported by cladistic analyses (Begun et al., 2012; Pugh, 2022). However, dryopithecines have been variously interpreted as pongines (e.g., Moyà-Solà and Köhler, 1995), hominines (e.g., Begun et al., 2012), or stem hominids (e.g., Alba, 2012; Alba et al., 2015; Pugh, 2022)—see discussion in Almécija et al. (2021). Such uncertainties led Gilbert et al. (2020b) to place dryopithecines in a trichotomy with crown hominids, in further agreement with some other cladistic analyses (Nengo et al., 2017; Gilbert et al., 2020a). Dryoptihecine genera differ from one another in cranial and postcranial features but are dentally conservative, although hispanopithecins appear somewhat more derived in the latter regard (e.g., the C^1 morphology of the of male individuals and the more peripheral dentine horns of the upper molars; Alba, 2012; Fortuny et al., 2021). Pugh's (2022) analyses did not find clear support that dryopithecins are less basal than kenyapithecines and, hence, the monophyly of dryopithecines as conceived here remains uncertain (Alba, 2012; Almécija et al., 2021; Pugh, 2022). Given the lack of a cladistic analysis including *Danuvius*, we group it with the hispanopithecins because it appears somewhat more derived than dryopithecins (Almécija et al., 2021).

Among dryopithecins, the distinctiveness of both *Pierolapithecus* and *Anoiapithecus* from *Dryopithecus* has been accepted by various researchers (Pickford, 2012; Fleagle, 2013; Böhme et al., 2019; Andrews, 2020) but questioned by Begun (2009, 2010, 2015), who argued that the two former might be junior synonyms of *Dryopithecus*, mostly based on claims of distortion (see SOM S3 for further details). However, preliminary results of a digital reconstruction of the *Pierolapithecus* cranium (Pugh et al., 2022) are consistent with its stem hominid status and difficult to reconcile with craniodental differences relative to *Anoiapithecus* (Moyà-Solà et al., 2009b; Pérez de los Ríos et al., 2012). In our opinion, the distinction of the three monotypic dryopithecin genera is supported by both dental and cranial differences (Moyà-Solà et al., 2004, 2009a, 2009b; Alba, 2012; Pérez de los Ríos et al., 2012; Alba et al., 2013; Fortuny et al., 2021), although more complete remains would be required to clarify further their phylogenetic relationships relative to both kenyapithecines and hispanopithecins. '*Sivapithecus*' *occidentalis* Villalta Comella and Crusafont Pairó, 1944, previously considered a nomen dubium (Moyà-Solà et al., 2004; Alba, 2012) or synonymized with *Neopithecus brancoi* (Schlosser, 1901) by Pickford (2012), is here included in the Dryopithecini as a species inquirenda following Alba et al. (2020), as this nominal species is potentially a junior synonym of either *Pi. catalaunicus* Moyà-Solà et al., 2004 or *An. brevirostris* Moyà-Solà et al, 2009b.

With regard to hispanopithecins, following the opinion of Begun and colleagues (Begun and Kordos, 1993; Kordos and Begun, 1997; Begun, 2002a), the binomen *Dryopithecus brancoi* (Schlosser, 1901) was formerly considered by many authors as a taxonomically valid species including the hispanopithecin remains from Hungary (e.g., Moyà-Solà and Köhler, 1995; Cameron, 2004, 2005; Ersoy et al., 2008; Kelley et al., 2008). In turn, the Spanish hispanopithecin remains were included in one or more species of *Dryopithecus* (e.g., Begun et al., 1990; Harrison, 1991; Begun, 1992b, 1994, 2002a; Moyà-Solà and Köhler, 1993, 1995, 1996). Alternatively, Andrews et al. (1996) considered *D. brancoi* a nomen dubium and advocated the inclusion of the Hungarian material in *Dryopithecus carinthiacus* Mottl, 1957, which is here considered a junior synonym of *D. fontani* (Begun, 2002a; Begun et al., 2006;

Casanovas-Vilar et al., 2011). Following most recent authors (Moyà-Solà et al., 2009a; Casanovas-Vilar et al., 2011; Begun, 2015; Alba et al., 2020; but see Pickford, 2012), both *Neopithecus* Abel, 1902 and *Neopithecus brancoi* are here considered nomina dubia. Furthermore, following Moyà-Solà et al. (2009a) and Begun (2009), *Dryopithecus* is restricted to Middle Miocene dryopithecines. Moyà-Solà et al. (2009a) resurrected *Hispanopithecus* not only for Late Miocene dryopithecines from Spain, as sometimes done by previous authors (Cameron, 1997a, 1999, 2004; Almécija et al., 2007), but also for those from Hungary, which were assigned by Begun (2009) to *Rudapithecus hungaricus* Kretzoi, 1969. Subsequently, Alba and coauthors (Casanovas-Vilar et al., 2011; Alba, 2012; Alba et al., 2012a, 2012b) distinguished *Hispanopithecus* and *Rudapithecus* only at the subgenus rank, but following most recent authors (e.g., Begun, 2015; Gunz et al., 2020; Urciuoli et al., 2021a) here both taxa are distinguished at the genus rank. The distinction of *Hispanopithecus crusafonti* (Begun, 1992b) from *Hispanopithecus laietanus* Villalta Comella and Crusafont Pairó, 1944 (Begun, 1992b, 2002a; Cameron, 1999) has been questioned by some authors (Harrison, 1991; Andrews et al., 1996; Ribot et al., 1996). However, they are here distinguished based on dental morphology (Alba, 2012; Alba et al., 2012a; Fortuny et al., 2021)—albeit recognizing that the proper genus allocation of *H. crusafonti* is difficult to evaluate due to the lack of more complete cranial remains.

The latest occurring dryopithecine (Agustí et al., 2020), ?*Udabnopithecus garedziensis* Burchak-Abramovich and Gabashvili, 1945, has been variously synonymized with *D. fontani* (e.g., Szalay and Delson, 1979) or left as incertae sedis within the Dryopithecinae (Andrews et al., 1996). More recently, it has been considered by some a distinct species of *Dryopithecus* (Gabunia et al., 2001; Agustí et al., 2020). Given the limited evidence available (a maxillary fragment with P^4–M^1) and the current more restricted usage of *Dryopithecus* (see above), the inclusion in *Dryopithecus* does not appear warranted and we prefer to provisionally leave ?*Udabnopithecus* as incertae sedis at the tribe rank, denoting the uncertain taxonomic validity of the genus with a question mark. We also leave '*Dryopithecus*' *wuduensis*, known on the basis of a partial mandible from the Late Miocene (~8–6 Ma) of China (Xue and Delson, 1988), as family incertae sedis. The inclusion of this species in *Dryopithecus* has been questioned (as ?*Dryopithecus wuduensis*) or even ruled out by several authors (Kelley, 2002; Harrison, 2005, 2006; Gilbert et al., 2020b), and most recently Pugh et al. (2020) identified closer similarities to stem hominoids. Given that the referral of this species to *Dryopithecus* can be discounted, we put the genus name within quotation marks until the allocation of the species is clarified.

3.7. Crown Hominidae

<u>Ponginae</u> Five genera of Miocene pongines are recognized here (Table 2), being recorded from the late Middle Miocene (~13 Ma) to the latest Miocene (~6 Ma; Table 1). Besides their geographic distribution in Asia, these genera are customarily considered pongines based on the possession of derived craniodental features displayed by extant orangutans (e.g., Kelley, 2002)—even though this has been disputed for *Lufengpithecus* Wu, 1987 during the last decade (see below). The most comprehensive cladistic analysis of crown hominids published so far (Pugh, 2022) found support for the inclusion of non-kenyapithecine hominids from Asia in the same clade as *Pongo*, with the single exception of a species thus far included in *Lufengpithecus*. To reflect the internal phylogenetic relationships of pongines, we follow Alba (2012) in distinguishing three tribes, with genera tentatively arranged in accordance with Pugh's (2022) results. The apparently most plesiomorphic pongines (*Ankarapithecus* and *Lufengpithecus*) are included in the tribe Lufengpithecini Alba, 2012, whereas

Indopithecus von Koenigswald, 1949 is included (together with *Sivapithecus* and the Pleistocene *Gigantopithecus*) in the Sugrivapithecini Simonetta, 1958 (regarding the year of publication of Simonetta's work, see SOM S2.3), and *Khoratpithecus* Chaimanee et al., 2004 is grouped with extant *Pongo* in the Pongini Elliot, 1913.

Sivapithecus, from the late Middle and Late Miocene of Indo-Pakistan (13.0–7.5 Ma), is the fossil pongine whose cranial morphology is the most complete, showing extensive similarities with orangutans; these include an airorynchous cranium, distinct supraorbital costae, tall and narrow orbits with their inferior margin well above the superior end of the nasal aperture, narrow interorbital space, and horizontal and procumbent premaxilla that considerably overlaps the hard palate, configuring a long and very narrow incisive canal as well as a smooth subnasal floor (Pilbeam, 1982; Ward and Pilbeam, 1983; Ward and Brown, 1986; Brown and Ward, 1988; Ward, 1997a; Kelley, 2002; Brown et al., 2005). In contrast, the postcranium of *Sivapithecus* appears much less derived than that of *Pongo*, combining some modern hominoid-like features (such as the morphology of the distal humerus) with an otherwise plesiomorphic postcranial morphology, more consistent with a pronograde body plan suitable for emphasis on powerful-grasping and cautious, above-branch arboreal quadrupedalism (Pilbeam et al., 1990; Rose, 1997; Madar et al., 2002; Morgan et al., 2015).

As a result of their cranial similarities, a close phylogenetic link between *Sivapithecus* and *Pongo* has received much support from cladistic analyses (Pugh, 2022 and references therein). The latter analysis, however, did not consistently recover a *Pongo* + *Sivapithecus* clade exclusive of all *Khoratpithecus* species. For this reason, we prefer to keep *Sivapithecus*, along with other extinct taxa presumably more closely related to it than to *Pongo*, in a different tribe. Although the intuitive name for this tribe would be Sivapithecini Pilbeam et al., 1977 (e.g., Andrews, 1992; Kelley, 2002), three names of the family group—

Ramapithecini Simonetta, 1958, Bramapithecini Simonetta, 1958, and Sugrivapithecini Simonetta, 1958—have priority. The latter was used by Szalay and Delson (1979) and Alba (2012) for the tribe including *Sivapithecus*, but neither of them qualify as First Reviser (ICZN, 1999: Art. 24.2; see SOM S2.3). We therefore act as First Reviser and choose Sugrivapithecini as the senior synonym of Ramapithecini and Bramapithecini for the tribe including *Sivapithecus*.

We follow Kelley (2002, 2005) in tentatively distinguishing three species of *Sivapithecus*, while recognizing that alternative taxonomic schemes (see discussion in Kelley, 2005; Pickford, 2010; Bhandari et al., 2018; Gilbert et al., 2019) might ultimately prove to be more satisfactory, because only *Sivapithecus parvada* Kelley, 1988 seems at present well diagnosed from other species of the genus based on dental size and shape (Kelley, 1988, 2002, 2005). For example, Kelley (2005) tentatively assigned the specimens from Haritalyangar to *Sivapithecus* cf. *sivalensis* (Lydekker, 1879), but admitted that this sample could alternatively include two different species, given the high levels of molar size variation and apparent sexual dimorphism (Scott et al., 2009). According to the present taxonomic arrangement, *Sivapithecus simonsi* Kay, 1982 is considered a synonym of *Sivapithecus indicus* Pilgrim, 1910 (Kelley, 2005).

We also include in the Sugrivapithecini the genus *Indopithecus*, from the Late Miocene (~8.9–8.6 Ma) of India and Pakistan. Its type species, *Indopithecus giganteus* (Pilgrim, 1915), was originally described in *Dryopithecus* based on a single lower molar and later transferred to *Indopithecus*. Subsequently, *Gigantopithecus bilaspurensis* Simons and Chopra, 1969 was described based on a relatively complete mandible. The two species were synonymized by Szalay and Delson (1979), who used the combination *Gigantopithecus giganteus*. However, during the last decades most authors have supported the generic distinction between

Indopithecus and *Gigantopithecus blacki* von Koenigswald, 1935 (Cameron, 2004; Alba, 2012; Begun, 2015; Zhang and Harrison, 2017; Chaimanee et al., 2022; Pugh, 2022), which displays more strongly molarized lower premolars and other dental differences relative to *Indopithecus* (Kelley, 2002; Zhang and Harrison, 2017). *Gigantopithecus* is recorded from the Pleistocene (~2.0–0.3 Ma) of China, Vietnam, and Thailand (Zhang et al., 2014; Zhang and Harrison, 2017), and its pongine status has been recently supported by paleoproteomic data (Welker et al., 2019). Similarities in molar occlusal morphology between *Indopithecus* and *Sivapithecus* could justify their inclusion in the same genus, but the larger size and some similarities in mandibular and P_3 morphology with the much younger and larger *Gigantopithecus* suggest that *Indopithecus* might be a basal member of the *Gigantopithecus* lineage (Kelley, 2002; Zhang and Harrison, 2017; Pugh, 2002).

The subnasal morphology of *Sivapithecus* and orangutans is also shared to a large extent by *Khoratpithecus*, which includes four species from the late Middle to latest Miocene (~12.4–6.0 Ma) of southeastern Asia (Begun and Güleç, 1998; Kelley, 2002; Begun, 2015; Chaimanee et al., 2019, 2022). The nasoalveolar configuration of a palate—initially attributed to cf. *Khoratpithecus* (Chaimanee et al., 2019) but recently assigned by Chaimanee et al. (2022) to the type species of the genus, *Khoratpithecus piriyai* Chaimanee et al., 2004—closely resembles the pongine condition shared by *Sivapithecus* and *Pongo* but displays larger incisive canal and fossa, thus being less derived than that of *Sivapithecus* (Chaimanee et al., 2019, 2022). In contrast, *Khoratpithecus* has been proposed as the pongine most closely related to orangutans based on its symphyseal morphology and the lack of anterior digastric fossa (Chaimanee et al., 2003, 2004, 2006, 2019, 2022; Jaeger et al., 2011). These features can be ascertained in both *Kh. piriyai* and *Khoratpithecus ayeyarwadyensis* Jaeger et al., 2011, which in our opinion supports the inclusion of the genus in the same tribe as orangutans. On the other hand, Pugh (2022) only recovered a sister-taxon relationship with *Pongo* in the case of *Kh. ayeyarwadyensis*—suggesting that additional cranial remains would be required to better ascertain the relationships between *Pongo*, *Sivapithecus*, and *Khoratpithecus*.

The inclusion of other non-kenyapithecine hominid genera from the Miocene of Asia (*Ankarapithecus* and *Lufengpithecus*) in the Ponginae, and their classification within a single tribe Lufengpithecini is more debatable because the group might ultimately prove paraphyletic. Both *Ankarapithecus meteai* Ozansoy, 1957 from the Late Miocene (9.8 Ma) of Turkey and the species previously included in *Lufengpithecus*, from the late Middle to latest Miocene of China, retain a more plesiomorphic stepped subnasal configuration (Begun and Güleç, 1998; Brown et al., 2005; Kelley and Gao, 2012; Ji et al., 2013) more similar to that of dryopithecines (Begun, 1994; Moyà-Solà and Köhler, 1995; Brown et al., 2005; Moyà-Solà et al., 2009a, 2009b; Pérez de los Ríos et al., 2012; Pugh, 2022). Nevertheless, the subnasal morphology of *Ankarapithecus* appears somewhat derived toward the condition of other pongines, being interpreted as the plesiomorphic condition for this subfamily—as further supported by cladistic analyses (Begun and Güleç, 1998; Pugh, 2022), although it could be alternatively interpreted as compatible with a stem hominid status (Alpagut et al., 1996; Kappelman et al., 2003).

The genus *Lufengpithecus* has traditionally been considered a pongine (e.g., Schwartz, 1990, 1997; Kelley, 2002; Alba, 2012; Begun, 2015), but evidence supporting its pongine status is more debatable than in the case of *Ankarapithecus* and further complicated by the existence of multiple species with a complex nomenclatural history (Harrison et al., 2002). Kelley (2002) tentatively distinguished three species of *Lufengpithecus*: *Lufengpithecus lufengensis* (Xu et al., 1978), which is the type species of the genus; *Lufengpithecus* *keiyuanensis* (Woo, 1957); and *Lufengpithecus hudienensis* (Zhang et al., 1987). In contrast, Harrison et al. (2002) and Harrison (2006) favored a two species taxonomic scheme, by considering that *L. hudienensis* was a junior subjective synonym of *L. keiyuanensis*. Yet another species, *Lufengpithecus yuanmouensis* Zheng and Zhang, 1997 was described based on a juvenile cranium from Yuanmou as the holotype, being considered a junior subjective synonym of either *L. hudienensis* or *L. keiyuanensis*, according to Kelley (2002) and Harrison et al. (2002), respectively. The redescription of juvenile crania attributed to *L. hudienensis* and *L.* cf. *lufengensis*, the two younger species of *Lufengpithecus* (~8–6 Ma), not only showed substantial differences between these species but also the lack of crown hominoid (either pongine or hominine) synapomorphies—not being attributable to their ontogenetic stage (Kelley and Gao, 2012; Ji et al., 2013). Subsequent cladistic analysis recovered *Lufengpithecus* as more closely related to dryopithecines than to *Pongo* or *Sivapithecus* (Nengo et al., 2017; Gilbert et al., 2020a), which could justify transferring the Lufengpithecini into the Dryopithecinae. Nevertheless, most recently Pugh (2022) did not recover the monophyly of *Lufengpithecus* and supported a pongine status for *L. lufengensis* but not *L. hudienensis*, while the older species *L. keiyuanensis* (~12 Ma) could not be analyzed.

On the basis that *Lufengpithecus* might be polyphyletic, Gilbert et al. (2020b) left this genus as incertae sedis within the Hominoidea. However, we consider more advisable to provisionally keep the Lufengpithecini (for *L. lufengensis*) within the Ponginae while transferring ‘*L.*’ *hudienensis* to a different genus, for which the nomen *Sinopithecus* Zhang et al., 1990 is available with this species as its type (Harrison et al., 2002; Harrison, 2006). This is consistent with the marked cranial differences previously noted between these taxa (Kelley and Gao, 2012; Ji et al., 2013; Kelley, 2017). We thus formally reassign the species to *Sinopithecus hudienensis*, which is left as subfamily incertae sedis until it is clarified whether it belongs to the Dryopithecinae, the Ponginae, or neither. The third and least well-known species of *Lufengpithecus* distinguished by Kelley (2002) and Ji et al. (2013) is further tentatively included in *Sinopithecus*, as previously done by Zhang et al. (1990), given the greater dental similarities with *S. hudienensis* (Harrison et al., 2002; Harrison, 2006). This arrangement must be considered very tentative until additional until additional evidence enables a better assessment of the phylogenetic relationships between *Lufengpithecus*, *Sinopithecus*, putative basal pongines (*Ankarapithecus*), and dryopithecines (particularly hispanopithecins). It is remarkable that the few postcranial remains of *Lufengpithecus*, unlike those of *Sivapithecus* (but similar to hispanopithecins such as *Hispanopithecus* and *Rudapithecus*, see above), are indicative (particularly based on phalangeal curvature) of suspensory behaviors (Deane and Begun, 2008; Begun, 2015; Zhang et al., 2020).

Graecopithecini The Late Miocene genera *Ouranopithecus* and *Graecopithecus* von Koenigswald, 1972, from the Late Miocene (9.7–7.2 Ma) of Greece and Turkey, are included in the tribe Gracopithecini Cameron, 1997b, whereas an isolated upper premolar from Bulgaria (7.2 Ma; Spassov et al., 2012; Böhme et al., 2017) is assigned to Graecopithecini indet. The genus *Graecopithecus* has been variously considered distinct from (Begun, 2002a, 2009, 2015; Koufos and de Bonis, 2005; Begun et al., 2012; Böhme et al., 2017; Fuss et al., 2017) or synonymous with (Martin and Andrews, 1984; Andrews et al., 1996; Cameron, 1997a, 1997b; Smith et al., 2004) *Ouranopithecus*, in which case the former would take precedence. Most authors favoring the latter view have indeed synonymized the respective type species, except for Cameron (1997b), who considered them distinct. In the light of recently published evidence (Fuss et al., 2017; Pugh, 2022), we favor the view that these two genera and species are distinct but likely closely related. Following the cladistic results summarized in the following paragraph, we include both *Graecopithecus* and

Ouranopithecus within a single tribe Graecopithecini Cameron, 1997b, with Ouranopithecini Begun, 2009 being considered its junior subjective synonym (see SOM S2.4 for further details).

Only the older graecopithecin species, *Ouranopithecus macedoniensis* (de Bonis et al., 1974) from Greece (9.7–8.8 Ma), is known from craniodental material (de Bonis et al., 1990; de Bonis and Koufos, 1993, 1994). This species is characterized by larger body size than dryopithecines (Kappelman et al., 2003), hyperthick molar enamel (Smith et al., 2004)—interpreted as an adaptation for a sclerocarpic diet (Ungar, 1996; Begun, 2009; DeMiguel et al., 2014)—and a subnasal morphology most similar to that of dryopithecines (de Bonis and Melentis, 1987; de Bonis and Koufos, 1994; Moyà-Solà and Köhler, 1995). The phylogenetic relationships of *Ouranopithecus* have been much debated, being interpreted as an early hominin by some authors (de Bonis et al., 1990, 1998; de Bonis and Koufos, 1993, 1994, 2004; Koufos and de Bonis, 2005), or alternatively as a stem pongine (Moyà-Solà and Köhler, 1995; Agustí et al., 1996; Köhler et al., 2001), a stem hominid (Alba, 2012), or a stem hominine (Begun, 1994, 2001, 2002a, 2009, 2010, 2015; Cameron, 2004). *Ouranopithecus* has been recovered as a stem hominine by cladistic analyses (Begun et al., 1997, 2012; Cameron, 1997a; Nengo et al., 2017; Gilbert et al., 2020a; Pugh, 2022). However, while Begun et al. (1997, 2012) recovered *Ouranopithecus* and dryopithecines as successive sister taxa of extant hominines, both Cameron (1997a) and more recent cladistic analyses (Nengo et al., 2017; Gilbert et al., 2020a; Pugh, 2022) supported a hominine status only for *Ouranopithecus*. It has also been recently argued that *Graecopithecus* is a hominin (Fuss et al., 2017) but such a contention has not been supported by subsequent cladistic analyses (Benoit and Thackeray, 2017; Pugh, 2022). Nevertheless, Pugh (2022) yielded tentative support to a clade of stem hominines including both *Ouranopithecus* and *Graecopithecus*.

Although we favor the view that these genera are closely related, following Pugh's (2022) results, we consider it premature to classify the Graecopithecini in the Homininae. While Pugh's (2022) analyses are thus far the most thorough in supporting the hominine status of graecopithecins, we consider that their hominine status is plausible but insufficiently supported at present (for further explanations, see SOM S4 and SOM Fig. S1), and even unlikely unless at least some dryopithecines are also considered hominines (e.g., Begun et al., 2012). Therefore, we provisionally prefer to leave graecopithecins as incertae sedis at the subfamily rank while noting that, on both morphologic and chronostratigraphic grounds, graecopithecins might have been derived from dryopithecines irrespective of whether they are closely related to *Nakalipithecus* Kunimatsu et al., 2007 and/or hominines (see below).

Homininae The ape record from the latest Middle and Late Miocene of Africa is quite meager compared to the panoply of Eurasian taxa during the same time interval. Isolated teeth from Middle Miocene (~12.8–12.0 Ma) localities of the Ngorora Formation, Kenya have been interpreted by some authors as hominines (Bishop and Chapman, 1970; Pickford and Senut, 2005) or stem hominoids (Hill and Ward, 1998; Hill et al., 2002), and the same applies to dental specimens from the latest Miocene (~6 Ma) of the Lukeino Formation (Pickford, 1975; Hill and Ward, 1988; Pickford and Senut, 2005), considered by some related to African apes (Pickford and Senut, 2005). All these samples are too meager to reach definite conclusions beyond a probable hominid status (e.g., Harrison, 2010a). A very fragmentary mandibular fragment, tentatively dated to the Late Miocene (Pickford et al., 2008, 2009b), records the presence of hominoids in Niger but does not allow further taxonomic precision (Harrison, 2010a)

Additionally, two great ape genera have been recognized from the Late Miocene in Africa, being represented by fragmentary dentognathic remains: *Nakalipithecus* from Kenya (9.9–

9.8 Ma) and *Chororapithecus* Suwa et al., 2007 from Ethiopia (~8.0 Ma). *Nakalipithecus* was originally proposed as a stem hominine likely related to *Ouranopithecus* (Kunimatsu et al., 2007)—as further favored by Harrison (2010a, 2010b), who on the basis of the more plesiomorphic dental features of *Nakalipithecus* supported an African origin of hominines. More recently, Pugh's (2022) cladistic results supported a stem hominine status for *Nakalipithecus* and, more tentatively, a possible link with European graecopithecins, but the features used in support of such links (Kunimatsu et al., 2007; Pugh, 2022) are too ambiguous (see SOM S4 for further details). *Chororapithecus* was originally interpreted as a member of the gorilla lineage based on some details of molar shape and overall size (Suwa et al., 2007), but this phylogenetic link has been questioned by Harrison (2010a), who suggested instead a link (and possible synonymy) with *Samburupithecus*. Pugh (2022) found the cladistic topology of *Chororapithecus* to be unstable because the available hypodigm does not preserve enough phylogenetically informative features to resolve its relationships and also owing to the fact that the purported gorillin synapomorphies identified by Suwa et al. (2007) have not been examined in a broad hominoid sample. Based on Pugh's (2022) results for *Nakalipithecus* and the purported similarities between *Chororapithecus* and gorillas noted by Suwa et al. (2007), we tentatively include both genera in the Homininae as tribe incertae sedis, given that additional remains would be required to better support the hypothesized relationships with graecopithecins and gorillins, respectively.

4. Miocene ape paleobiodiversity, phylogeny, and paleobiogeography

4.1. Paleobiodiversity dynamics

The chronostratigraphic range and geographic distribution of Miocene ape species are summarized in Table 3, whereas species-locality occurrences with primary references and the age of each Miocene ape-bearing locality are reported respectively in SOM Tables S1 and S2. Up to 56 species of Miocene apes are considered valid in this work (plus two species of uncertain taxonomic validity), being included in 35 genera (plus two of doubtful or uncertain taxonomic validity). The geographic distribution of these taxa, including occurrences indeterminate at the species rank, during the Early, Middle, and Late Miocene is depicted in Figures 3, 4, and 5, respectively. In turn, the chronostratigraphic ranges reported in Table 3 for Miocene ape species, together with other citations indeterminate to species rank, have been summarized at the genus level in Figure 6.

The chronostratigraphic ranges reported in Table 3 simultaneously reflect the occurrence of each species in differently aged localities and the dating uncertainties for these localities, but may be used to provide a first approximation to the paleobiodiversity dynamics of Miocene apes through time (Foote, 2000; see SOM S5 and SOM Table S3 for further details). Range-through (total) diversity (Fig. 7a) and standing diversity (Fig. 7b) at the species level yield similar diversity patterns, with a diversity peak during the Early Miocene (~21–20 Ma) and an even more marked peak during the Late Miocene (~9–8 Ma). Both metrics reflect a more or less marked decrease in diversity during the late Early Miocene, followed by an irregular recovery throughout the Middle Miocene until reaching the highest diversity well within the Late Miocene, followed by an abrupt decline thereafter. Changes in diversity through time are more marked in the plot based on standing diversity (Fig. 7b), which more adequately minimizes sampling biases than total diversity counts (Fig. 7a). However, both patterns support that the Middle (Fig. 4) and Late (Fig. 5) Miocene ape radiation—largely driven by the diversification of great apes throughout Eurasia—was of comparable magnitude to (if not greater than) the Early Miocene radiation of putative stem apes (Fig. 3)—confined to Afro-Arabia except for the Engelswies tooth fragment.

It is noteworthy that the Mid-Miocene Climatic Optimum (Foster et al., 2012) is characterized by a low diversity of Miocene apes, which is followed by a progressive increase in diversity that continues into the Late Miocene despite a progressive trend toward increased cooling and seasonality initiated at ~14 Ma. This supports the interpretation that climatic 'deterioration' and associated paleoenvironmental changes might have triggered the adaptive radiation of crown hominoids in Eurasia (Casanovas-Vilar et al., 2011), as a result of progressive locomotor and dietary specialization (DeMiguel et al., 2014). A temporary drop in diversity at ~11 Ma appears artifactual to a large extent, both in Eurasia (where the poor sampling of hominoids by this time has been previously noted; Alba et al., 2022) and in Africa (as indeterminate remains older than 12 Ma and the presence of several taxa from 10 Ma onward suggest a greater diversity than currently recorded around the Middle/Late Miocene boundary). In contrast, the marked decline in diversity during the latest Miocene mostly reflects the local extinction of hominoids in Western Eurasia and their progressive decline in Eastern Eurasia and probably Africa (hominins excluded). This has been interpreted as the result of changes in vegetation structure related to progressive climate cooling and aridification (Agustí et al., 2003; Casanovas-Vilar et al., 2011; Marmi et al., 2012; Almécija et al., 2021), roughly coinciding with the spread or more open and arid environments across the Old World (Kaya et al., 2018).

4.2. Phylogenetic uncertainties: Craniodental vs. postcranial evidence

Although both climatic and paleogeographic factors seemingly played a role in Miocene ape diversification, important paleobiogeographic issues remain to be deciphered due to phylogenetic uncertainties. For example, it is unclear whether hominids and hylobatids diverged in Africa during the Early Miocene and separately dispersed into Eurasia by the

Middle Miocene, or whether they diverged in Eurasia following a single dispersal event. It is similarly uncertain whether hominines and pongines evolved as a result of a vicariant event in Eurasia and Africa, respectively, or whether they diverged in one of these continents and subsequently dispersed to the other. Gilbert et al. (2020b) examined several recent phylogenetic hypotheses from a paleobiogeographic perspective and concluded that they implied between one and four hominoid dispersal events between Africa and Eurasia and zero to two between Europe and Asia. Later in this section, we will discuss the pros and cons of various competing paleobiogeographic scenarios in the light of phylogenetic evidence, but before doing so it is worth discussing to what extent the phylogenetic relationships favored by cladistic analyses published during the last decade (Nengo et al., 2017; Rossie and Hill, 2018; Gilbert et al., 2020a; Pugh, 2022) appear reliable.

Discrepancies between most parsimonious topologies and chronostratigraphic ranges are to be expected due to the multiple biases of the fossil record, but can also by caused by inaccurate phylogenies, particularly in the light of abundant postcranial homoplasy. Previous attempts to determine whether craniodental or postcranial features are more homoplastic proved rather inconclusive, finding higher levels in craniodental (Finarelli and Clyde, 2004) or postcranial (Young, 2005) characters. Any attempt to estimate craniodental and postcranial homoplasy based on a most parsimonious cladogram derived from both anatomical areas simultaneously results in circular reasoning and is biased by the number of characters in each subset and their actual degree of homoplasy (which is unknowable). An alternative way to tackle this issue is to compare the results provided by separate analyses of craniodental and postcranial features, as done by Pugh (2022).

The most parsimonious cladograms obtained by Pugh (2022: Fig. 4) based on craniodental and postcranial characters separately evince important similarities and differences, and further highlight those phylogenetic links that are exclusively or mostly based on craniodental data. The results supported by both craniodental and postcranial evidence include the sequential branching of equatorines, kenyapithecines, and dryopithecines. Hispanopithecines are also recovered as less basal than dryopithecins + kenyapithecines in all analyses, but the craniodental evidence supports *H. laietanus* as a pongine and *R. hungaricus* as a hominine—casting even more doubts on the monophyly of dryopithecines as conceived here. The results of the total morphological evidence analysis that are only supported by craniodental data include: (1) the stem hylobatid status of the clade constituted by *Oreopithecus* and *Samburupithecus*; (2) the polyphyly of *Lufengpithecus* s.l. and *Khoratpithecus*; and (3) the recovery graecopithecins in a hominine clade also including *Nakalipithecus*. This is not surprising given that most of these taxa were not included in the postcranial analysis, with the exception of *Oreopithecus*. However, it is noteworthy that the clade including graecopithecins + *Nakalipithecus* is not recovered as sister to crown hominines, but as sister of hominins—supporting the view that, unless interpreted as basalmost hominins (e.g., de Bonis and Koufos, 2004), the hominine status of these taxa in the total morphological evidence analysis is influenced by craniodental convergences with hominins related to powerful mastication (see discussion in Pugh, 2022).

Most noteworthy for assessing the reliability of Pugh's (2022) results based on total morphological evidence are the differences between the postcranial and craniodental results. The cladogram based on the former recovers the monophyly of crown hominoids, hylobatids, hominids, and hominines, but excludes from these clades all the analyzed Miocene apes except *Si. sivalensis* and *Oreopithecus*, which are recovered as crown hominids. Thus, besides failing to recover the pongine status of *Sivapithecus*, the postcranial data support a much less basal branching for both hylobatids and *Oreopithecus*. As a result, most of the Miocene apes recovered as hominids in the craniodental analysis (equatorines, kenyapithecines, dryopithecines, and *Si. sivalensis*) are recovered as stem hominoids based on the postcranial data. *Oreopithecus* exhibits the most extreme incongruency between craniodental and postcranial data, but the contrasting results obtained for hylobatids are also worrisome for the reliability of their topology in the total morphological evidence cladogram—intermediate between equatorines and kenyapithecines + dryopithecins—given its implications for distinguishing stem from crown hominoids. As in the case of *Oreopithecus*, the branching topology of hylobatids appears strongly influenced by postcranial similarities with hominids, which are functionally related to orthograde behaviors and most likely evolved in parallel to a large extent, as illustrated by *Sivapithecus* and *Pierolapithecus* (e.g., Larson, 1998; Moyà-Solà et al., 2004; Alba, 2012; Ward, 2015) and further favored by Pugh (2022).

To account for the potential bias introduced by crown hominoid postcranial similarities, in Figure 8b we have depicted a cladogram that better reflects current main uncertainties about Miocene ape phylogeny while hypothesizing a more basal divergence of hylobatids (more consistent with the craniodental results) instead of the less basal divergence hypothesis currently favored by most parsimonious cladograms. The cladogram depicted in Figure 8b thus mainly differs from that of Figure 8a in the position of afropithecines and equatorines, which are considered basalmost stem hominids instead of advanced stem hominoids (leaving unresolved if they constitute a clade or successive sister taxa). Based on the consistency between craniodental and postcranial results about the more derived status of hispanopithecins, in Figure 8b we have further considered them less basal than dryopithecins while leaving unresolved if the latter constitute a clade with kenyapithecines.

In the following subsections, we discuss some of the most vexing unresolved enigmas of Miocene ape evolution in terms of phylogeny and paleobiogeography by taking into account not only molecular estimates of divergence times and the additional evidence provided by the fossil record (chronostratigraphic ranges and geographic distribution), but also the more vs. less basal divergence hypotheses for hylobatids depicted in Figure 8. These unresolved issues are the following: (1) What are the closer phylogenetic relationships of *Oreopithecus*; (2) What is the evolutionary origin of hylobatids, i.e., where do we draw the cladistic boundary between stem and crown hominoids; (3) When and where did pongines and hominines diverge, and what is the role that dryopithecines and graecopithecins played in the origin and subsequent diversification of the hominid clade.

4.3. The perplexing enigma of Oreopithecus

Uncertainties about the phylogenetic relationships of *Oreopithecus*, from the Late Miocene of Italy, are "especially perplexing because *Oreopithecus* is one of the best-known fossil primates" (Harrison and Rook, 1997: 328). A skeleton discovered in 1958 led Straus (1963) to conclude that *Oreopithecus* was either a 'hominid' s.s. or a member of a separate hominoid family, whereas Hürzeler (1958, 1968) more explicitly considered *Oreopithecus* a side branch of the human lineage. However, the bizarre dental morphology of *Oreopithecus*, coupled with its peculiar cranial morphology and modern hominoid-like postcranium led to varied interpretations over the years (see review in Delson, 1986). Harrison (1986, 1987a) advocated a phylogenetic link between *Oreopithecus* and nyanzapithecids, while supporting its hominoid status based on the contention that its postcranial similarities with extant apes "are so detailed that there seems little possibility that they could have been developed independently" (Harrison, 1987a: 541). Similar views were stated by Sarmiento (1987: 35):

"given the evidence of the forelimb anatomy and associated shape of the thorax, this form [*Oreopithecus*] cannot be interpreted as anything but a hominoid". Sarmiento (1987) noted that, in some aspects, *Oreopithecus* is more hylobatid-like than great ape-like, and put forward two possible interpretations: either *Oreopithecus* retained the crown-hominoid plesiomorphic condition; or *Oreopithecus* is a large-bodied hylobatid.

Given Harrison's (1986, 1987a, 1987b) views about the synapomorphic nature of crown hominoid postcranial similarities (see Section 2.3), Harrison and Rook (1997: 347) still maintained that "the postcranial characteristics shared by *Oreopithecus* and the extant hominoids are so pervasive throughout the skeleton that it is almost impossible to consider that these could have been developed independently to such a remarkable degree of detail in *every* anatomical region." The same opinion was held by Pilbeam (1996, 1997), who considered *Oreopithecus* as the most secure modern Miocene hominoid. Nevertheless, Harrison and Rook (1997) abandoned Harrison's (1986, 1987a) former views about a close phylogenetic link with nyanzapithecids and, like Moyà-Solà and Köhler (1997), hypothesized that *Oreopithecus* is a derived dryopithecine. The postcranial similarities between *Oreopithecus* and *Hispanopithecus* (Moyà-Solà and Köhler, 1996) were determinant in these proposals of a great ape status for *Oreopithecus*, even if also supported by some cranial features—such as the configuration of the incisive canal and the lack of subarcuate fossa (Harrison and Rook, 1997; Moyà-Solà and Köhler, 1997), whose reliability as hominid synapomorphies is currently doubtful (see next subsection). A hominid status for *Oreopithecus* would not only imply dental convergences with nyanzapithecids (see discussion in Rossie and Cote, 2022), but also that its cranial morphology is autapomorphic (Harrison and Rook, 1997; Moyà-Solà and Köhler, 1997; Alba et al., 2001) rather than symplesiomorphic for crown hominoids, as generally assumed (Harrison, 1987a; Sarmiento, 1987; Begun et al., 1997; Begun, 2002a, 2013, 2015; Pugh, 2022).

Begun et al.'s (1997, 2012) cladistic analyses recovered *Oreopithecus* as a stem hominid, and its hominid status was generally accepted until about a decade ago (e.g., Wood and Harrison, 2011; Alba, 2012), with some exceptions restating the link with nyanzapithecids (Benefit et al., 1998; Benefit and McCrossin, 2001). Subsequent cladistic analyses, including a wider representation of Early and Middle Miocene apes, recovered *Oreopithecus* as deeply nested within the nyanzapithecid clade (Nengo et al., 2017; Gilbert et al., 2020a)—in agreement with Harrison's (1986, 1987a) former opinion. Most recently, Pugh's (2022) analyses hinted at a possible close relationship between *Oreopithecus* and *Samburupithecus* and provided some support for considering both taxa as stem hylobatids. The link between *Oreopithecus* and *Samburupithecus*, given the previously noted dental similarities between the latter taxon and nyanzapithecids (Harrison, 2010a), is consistent with previous cladistic analyses supporting that *Oreopithecus* is a derived nyanzapithecid (Nengo et al., 2017; Gilbert et al., 2020a), in further agreement with previously noted similarities between *Oreopithecus* and members of this family (Leakey, 1968; Harrison, 1986, 1987a, 1992, 2010a). In contrast, the stem hylobatid status recovered by Pugh (2022) must be considered poorly supported at present, given the lack of nyanzapithecids in her analyses and the highly divergent results obtained for *Oreopithecus* based on craniodental and postcranial characters. As noted by Pugh (2022), similarities between *Oreopithecus* with hylobatids include a few craniodental features present in some putative stem hominoids (e.g., elongate fourth premolars as in nyanzapithecids) and even stem catarrhines (an anteriorly protruding rhinion), thus being likely symplesiomorphic, coupled with multiple modern hominoid-like postcranial characteristics that are most likely homoplastic between crown hominoids.

Therefore, Pugh (2022) concluded that *Oreopithecus* is most reasonably interpreted as a stem hominoid.

That the link between *Oreopithecus* and hylobatids retrieved by Pugh (2022) is not entirely attributable to postcranial similarities is confirmed by the fact that craniodental features alone support this link (while postcranial characteristics favor a more advanced status toward hominids). Nevertheless, a stem hominoid status for *Oreopithecus* is further supported by the morphology of the inner ear semicircular canals, which despite some similarities in proportions with extant great apes is much more primitive and does not show particular similarities with that of hylobatids (Urciuoli et al., 2020, 2021a, 2021b). On the other hand, the homologies hypothesized between *Oreopithecus* and nyanzapithecids in lower molar cristids (Rossie and Cote, 2022) are suggestive but questionable, so it is probably too early to confidently rule out their independent evolution. Analyses of enamel–dentine junction shape (currently underway) would be required to better evaluate these dental similarities, but preliminary results indicate close morphometric affinities between *Oreopithecus* and stem catarrhines (Zanolli et al., 2022a), supporting further that the former is not a crown hominoid. Taken overall, current evidence lends greater support to the hypothesis that *Oreopithecus* is a late descendant of an ancient hominoid lineage (maybe nyanzapithecids) that dispersed from Africa into Tusco-Sardinia sometime before 8 Ma and acquired orthograde-related features independently from crown hominoids. However, given that the branching order between nyanzapithecids and crown hominoids does not appear reliable (see Section 5.1), the possibility that *Oreopithecus* and some nyanzapithecids are stem hylobatids deserves further consideration in the future.

4.4. The vexing problem of hylobatid origins

The fossil record indicates that hominoids originated in the Oligocene (Stevens et al., 2013; Hammond et al., 2019) and first radiated during the Early Miocene in Afro-Arabia (Harrison, 2010a), when this continent was isolated from Eurasia by the Tethys Seaway (Bernor, 1983; Seiffert, 2012; Begun et al., 2012). By ~19 Ma, the emergence of an intermittent land-bridge allowed intercontinental faunal exchanges between Africa and Eurasia (Harzhauser et al., 2007), even if temporarily interrupted by the Langhian transgression at ~16 Ma (Rögl, 1999), leading to the eventual dispersal of multiple catarrhine lineages into Eurasia at different times (Roos et al., 2019; Gilbert et al., 2020b). Stem catarrhines (pliopithecoids) were apparently the first group to disperse, being first recorded at ~19–18 Ma in Asia (Harrison and Gu, 1999; Begun, 2002b, 2017; Harrison, 2013; Harrison et al., 2020). Large-bodied putative hominids followed soon thereafter, being first recorded by kenyapithecines (*Griphopithecus* and *Kenyapithecus*) at ~16.5–14 in Europe and Turkey (Heizmann and Begun, 2001; Andrews and Kelley, 2007; Casanovas-Vilar et al., 2011), and subsequently by dryopithecines in Europe and pongines in Asia from ~13–12.5 Ma onward (Kelley, 2005; Alba, 2012; Begun, 2015; Gilbert et al., 2020b). However, the scarce record of Miocene hylobatids (Harrison, 2016; Ji et al., 2022), coupled with phylogenetic uncertainties (Fig. 8), hinders an adequate understanding of hylobatid origins.

Molecular estimates strongly support that hylobatids and hominids diverged during the Early Miocene (i.e., before the Langhian transgression), probably ~20–17 Ma, although the large confidence intervals of some of these estimates do not completely rule out a later divergence in the early Middle Miocene: 20.3 (24.2–16.5) Ma (Perelman et al., 2011), 17.4 (23.9–12.4) Ma (Springer et al., 2012), 20.3 (23.5–17.4) Ma (Finstermeier et al., 2013), and 16.8 (17.6–15.9) Ma (Carbone et al., 2014). Given that their oldest unambiguous fossil record (*Yuanmoupithecus*) dates to the latest Miocene (8.2–7.1 Ma; Harrison, 2016; Ji et al., 2022), hylobatids have a long ghost lineage. Furthermore, molecular data indicate that crown members of the group did not diverge from one another until the latest Miocene (Perelman et al., 2011; Springer et al., 2012; Finstermeier et al., 2013; Carbone et al., 2014), which implies that stem hylobatids might lack most of the derived features shared by *Yuanmoupithecus* and crown hylobatids.

Decades ago, pliopithecoids were considered broadly ancestral to hylobatids (Hürzeler, 1954; Zapfe, 1958, 1961; Simons and Fleagle, 1973; Andrews and Simons, 1977). However, such an assumption was based on superficial cranial and postcranial similarities and is no longer tenable given the widely-accepted stem catarrhine status of pliopithecoids (e.g., Zalmout et al., 2010; Stevens et al., 2013; Nengo et al., 2017; Gilbert et al., 2020a; Urciuoli et al., 2021b). The latter is supported by the lack of crown catarrhine synapomorphies and the retention of multiple plesiomorphic features (e.g., incompletely ossified ectotympanic, entepicondylar foramen in the distal humerus, and single hinge-like carpometacarpal thumb joint; Zapfe, 1961; Harrison, 1987b, 2005; Andrews et al., 1996; Begun, 2002b, 2017). According to this interpretation, hylobatids must represent an independent dispersal event from those of pliopithecoids. It has generally been assumed that hylobatids and large-bodied hominoids from Eurasia are the result of at least two different dispersal events from Africa (Moyà-Solà et al., 1999b; Roos et al., 2019; Gilbert et al., 2020a), either synchronous or diachronous. Gilbert et al. (2020a) suggested that this dispersal event took place from Africa into Asia just after the Mid-Miocene Climatic Optimum. However, in the light of the molecular estimates of crown hominoid divergence time reported above, hylobatids could have alternatively dispersed somewhat earlier, before than Langhian transgression (19–16 Ma), like pliopithecoids (see above). Both alternatives are possible, as a pre-Langhian divergence time does not exclude a later dispersal event of hylobatid ancestors from Africa into Eurasia.

Gilbert et al. (2020a) further hypothesized that hylobatids might have originated from a dendropithecid or purported stem hominoid (Proconsulidae s.l.) from the Early Miocene of Africa. Hypothetical basalmost hylobatids might be simply unknown or currently unrecognized as such among the multiple small-bodied catarrhine genera of uncertain affinities from Early Miocene of Africa. An origin from dendropithecids (sensu Harrison, 2010a) is plausible on chronological grounds, as they are first recorded in the Early Miocene (e.g., Harrison, 2010a), but would imply that at least some dendropithecids are crown hominoids instead of the stem catarrhines (as supported by Rossie and Hill, 2018, who recovered *Dendropithecus* Andrews and Simons, 1977 and *Simiolus* Leakey and Leakey, 1987 as basal nyanzapithecids). Cladistic analyses have generally recovered dendropithecids as stem catarrhines (Nengo et al., 2017; Gilbert et al., 2020a) or as stem hominoids at most (Rae, 1999, 2004; Zalmout et al., 2010; Alba et al., 2015; Rossie and Hill, 2018), such that a crown hominoid status for dendropithecids lacks cladistic support except perhaps for *Micropithecus*. Originally interpreted as a hylobatid relative based on facial morphology (Fleagle and Simons, 1978), *Micropithecus* and other dendropithecids were subsequently reinterpreted as stem catarrhines given the lack of crown catarrhine postcranial synapomorphies (e.g., Harrison, 1987b, 2002, 2010a), with cranial similarities with hylobatids being interpreted as symplesiomorphic. However, *Micropithecus* was tentatively considered a hominoid (‘proconsuloid’) by Begun (2015) based on its moderately developed molar cingula, and most recently recovered as a stem hylobatid more basal than *Yuanmoupithecus* by Ji et al. (2022). Even if the latter authors attributed this result to dietary convergence, the possibility that hylobatids may be closely related to some dendropithecids should be scrutinized further when more complete material becomes available.

Alternatively, hylobatids (or even crown hominoids as a whole) might have evolved from putative stem hominoids from the Early or Middle Miocene of Africa, i.e., proconsulids or nyanzapithecids. The Oligocene record of both proconsulids and nyanzapithecids (Stevens et al., 2013; Hammond et al., 2019) supports an early divergence between these families, while afropithecids are not recorded until later. Although some recent cladistic analyses recovered a monophyletic nyanzapithecid clade that nests within afropithecids (Nengo et al., 2017; Gilbert et al., 2020a; but see Rossie and Hill, 2018 for a different topology), the Oligocene age of *Rukwapithecus* and another indeterminate nyanzapithecids (Stevens et al., 2013; Hammond et al., 2019) is at odds with its nesting well within the nyanzapithecid radiation. This suggests that the relationships between nyanzapithecids, afropithecids, and crown hominoids are not well resolved. The less basal divergence hypothesis for hylobatids (Fig. 8a) suggests that they are a dwarfed lineage (Pilbeam, 1996; Reichard et al., 2016) evolved from an afropithecid-like ancestor, which is compatible with molecular estimates and with either one or two dispersal events of crown hominoids into Eurasia during the Early and/or Middle Miocene. In contrast, the basal divergence hypothesis for hylobatids (Fig. 8b) favored by craniodental data suggests that they originated from a nyanzapithecid-like (or proconsulid-like) ancestor, is in better agreement with average divergence times estimated from molecular evidence, and requires two dispersal events of crown hominoids into Eurasia. The craniodental similarities shared between nyanzapithecids and hylobatids (e.g., relatively short face, broad interorbital distance, and projecting orbits; Nengo et al., 2017) may be interpreted as the plesiomorphic condition for crown hominoids and, hence, neither favor nor contradict a possible origin of hylobatids from more or less derived nyanzapithecids (which would imply that the latter are paraphyletic). Dendropithecids and proconsulids seem more unlikely ancestors for hylobatids given the results of cladistic analyses, but the plausibility of an afropithecid-like—as opposed to nyanzapithecid-like—ancestor, or a Eurasian divergence between hylobatids and hominids following a single dispersal event from Africa, largely depends on the extent to what most parsimonious cladistic analyses are biased by postcranial homoplasy between hylobatids and hominids.

4.5. The elusive origin of the great ape and human clade

Equatorines The uncertain monophyly and phylogenetic relationships of afropithecids are illustrated by the fact that they have been hypothesized as stem hominids by various researchers (Andrews, 1992, 1996; Ward and Duren, 2002) whereas others have considered that at least afropithecines would precede the hylobatid–hominid divergence (e.g., Moyà-Solà et al., 2009b; Casanovas-Vilar et al., 2011; Alba, 2012; Begun, 2015; Andrews, 2020). As discussed in the preceding subsection, deciding whether afropithecids are stem hominoids, as favored by most parsimonious cladograms (Nengo et al., 2017; Gilbert et al., 2020a; Pugh, 2022), instead of stem hominids, as supported by craniodental evidence (Pugh, 2022), depends on their branching sequence relative to hylobatids (Fig. 8). Afropithecids are recorded in the Early Miocene before 17 Ma, and probably at least by 20 Ma if the older dating of *Morotopithecus* is correct (see Section 3.4), which roughly coincides with the average divergence time between hylobatids and hominids estimated on molecular grounds, and is thus compatible with both possibilities.

The phylogenetic relationships of the equatorine *Nacholapithecus* are particularly controversial. Some authors have considered it as a stem hominid (Alba, 2012; Kunimatsu et al., 2019) largely based on the possession of an elongated and procumbent premaxilla that slightly overlaps the maxillary palatine process (Ishida et al., 2004; Kunimatsu et al., 2004; Nakatsukasa and Kunimatsu, 2009). This condition is more derived than that of hylobatids, which differ from both pongines and hominines in the lack of premaxillary-maxillary overlap (Ward and Kimbel, 1983; McCollum et al., 1983; McCollum and Ward, 1997). Except pongines, other Miocene apes also lack a clear overlap, although dryopithecines (and maybe afropithecines to a lesser extent) display a more derived condition than proconsulids and hylobatids, with the posterior pole of the premaxilla closely approaching or minimally overlapping the palatine process of the maxilla (Ward and Kimbel, 1983; Begun, 1994; Moyà-Solà and Köhler, 1995; McCollum and Ward, 1997; Brown et al., 2005; Moyà-Solà et al., 2009a; Pérez de los Ríos et al., 2012; Pugh, 2022). Based on current fossil evidence, it is not possible to determine whether the divergent subnasal configuration of orangutans and African apes independently evolved from a dryopithecine-like condition, or whether gorillas retain the plesiomorphic configuration for crown hominids. This makes it difficult to interpret whether the derived condition of *Nacholapithecus* is homologous with that of crown hominids (Kunimatsu et al., 2019) or merely homoplastic (Pugh, 2022)—although the more plesiomorphic subnasal configuration of dryopithecines supports the latter view as long as they are interpreted as stem hominids less basal than equatorines.

The potential stem hominid status of *Nacholapithecus* has been reinforced by the report that this taxon has an obliterated subarcuate fossa (Kunimatsu et al., 2019), which is similarly absent or very shallow in dryopithecines (*Hispanopithecus* and *Rudapithecus*; Moyà-Solà and Köhler, 1993, 1995; Kordos and Begun, 1997, 2001). However, as admitted by Kunimatsu et al. (2019), a well-developed subarcuate fossa is variably absent in cercopithecoids and hylobatids (Spoor and Leakey, 1996), indicating that its phylogenetic value must be interpreted with care, given its variability and the possibility that its obliteration could be homoplastic in various stem hominoids (Pugh, 2022). The latter contention is further reinforced by the lack of the subarcuate fossa in *Oreopithecus* (Harrison and Rook, 1997; Moyà-Solà and Köhler, 1997), currently most parsimoniously interpreted as a stem hominoid (see Section 4.3).

Current morphological support for the stem hominid status of *Nacholapithecus* is thus somewhat ambiguous, although craniodental data support equatorines as stem hominids when postcranial features are ignored (Pugh, 2022) and this systematic position appears most likely under a basal divergence hypothesis for hylobatids (Fig. 8b). As remarked by Kunitmatsu et al. (2019), a hominid status for *Nacholapithecus* would provide additional support to the contention that not only suspensory behaviors (Moyà-Solà et al., 2004; Pugh, 2022) but also an orthograde body plan (Alba, 2012) would have been independently acquired by hylobatids and hominids. Given that equatorines roughly coincide in age (~16–15 Ma) with crown hominid divergence average dates estimated from molecular data—16.5 (19.7–13.5) Ma (Perelman et al., 2011) and 15.1 (20.8-11.0) Ma (Springer et al., 2012)—these neither favor nor preclude a crown hominid (e.g., hominine) status for *Nacholapithecus*. However, this possibility is not favored by most parimonious cladograms even if based on craniodental evidence alone (Pugh, 2022), and hence it is much more unlikely that a stem hominid status.

<u>Kenyapithecines and dryopithecines</u> Unlike in the case of *Nacholapithecus*, the hominid status of *Kenyapithecus* is much better supported by cladistic analyses, albeit with some discordant results. Begun et al. (1997) recovered *Kenyapithecus* s.l. (including *Equatorius*) as a stem hominoid, while Begun et al. (2012) recovered *Griphopithecus* as a stem hominoid and *Kenyapithecus* as a stem hominid. More recently, *Kenyapithecus* was supported as a pongine (Nengo et al., 2017; Gilbert et al., 2020a) or as a stem hominid together with

Griphopithecus (Pugh, 2022). The latter view had been favored by Alba (2012), in agreement with many previous authors (see Section 3.6) and the interpretation that the craniodental similarities between *Kenyapithecus* and pongines are symplesiomorphic (Harrison, 1992, 2010a).

Kenyapithecus stands out from a paleobiogeographic viewpoint because it is the only Miocene ape genus thus far recorded both in Africa and Eurasia, but a clear-cut interpretation of this fact is obscured by its uncertain phylogenetic relationships with dryopithecines and crown hominids (Almécija et al., 2021). Based on the record of a possible kenyapithecine in Europe before the Langhian transgression (Heizmann and Begun, 2001; Casanovas-Vilar et al., 2011), Gilbert et al. (2020b) suggested that apes might have followed a more westward dispersal route from Africa into Eurasia than the ancestors of pliopithecoids, subsequently dispersing into Asia sometime between 16 and 13 Ma. However, the larger samples of *Griphopithecus* and *Kenyapithecus* (Alpagut et al., 1990; Begun, 1992c, 2002a; Begun et al., 2003b; Kelley et al., 2008) are not recorded until somewhat later (~14.5–14.0 Ma) in Turkey (see discussion in Casanovas-Vilar et al., 2011 and Gilbert et al., 2020b, regarding the older dates favored for these sites by some other authors). It is generally assumed that *Kenyapithecus* dispersed from Africa into Eurasia (Andrews and Kelley, 2007; Alba, 2012) rather than the other way around, as an excessively literal reading of the fossil record might suggest (Begun, 2000). However, it is uncertain whether Eurasian kenyapithecines originated from a single dispersal event (as suggested by the close phylogenetic link between *Kenyapithecus* and *Griphopithecus* recovered by Pugh, 2022) or two (pre- and post-Langhian) dispersals from Africa.

Sometime after kenyapithecines are first recorded in Turkey, both pongines and dryopithecines are recorded in Asia and Europe, respectively, ~13.0–12.5 Ma. Not surprisingly, thus, transcontinental dispersal events followed by vicariant divergence have played a major role in the interpretation of the Eurasian hominoid radiation (Agustí et al., 1996; Andrews and Bernor, 1999; Begun, 2005). However, the recognition that at least some species formerly included in *Lufengpithecus* lack pongine synapomorphies (Kelley and Gao, 2012; Ji et al., 2013; Pugh, 2022) requires a more complicated paleobiogeograpic interpretation (Begun and Kelley, 2016), which is nevertheless obscured by phylogenetic uncertainties regarding dryopithecines and graecopithecins (see Section 3.7). Agustí et al. (1996) and Köhler et al. (2001), following Moyà-Solà and Köhler (1993, 1995), hypothesized that, after the hominoid dispersal into Eurasia, hominines evolved in Africa, with dryopithecines and graecopithecins being successive members of the pongine stem lineage less closely related to orangutans than *Sivapithecus*. This scenario is very reasonable from a paleobiogeographic perspective (Andrews and Bernor, 1999), but not supported by most parsimonious cladograms, which favor a stem hominid status for dryopithecines (Alba et al., 2015; Pugh, 2022). In contrast, based on the hominine hypothesis for both dryopithecines and graecopithecins, Begun and coauthors initially discussed different paleobiogeograpic scenarios (Begun, 1994, 1995; Begun et al., 1997) but ultimately more actively promoted a Eurasian origin and early divergence of crown hominids, followed by a subsequent back-to-Africa dispersal of the latter in the Late Miocene (Begun, 2001, 2002a, 2005, 2009, 2010, 2013, 2015, 2016; Begun et al., 2003a, 2012; Begun and Nargolwalla, 2004).

Moyà-Solà et al. (2009b) advocated the view that dryopithecines are closely related to kenyapithecines and considered likely a Eurasian origin of crown hominids, but did not discount an independent evolution of hominines and pongines in Africa and Eurasia, respectively, from similar kenyapithecine ancestors—which is essentially the same hypothesis proposed by Agustí et al. (1996). Alba (2012), despite classifying dryopithecines as stem hominids, further commented on the possibility that pongines and hominines evolved separately in different continents from similar kenyapithecine ancestors. According to this hypothesis, dryopithecines would be more closely related to pongines—in which case, as noted by Alba (2012) and Almécija et al. (2021), orthogrady would have had to independently evolve not only between hylobatids and hominids, but also between hominines, pongines (as currently conceived), and dryopithecines. While the latter is plausible in the light of the postcranial evidence available for taxa such as *Pierolapithecus* and *Sivapithecus* (see Section 3.7), the cranial similarities noted by some previous authors between dryopithecines and pongines (Moyà-Solà and Köhler, 1993, 1995; Pérez de los Ríos et al., 2012) do not provide sufficient support to this hypothesis according to most recent cladistic analyses (Pugh, 2022) and support instead that even hispanopithecins (which appear less basal than kenyapithecines and dryopithecins) are stem hominids. The inclusion of *Danuvius*—chronologically intermediate between dryopithecins and hispanopithecins (Böhme et al., 2019)—in a formal cladistic analysis might help disentangle the phylogenetic relationships between dryopithecins and hispanopithecins, given that this genus also appears morphologically intermediate between them (Almécija et al., 2021). However, clarifying the phylogenetic relationships of dryopithecines would probably require as well more complete fossils around the Middle/Late Miocene from Europe (Alba et al., 2022) and China (Begun and Kelley, 2016).

Although Pugh’s (2022) analyses generally support hispanopithecin monophyly, the support of *H. laietanus* as a stem pongine and of *R. hungaricus* as a stem hominine by her craniodental analyses parallels the previous cladistic results by Cameron (1997a), which led this author to resurrect *Hispanopithecus*. If supported by additional evidence, this topology would imply a Eurasian divergence of crown hominids—albeit not in the usual sense in which hispanopithecines are all considered hominines (e.g., Begun, 2005). Pugh's (2022) support for the stem hominine status of graecopithecins is also consistent with a Eurasian divergence of crown hominids followed by a Late Miocene dispersal of hominines into Africa. However, as explained in Section 3.7 (see also SOM S4), we do not consider this phylogenetic link to be sufficiently supported at present. In any case, its paleobiogeographic implications would be less straightforward than the purported hominine status for some dryopithecines, given the stem hominine status further supported by Pugh (2022) for *Nakalipithecus* from the Late Miocene of Africa.

Before the finds of *Nakalipithecus* and *Chororapithecus* (Kunimatsu et al., 2007; Suwa et al., 2007), the lack of unambiguous great apes during the late Middle Miocene and early Late Miocene of Africa was used to support the view that hominines originated in Europe (e.g., Begun, 2001)—even though, as pointed by Cote (2004), the absence of ape fossils was largely attributable to low sampling effort or inadequate habitat sampling. The existence of such a gap in the African hominid record is no longer tenable for the Late Miocene, although the support for the hominine status of *Nakalipithecus* and *Chororapithecus* is tenuous at best. Both the oldest graecopithecin (*O. macedoniensis*) and *Nakalipithecus* predate the average molecular dates between gorillins and other hominines—8.3 (10.1–6.6) Ma (Perelman et al., 2011) or 8.0 (11.7–5.5) Ma (Springer et al., 2012). This fact suggests that these taxa, unlike *Chororapithecus*, are unlikely to be crown hominines based on their chronology, although this remains a possibility given the uncertainty range of molecular divergence dates.

While the phylogenetic relationships of *Chororapithecus* cannot be properly evaluated (see Section 3.7), the potential link between *Nakalipithecus* and graecopithecins, if confirmed, would be suggestive of an intercontinental connection during the Late Miocene.

Nevertheless, the less derived morphology of *Nakalipithecus* (Kunimatsu et al., 2007), in agreement with its slightly older dating, might be interpreted to support instead an African origin and subsequent dispersal into Eurasia of graecopithecins. A European origin of graecopithecins from derived dryopithecines such as hispanopithecins would be consistent with their known fossil record in chronological terms. However, according to Pugh's (2022) results—which recover hispanopithecins as advanced stem hominids and graecopithecines as stem hominines—this would imply that hispanopithecins gave rise to both pongines and hominines, which is at odds with the older (>2 Myr) record of pongines as compared with hispanopithecins.

Other possibilities would be: (1) graecopithecins represent a dispersal event of stem hominines from Africa into Eurasia (also consistent with the most parsimonious results of Pugh, 2022); (2) graecopithecins are stem hominids evolved from hispanopithecins that represent an evolutionary dead-end (not supported by the results of Pugh, 2022); or (3) ouranopithecins and at least some hispanopithecins are stem hominines (only supported by the craniodental analysis of Pugh, 2022). Only the latter possibility necessarily entails a hominine dispersal back to Africa, whereas Pugh's (2022) best supported alternative implies a dispersal event that might have been in either direction. Therefore, the place of origin of hominines seems difficult to determine until more complete Late Miocene hominids from Africa are discovered, although the various alternatives discussed above illustrate why clarifying the phylogenetic relationships of dryopithecines is also key for clarifying this question.

5. Discussion

5.1. Something is rotten in Miocene ape phylogeny

Despite the progress made during the last decades in terms of Miocene ape systematics, many phylogenetic and paleobiogeographic uncertainties persist. Some of them, such as the systematic status of equatorines and the potential paraphyly of dryopithecines, might seem of relatively minor relevance for understanding the big picture of hominoid evolution, even if they have potentially deeper implications for the origin of crown hominids. In contrast, the enduring uncertainties about origin of hylobatids appear of utmost importance, given the implications of its branching topology to determine the systematic (stem vs. crown hominoid) status of Early Miocene apes.

The parsimony analyses published during the last decade support a less basal divergence of hylobatids that implies a stem hominoid status for all Early and Middle Miocene apes from Africa except *Kenyapithecus*. This is the view that—coupled with some uncertainties regarding some Eurasian taxa (such as oreopithecins and graecopithecins)—has been reflected it in the systematic classification used in this work. Nevertheless, several lines of evidence strongly suggest that such an advanced branching of hylobatids is probably amiss: (1) Molecular estimates for the hylobatid–hominid divergence predate by several million years the oldest record of stem hominids and hylobatids; (2) A separate analysis of craniodental and postcranial data yields strikingly different topologies for hylobatids—with postcranial data excluding most Miocene apes from the crown hominoid clade, and craniodental evidence supporting the crown hominoid status of equatorines; and (3) Bona fide Miocene great apes (especially *Pierolapithecus* and *Sivapithecus*) support the independent evolution of suspensory and orthogrady-related features along various crown hominoid lineages.

Discrepancies between two subsets of data taken from a single taxon-character matrix are inevitable, as the resulting most parsimonious cladograms will be but sampling estimates of the true (parametric) phylogeny (Rodrigo et al., 1993). However, highly discrepant results may also highlight the presence of insufficient (or misleading) phylogenetic signal in one or all of the analyzed subsets. In general, combining different morphological datasets in a total evidence analysis is preferable, as this procedure may reveal hidden support that is not evident from each dataset separately (de Queiroz and Gatesy, 2007). Nevertheless, if one dataset is systematically affected by homoplasy in a particular given direction (as in the assumption of postcranial paralellism between hylobatids and hominids), then the results of the total evidence analysis might be less accurate than those yielded by the other dataset (i.e., craniodental data). This suggests that the relative branching order among hylobatids and putative stem hominoids from Africa other than proconsulids might be less reliable (potentially less accurate) than other phylogenetic relationships recovered by the analysis.

Pugh's (2022) results based on postcranial data evoke Pilbeam's (1997) contention that most Miocene apes except *Oreopithecus* likely belong to an 'archaic' radiation not directly related to modern hominoids. Paradoxically, *Oreopithecus* is the taxon that most clearly evinces the contradictory signal provided by craniodental and postcranial data. The detailed phylogenetic affinities of *Oreopithecus* deserve further investigation but multiple lines of craniodental evidence (from the facial morphology to the inner ear anatomy and tooth endostructural shape) support that it is a late descendant of an ancient lineage more basal than crown hominoids. The incongruent signal displayed by *Oreopithecus* is the opposite of that of *Sivapithecus* but highlights the same problem.

Pilbeam (1997) and Harrison and Rook (1997) argued that the traditional tendency to invoke postcranial rather than cranial homoplasy was a historical bias owing to the scarcity of hominoid postcranial remains. However, these views were soon challenged by Larson (1998), who advocated parallelism between lesser and great apes. Subsequent discoveries have largely supported Larson's (1998) views that there are good reasons to mistrust the purported postcranial synapomorphies of crown hominoids (Moyà-Solà et al., 2004; Alba, 2012; Ward, 2015): the fact that *Pierolapithecus* and *Sivapithecus* are recovered as a stem hominid and as a pongine, respectively, by most parsimonious cladograms (Pugh, 2022), despite lacking some of the derived postcranial features shared by crown hominids, supports the view that these features are homoplasies rather than true synapomorphies. Under this view, the hominoid postcranium would be prone to evolve the same features again and again as long as it is subject to similar positional selection pressures. The fact that cladistic analyses can resolve the *Sivapithecus* dilemma could be taken as an indication that postcranial homoplasy can be readily overcome by parsimony analysis. However, in reality we cannot know how often and to what extent the potentially misleading evidence provided by the postcranial remains may override the true phylogenetic signal.

The problem of abundant homoplasy has long been recognized in paleoanthropology (e.g., Fleagle, 1997; Larson, 1998; Lockwood and Fleagle, 1999; Young, 2003; Begun, 2007). Although homoplasies may result from character misscoring, in most cases they reflect a real biological phenomenon resulting from evolutionary constraints and/or recurrent selective pressures during evolution (Felsenstein, 1978; Lockwood and Fleagle, 1999; Begun, 2007). The fact that, on epistemological grounds, homoplasies cannot be determined a priori but must be identified a posteriori based on most parsimonious cladograms (see SOM S1.3) does not mean that they can be discarded as uninteresting ad hoc hypotheses or phylogenetic 'noise'—rather the contrary, they should be scrutinized on the basis of morphofunctional and developmental considerations (Fleagle, 1997; Lockwood and Fleagle, 1999; Begun, 2007). Nevertheless, this is more easily said than done. In practice, there is no other option but to rely on most parsimonious cladograms based on all available evidence, even if it suspected (as in this case) that homoplasy is more prevalent in a particular anatomical area. This does not prevent the results from being potentially biased by differential degrees of homoplasy between the cranium and the postcranium because the result will be "heavily dependent on which morphological area can muster the greater number of characters" (Andrews and Pilbeam, 1996: 124).

The fact that most cladistic studies show a large minimum level of homoplasy (Fleagle, 1997; Begun, 2007) represents a caveat for retrieving phylogenetic signal because morphological characters, in practice, are potentially exhaustible (Felsenstein, 1978) so that data matrices can become saturated by excessive homoplasy as clades age (Wagner, 2000). This saturation erodes and can even override true phylogenetic signal, leading to a long-branch attraction problem (Wagner, 2000; Bergsten, 2005). The latter occurs when lineages that have undergone many changes artifactually appear too closely related (Bergsten, 2005), either because phylogenetic signal has been saturated or because the long branches converge on similar morphologies. Cladistic analyses are expected to be more prone to long-branch attraction than other methods of phylogenetic inference because parsimony does not take into account the lengths of the branches and hence tends to underestimate the amount of change in long branches (Pagel, 1999).

To conclude that postcranial homoplasies are causing a long-branch attraction problem between hylobatids and hominids we would need independent evidence that most parsimonious cladograms are yielding inaccurate results (Brower, 2017). Of course, we do not have such evidence, but the highly contradictory results yielded by craniodental and postcranial datasets (Pugh, 2022) point to this direction. Hylobatids, hominids, and *Oreopithecus* are the longest branches of hominoid phylogeny from the viewpoint of their duration and they all display postcranial adaptations for antipronograde behaviors.

Therefore, the conditions for a long-branch attraction problem are undoubtedly met, being further aggravated by the high number of missing data. According to this, parsimony analyses might potentially recover hylobatids and hominids as more closely related than they actually are (relative to Early and Middle Miocene hominoids) simply because they have had more time to accumulate morphological changes.

5.2. Future directions of work

The possibility that Miocene ape most parsimonious cladograms are biased by a long-branch attraction problem that systematically recovers hylobatids as too closely related to hominids has far-reaching implications: even if Pilbeam's (1996, 1997) views about the synapomorphic nature of extant hominoid postcranial similarities have been progressively abandoned during the last two decades, they would still exert a powerful—even if largely unconscious—influence simply because of the way cladistics works (see SOM S1.3) and the fragmentary nature of the ape fossil record. Abandoning postcranial characters in Miocene ape phylogenetic inference is not an option, both from an epistemological perspective and on more practical grounds. We agree with previous authors (e.g., Ward, 2015; Pugh, 2022) that the incongruence between craniodental and postcranial features does not imply that the latter are not useful in hominoid phylogenetics. So, how can we make progress? In the following, we outline future directions of research, with emphasis on the possibilities offered by recent developments in phylogenetic inference.

<u>More and better fossils and analyses</u> From the viewpoint of fieldwork, finding additional remains of Miocene apes will always be most helpful, not only to increase taxon sampling but especially to reduce the proportion of missing data. Too many Miocene ape genera are still known mainly from fragmentary dentognathic remains, so that partial skeletons of

Miocene apes with associated craniodental remains would be particularly welcome. This is not an easy task because fossil hominoids tend to be comparatively less abundant than many other mammalian taxa, and thus their finding generally requires a large sampling effort (Cote, 2004; Alba et al., 2017).

More detailed morphological analyses could also increase the number of phylogenetically informative characters analyzed. These efforts should ideally be focused on craniodental features that embed strong phylogenetic signal (sensu Blomberg and Garland, 2002)—such as the semicircular canals of the inner ear (Urciuoli et al., 2020, 2021a, 2021b) or enamel–dentine shape (Zanolli et al., 2022b)—because a priori they appear less prone to (albeit not entirely devoid of) homoplasy than other features with a greater functional signal (such as postcranial remains; e.g., Arias-Martorell et al., 2021). Automated quantitative morphometric methods would further reduce the inherent subjectivity of cladistic analyses. One of the main merits of cladistics—besides the computer-assisted analysis of large amounts of data—is the obligation to be transparent about the data upon which most parsimonious cladograms are based, by elaborating taxon-character matrices that can be scrutinized by other scholars. Nevertheless, in morphology-based phylogenetic inference there is still a subjective component in the selection, definition, and scoring of the characters employed (Pilbeam and Young, 2001; Cartmill, 2018). This subjectivity is much greater than in molecular phylogenetics (Scotland et al., 2003), to the extent that the “often subjective nature of discrete character coding can generate discordant results that are rooted in individual researchers’ subjective interpretations” (Parins-Fukichi, 2017: 328). This makes obtaining different results unavoidable, largely depending on the researchers’ unconscious preconceptions, informed preferences, and anatomical expertise. The *Ramapithecus* debate illustrates “the power of preconceptions” as we as paleoanthropologists—like all scientists—

are all “guided to some degree by a set of assumptions, usually implicit rather than explicit” (Lewin, 1987: 126).

Given that morphology can be discretized ad infinitum, there is no objective solution regarding how many characters or character states a particular anatomical area requires, further resulting in the loss of potentially informative data. Therefore, it is always desirable to develop more objective ways to quantitatively analyze shape from a phylogenetic viewpoint. Additional efforts would be thus required to determine the most suitable methods to code continuous data (Goloboff et al., 2006; Pugh, 2022) as well as to more fully integrate 3D geometric morphometric data with cladistics (Almécija et al., 2021). This synthesis is already underway thanks to recent methodological developments based on landmarks (Catalano et al., 2010; Goloboff and Catalano, 2011, 2016). Nevertheless, landmark-free methods (e.g., Urciuoli et al., 2020) should ideally be employed, as landmark protocols may introduce some biases of their own. If bone morphology could be analyzed using parsimony by entirely relying on automatic coding methods based on geometric morphometric techniques, the subjectivity of character and character state definition would be drastically reduced.

In the midterm, paleoproteomics (based on the retrieval of phylogenetically informative amino acid sequences from fossil remains) might also provide invaluable data for deciding among some of the most controversial hypotheses about Miocene ape phylogeny and paleobiogeography (Almécija et al., 2021). Thus far, paleoproteomic data have confirmed that Early Pleistocene (1.9 Ma) *Gigantopithecus* is a pongine distantly related to orangutans (Welker et al., 2019), with an estimated divergence date of 12–10 Ma, compatible with being more closely related to the sugrivapithecins *Sivapithecus* and *Indopithecus*. If technological advances eventually enable the retrieval of phylogenetically informative paleoproteomic data from key Miocene apes (such as *Oreopithecus* or dryopithecines), this might be enough to confidently anchor them in the phylogeny of extant species and use it as an extended molecular backbone in cladistic analyses—hopefully resulting in a more accurate phylogeny of Miocene apes as a whole.

Beyond parsimony Besides the various aspects mentioned in the paragraphs above, it is worth emphasizing that further progress in Miocene ape phylogeny could potentially be made based on currently available paleontological data. The most obvious next step would be to increase taxon sampling and replicate Pugh's (2022) joint and separate analyses of craniodental and postcranial characters—including taxa such as afropithecines, more proconsulids, putative stem hylobatids, and dendropithecids—to better assess the potential long-branch attraction problem hypothesized above. The application of character weighting methods (e.g., Goloboff, 1993, 1997) to Pugh (2022) and others' cladistic matrices might potentially help cope with differential homoplasy between anatomical regions as well. Finally, and most importantly, Miocene ape phylogenetics could take advantage of recent methodological advances that have yet to be applied to these taxa.

The inclusion of extinct taxa in morphology-based cladistic analysis has a very positive effect because they are closer in time to ancestral nodes and display combinations of primitive and derived features not found among extant taxa, thus helping determine the polarity of change and better discriminate between homoplasy and homology (Gauthier et al., 1988; Donoghue et al., 1989; Huelsenbeck, 1991; Smith, 1998; Smith and Turner, 2005; Hunt and Slater, 2016; Mongiardino Koch et al., 2021). Methods of phylogenetic inference other than morphology-based cladistics are not immune either to the problems of pervasive homoplasy, subjectivity in character selection and definition, and abundant missing data. However, parsimony arguably lags behind because of its inability to incorporate one of the main contributions of paleontology to evolutionary biology: deep time. To solve this problem, several decades ago some paleontologists advocated a modified concept of parsimony incorporating stratigraphic data a priori, as in stratocladistics, which maximizes explanatory power based on a modified parsimony criterion (Fisher, 2008; see SOM S1.4 for further details). Although this method was criticized by some other paleontologists, if stratigraphic data are considered relevant for inferring phylogeny there is no reason why the former cannot overturn parsimony considerations based exclusively on morphological data (Grantham, 2004), in agreement with the principle of total evidence frequently advocated in cladistics (SOM S1.4).

Despite criticisms, stratocladistic analyses performed well (Clyde and Fisher, 1997) and simulation studies supported that stratocladistics outperforms the accuracy of conventional cladistics (Fox et al., 1999), being eventually applied to Miocene apes (Finarelli and Clyde, 2004). But despite the development of a computer program to perform automated stratocladistic searches (Marcot and Fox, 2008), this approach never became mainstream. This might be attributable to the development in the 2000s of Bayesian methods of phylogenetic inference using Markov chain Monte Carlo techniques applicable to discrete morphological data (e.g., Nylander et al., 2004; see SOM S1.5 for further details). According to simulations, Bayesian analyses yield more accurate (Puttick et al., 2019)—although less resolved (O'Reilly et al., 2016)—cladograms than parsimony analyses, even when extinct taxa are incompletely preserved and there are high levels of homoplasy, being less sensitive to long-branch attraction (see additional references in SOM S1.5). Instead of incorporating a molecular backbone in morphology-based cladistic studies or deriving molecular estimates of divergence times based on bounds taken from the fossil record ('node dating'), total-evidence Bayesian analyses based on morphologic, chronostratigraphic, and molecular data produce time-calibrated phylogenies (‘tip dating’; e.g., Ronquist et al., 2016; Zhang et al., 2016; Pozzi and Penna, 2022).

Despite various criticisms and limitations (e.g., O’Reilly et al., 2016; Goloboff, 2018; see discussion in Pugh, 2022 and SOM S1.5), simulation studies support that tip-dated phylogenies generally have a better fit with stratigraphic data and a greater accuracy than other methods (King, 2021; Mongiardino Koch et al., 2021). Therefore, it is somewhat surprising that tip-dating methods have yet to be applied in Miocene ape phylogenetics. Thus far, the application of these methods to primates is still limited (see review in Pozzi and Penna, 2022). This is probably because it takes time to introduce methodological advances in phylogenetic inference into paleoanthropology (see Section 2.2. regarding the slow introduction of cladistics)—which, as a discipline, has played a much more important role in the development of geometric morphometrics (Slice, 2007).

Only recently, Pugh (2022) compared the results of parsimony and Bayesian methods for inferring the phylogeny of Miocene apes, obtaining a better resolution using the former, in agreement with simulation results (O’Reilly et al., 2016). However, Pugh (2022) did not take advantage of Bayesian tip-dating methods to obtain a time-calibrated phylogeny of Miocene apes. Although various aspects of Bayesian analyses are not sufficiently understood yet (Almécija et al., 2021; Pugh, 2022), total-evidence (tip-dating) methods are very appealing in the light of recent simulation results, which support that “fossils help to extract true phylogenetic signals from morphology” not only because of “their distinctive morphology” but also because of “their temporal information” (Mongiardino Koch et al., 2021: 1). Therefore, performing a tip-dated Bayesian total evidence analysis and comparing the results with those of parsimony with implied character weighting should be a must for Miocene ape phylogenetics in the midterm.

6. Summary and conclusions

Miocene apes are much more diverse than their extant counterparts, evincing a suite of mosaic morphologies that are essential to reconstruct the evolutionary history of the Hominoidea. Here we review Miocene ape evolution with emphasis on their phylogenetic relationships and the paleobiogeographic scenarios that derive from them. The oldest hominoids from the Oligocene, Miocene catarrhines of uncertain affinities, and Late Miocene purported hominins are excluded from this review.

First, we provide a historical account of the progress made in hominoid phylogeny and paleobiogeography during the last one hundred and fifty years, with emphasis on the *Ramapithecus* debate, the molecular revolution, the spread of the cladistic paradigm, the *Sivapithecus* dilemma, the enigmatic ape *Oreopithecus*, and the synapomorphic vs. homoplastic nature of the postcranial similarities shared by extant apes. Second, based on our interpretation of the most parsimonious results yielded by recent cladistic analyses, we report an updated classification of Miocene apes. Our classification tentatively distinguishes three families of putative stem Hominoidea (Proconsulidae, Afropithecidae, and Nyanzapithecidae), a new subfamily Yuanmoupithecinae for stem Hylobatidae, and two subfamilies of stem Hominidae (Kenyapithecinae and Dryopithecinae), while the tribes Oreopithecini and Graecopithecini are provisionally left as subfamily incertae sedis. Third, we report a list of Miocene ape species-locality occurrences accompanied by an analysis of their paleobiodiversity dynamics and a discussion of the highly contradictory results yielded by parsimony analyses based on craniodental and postcranial features. On the basis of the latter, we argue that the less basal divergence of hylobatids relative to putative stem hominoids, as currently favored by most parsimonious cladograms, is far from being definitively settled and that a more basal divergence is likely given the abundant postcranial homoplasy between hylobatids and hominids. With these two competing hypotheses (more vs. less basal divergence for hylobatids) in mind, we discuss ongoing debates about the origin of hylobatids, *Oreopithecus*, and hominoids from a phylogenetic and paleobiogeographic perspective.

Hylobatid origins remain uncertain because their branching topology relative to nyanzapithecids and afropithecids is unreliable, given the contrasting phylogenetic signal provided by craniodental and postcranial features. However, if the suspicion that recent cladistic analyses are biased toward a too advanced divergence of hylobatids were correct, an initial divergence of crown hominoids in Africa followed by two independent dispersal events into Eurasia would be most likely. It remains to be more conclusively determined whether equatorines are stem hominids rather than stem hominonids, as favored by most recent cladistic analysis, whereas kenyapithecines appear as the most likely stock from which crown hominids might have evolved. In contrast, current data favor the view that *Oreopithecus* is a stem hominoid rather than a stem hominid or hylobatid. The geographic origin of crown hominids remains unresolved due to phylogenetic uncertainties regarding dryopithecines and graecopithecins. The possibility that a dispersal event from kenyapithecines into Eurasia set the initial divergence between hominines and pongines remains a plausible interpretation but lacks cladistic support (unless European dryopithecines originated from a second dispersal event of stem hominids from Africa). Alternatively, the pongine–hominine divergence might have occurred in Eurasia, in agreement with the view that graecopithecins and at least some dryopithecines are hominines, which we consider insufficiently supported at present.

The less basal divergence of hylobatids favored by most parsimonious cladograms might artifactually result from a long-branch attraction problem caused by the numerous postcranial similarities shared by extant hylobatids and hominids (which appear largely homoplastic), coupled with abundant missing data from Miocene apes. Although is it currently recognized that postcranial features functionally related to antipronograde behaviors likely evolved in parallel along various ape lineages, they still exert a strong influence in the outcome of parsimony analyses because homoplasy can only be identified a posteriori and branch lengths are not considered. Although it is not possible to determine to what extent this potential problem might affect the accuracy of most parsimonious cladograms, it could be ameliorated by the discovery of additional Miocene ape fossils (leading to increased taxon sampling and/or a decrease of missing data), the implementation of character weighting methods, the scoring of new characters from anatomical areas embedding high phylogenetic signal, and the integration of geometric morphometric continuous data in cladistic analyses. Paleoproteomic analyses offer even more promising prospects to more reliably reconstruct the evolutionary history of hominoids if future technological advances allow the retrieval of molecular data from Miocene apes of controversial systematic position.

Finally, we further advocate incorporating chronostratigraphic information in phylogenetic inference by taking advantage of recent methodological advances. In particular, total-evidence (tip-dating) Bayesian methods of phylogenetic inference appear to outperform parsimony methods and provide time-calibrated phylogenies based on the simultaneous analysis of molecular, morphologic, and chronostratigraphic data. Performing these analyses and comparing their results with more conventional parsimony analyses would hopefully allow to ascertain if, as we suspect, our current concept of the hominoid stem lineage is artifactually inflated by a long-branch attraction problem between hylobatids and hominids. The data required to perform such analyses are already out there.

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Figure legends

Figure 1. Schematic cladogram showing the relationships between extant catarrhine main clades and hypothetical extinct clades to illustrate the concepts of stem lineage, crown group, and total group based on a stem-based definition of the Hominoidea (black arrow). A crown-based definition would restrict the taxon to the crown clade. An apomorphy-based definition would imply that the hominoid last common ancestor would depend on the crown hominoid synapomorphy selected as definitory of the group (character state 1 in the example of the figure).

Figure 2. Schematic cladograms summarizing the phylogenetic relationships of the hominoid families distinguished here relative to cercopithecoids and the most advanced stem catarrhines (pliopithecoids and dendropithecids) according to the contrasting cladistic results of various authors: a) based on Nengo et al. (2017) and Gilbert et al. (2020a); b) based on Rossie and Hill (2018). The hominoid stem lineage is denoted in light gray whereas the hominoid crown group is denoted in dark gray. Note that, according to Rossie and Hill (2018), Dendropithecidae s.s. (*Dendropithecus* and *Simiolus*) would be stem hominoids but

Dendropithecidae s.l. (including *Micropithecus*) would be polyphyletic. Abbreviation: LCA = last common ancestor.

Figure 3. Geographic distribution of Early Miocene apes. The information reported mostly comes from Table 2 but further includes the following species-locality occurrences (see SOM Table S1 for further details and SOM Table S2 for references): Hominoidea indet. from Moruorot (Kenya; 17.5 Ma); Nyanzapithecidae indet. from Ryskop (South Africa; 16.0 Ma); and cf. Kenyapithecinae indet. from Engelswies (Germany; 16.5–16.0 Ma). Base map downloaded from ArcGIS Online (https://www.esri.com/it-it/arcgis/products/arcgis-online/); image sources: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community.

Figure 4. Geographic distribution of Middle Miocene apes. The information reported mostly comes from Table 2 but further includes the following species-locality occurrences (see SOM Table S1 for further details and SOM Table S2 for references): Nyanzapithecidae indet. from Fort Ternan and Kapsibor (Kenya; 13.7 Ma); Kenyapithecinae indet. from Thannhausen (Germany; 14.0 Ma); cf. *Kenyapithecus* sp. from Berg Aukas (Namibia; 13.0–12.0 Ma); Hominidae indet. from Ngorora (Kenya; 12.8–12.0 Ma). Base map downloaded from ArcGIS Online (https://www.esri.com/it-it/arcgis/products/arcgis-online/); image sources: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson,

NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community.

Figure 5. Geographic distribution of Late Miocene apes. The information reported mostly comes from Table 2 but further includes the following species-locality occurrences (see SOM Table S1 for further details and SOM Table S2 for references): Hominoidea indet. from N 885 (Niger; 11.0–5.0 Ma); Nyanzapithecinae indet. from Nakali (Kenya; 9.9–9.8 Ma); Hominidae indet. from Maragheh (Iran; 7.5 Ma); Dryopithecinae indet. from Wissberg (Germany; 13.7–7.5 Ma), Neuhausen, Egingen, and Trochtelfingen (Germany; 11.0–9.0 Ma), Melchingen (Germany; 11.2–7.5 Ma), and Salmendingen (Germany; 11.6–7.5 Ma); Graecopithecini indet. from Azmaka (Bulgaria; 7.2 Ma); and Hominidae indet. from Kapsomin and Cheboit, Lukeino (Kenya; 6.2–5.7 Ma). Base map downloaded from ArcGIS Online (https://www.esri.com/it-it/arcgis/products/arcgis-online/); image sources: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community.

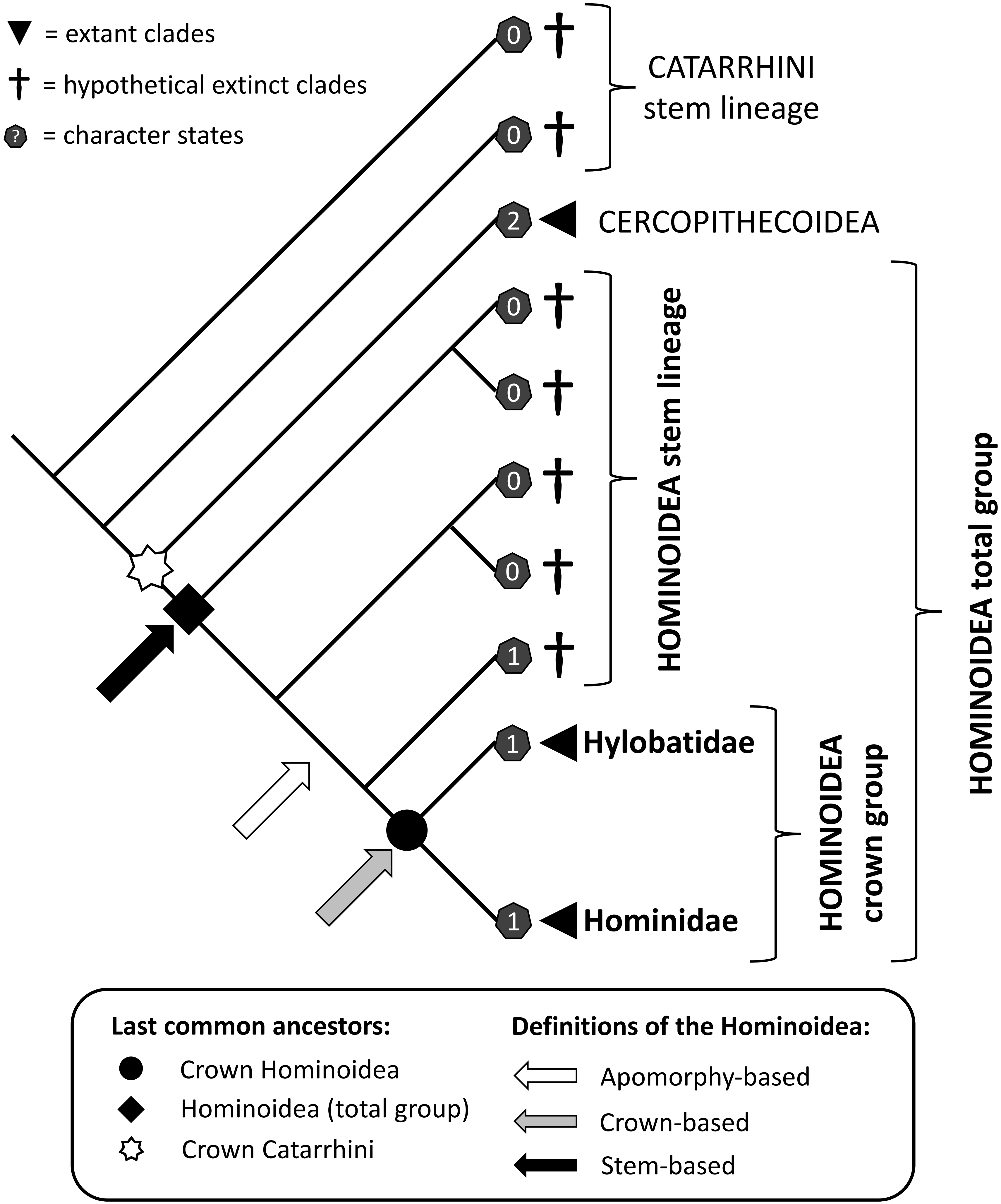
Figure 6. Chronostratigraphic ranges and broad geographic distribution of Miocene apes summarized at the genus level and organized according to the classification reported in Table 1; family names are colored as in Figures 3–5. Chronostratigraphic ranges are organized from oldest to youngest (left to right) for each (sub)family and colored based on geographic distribution at the continental level (gray denotes geographic uncertainty due to lack of record for taxa represented in more than a single continent). The depicted genus

ranges are reported in Table 2. Also depicted are the ranges for some taxa not identified to the genus rank (see SOM Table S1 for further details and SOM Table S2 for references): cf. Kenyapithecinae from Engelswies (Germany; 16.5–16.0); and Nyanzapithecidae indet. from Fort Ternan, Kapsibor (Kenya; 13.7 Ma) and Nakali (Kenya; 9.9–9.8 Ma).

Figure 7. Paleobiodiversity curve of Miocene apes through time: range-through or total diversity (top) and estimated standing diversity (bottom). Diversity metrics are based on the data reported in Table 3, see SOM Table S3 for further details.

Figure 8. Alternative phylogenetic hypotheses discussed in this paper as depicted by schematic time-calibrated cladograms at the (sub)tribe rank: a) phylogenetic hypotheses favored in this paper based on our interpretation of the current state of knowledge according to most parsimonious cladograms; b) alternative hypothesis of a more basal divergence for hylobatids coupled with multiple polytomies to highlight current phylogenetic uncertainties. Colored rectangles represent the chronostratigraphic ranges of the depicted taxa (color-coded as in Figs. 3–6 based on geographical distribution; gray denotes geographic uncertainty due to lack of record for taxa represented in more than a single continent); colored dots at the tips of extant lineages denote their current geographic distribution. Gray semitransparent rectangles represent the maximum-minimum divergence age estimates for crown clades. Internal nodes have been depicted arbitrarily 0.5 Myr before the oldest record of the group or relative to the oldest node that immediately follows, with the exception of crown groups, for which average estimated divergence times (Perelman et al., 2011) have been used (except when they are too close or even younger than the oldest record of the

group). Note that no Plio-Pleistocene ranges are depicted, whereas in contrast the Oligocene range of proconsulids and nyanzapithecines has been depicted.


▼ = extant clades
† = hypothetical extinct clades
? = character states
CATARRHINI stem lineage
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CERCOPITHECOIDEA
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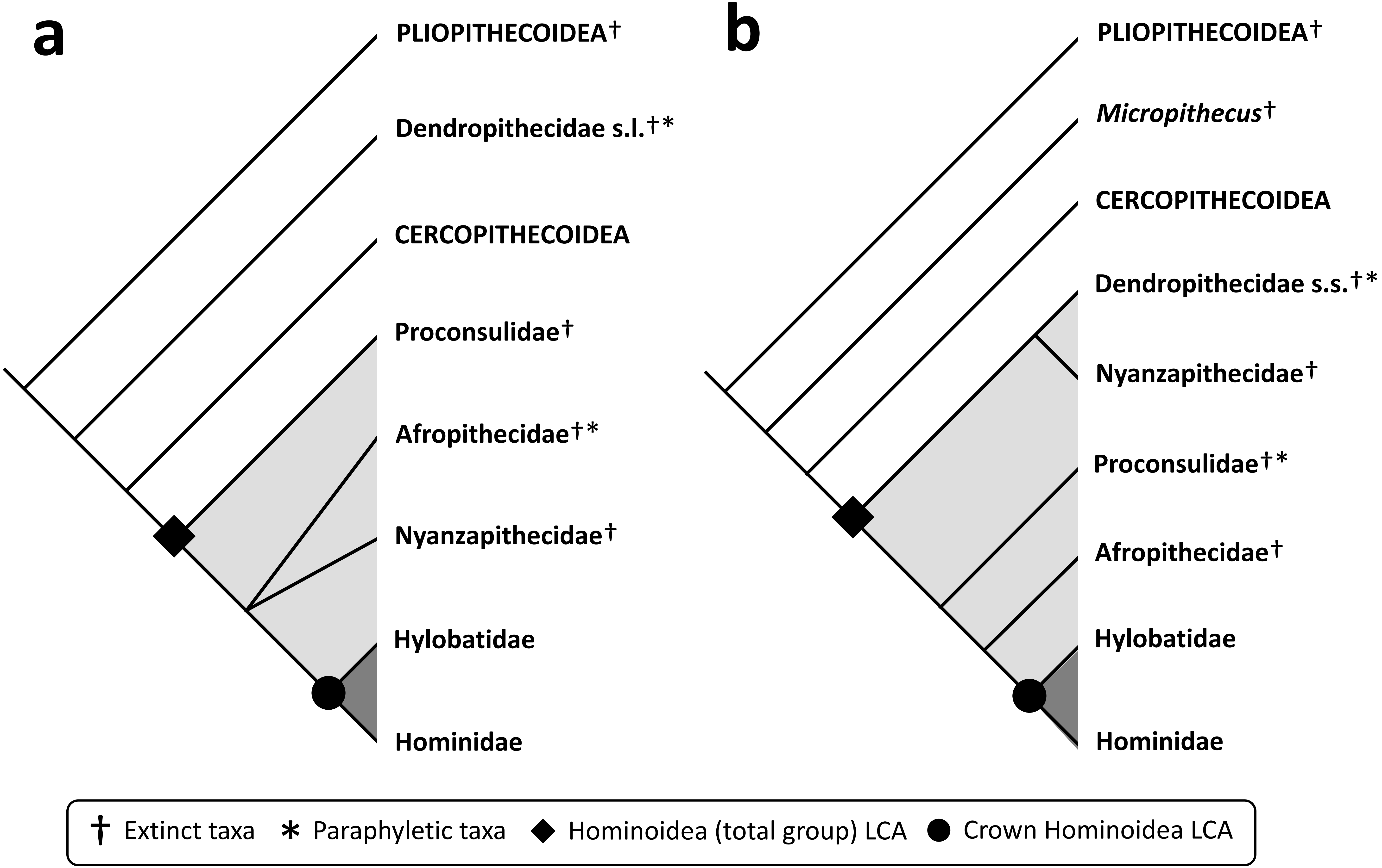
1
HOMINOIDEA stem lineage
HOMINOIDEA total group
1
Hylobatidae
1
Hominidae
HOMINOIDEA crown group
Last common ancestors:
● Crown Hominoidea
◆ Hominoidea (total group)
✡ Crown Catarrhini
Definitions of the Hominoidea:
Apomorphy-based
Crown-based
Stem-based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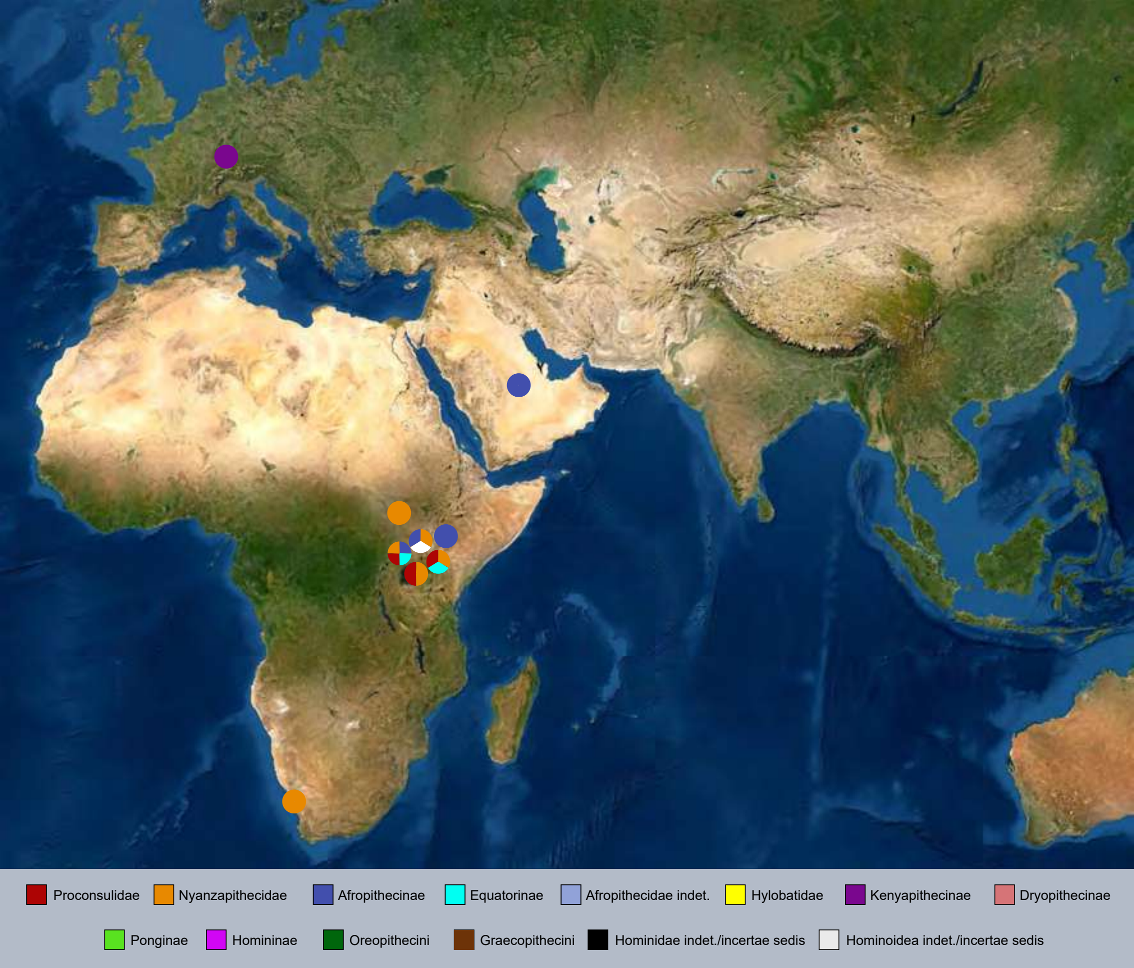
PLIOPITHECOIDEA†
Dendropithecidae s.l.†*
CERCOPITHECOIDEA
Proconsulidae†
Afropithecidae†*
Nyanzapithecidae†
Hylobatidae
Hominidae
b
PLIOPITHECOIDEA†
Micropithecus†
CERCOPITHECOIDEA
Dendropithecidae s.s.†*
Nyanzapithecidae†
Proconsulidae†*
Afropithecidae†
Hylobatidae
Hominidae
† Extinct taxa
* Paraphyletic taxa
◆ Hominoidea (total group) LCA
● Crown Hominoidea LCA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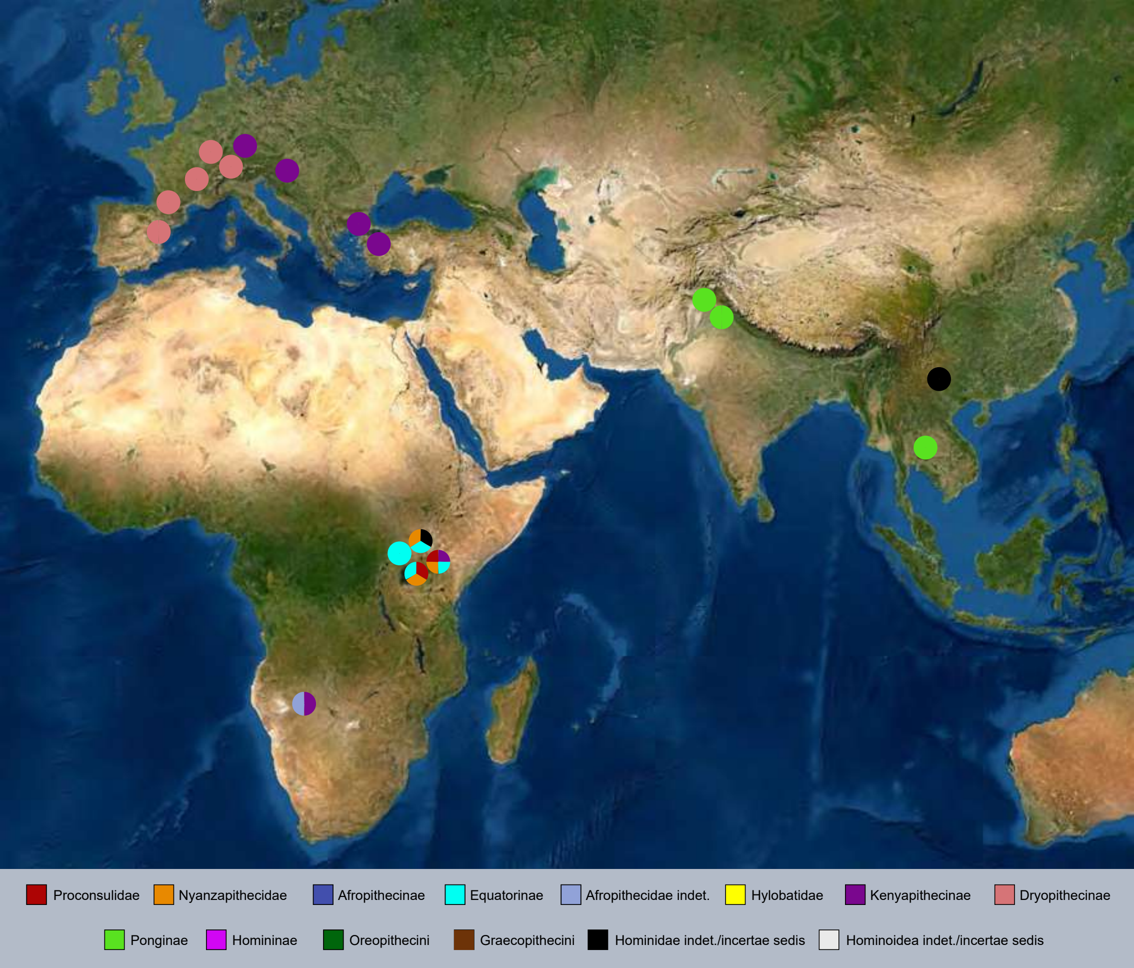
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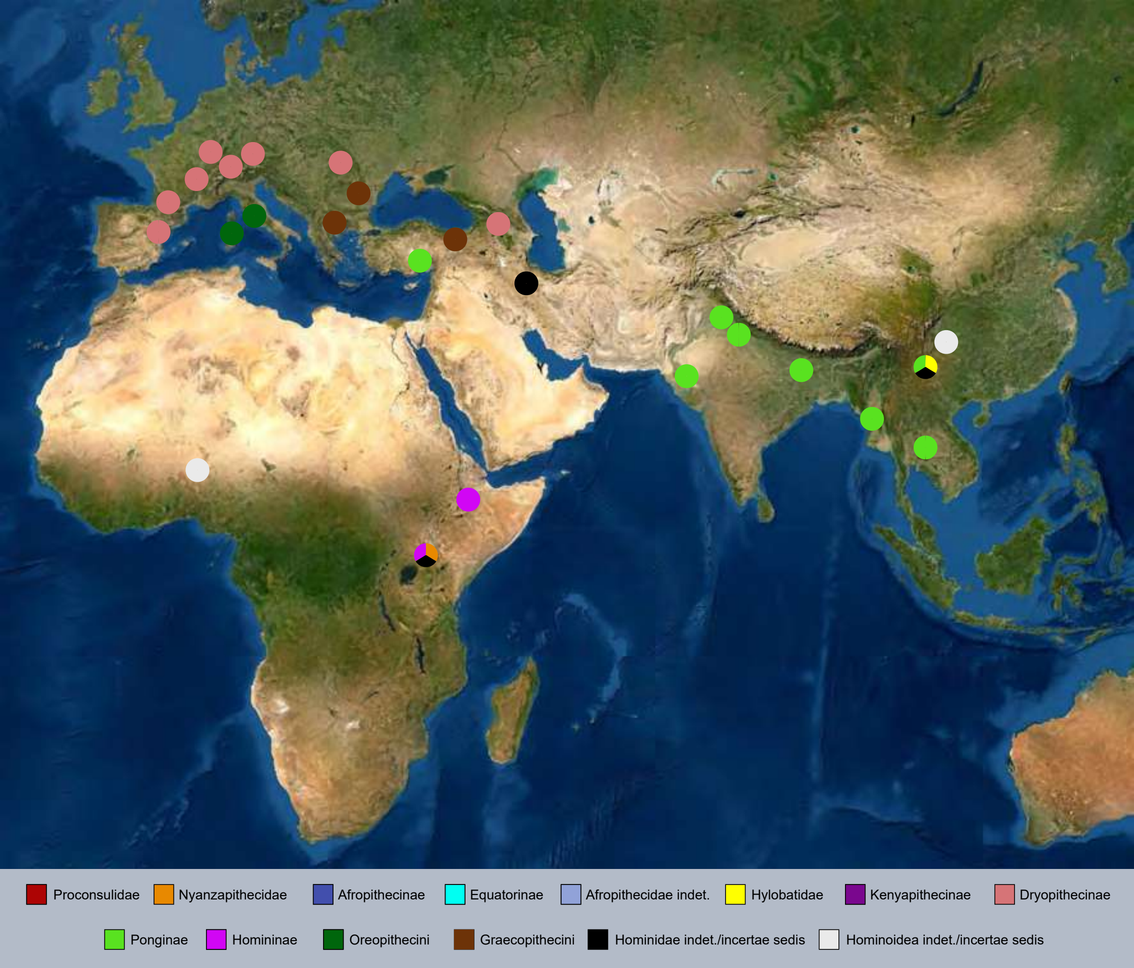
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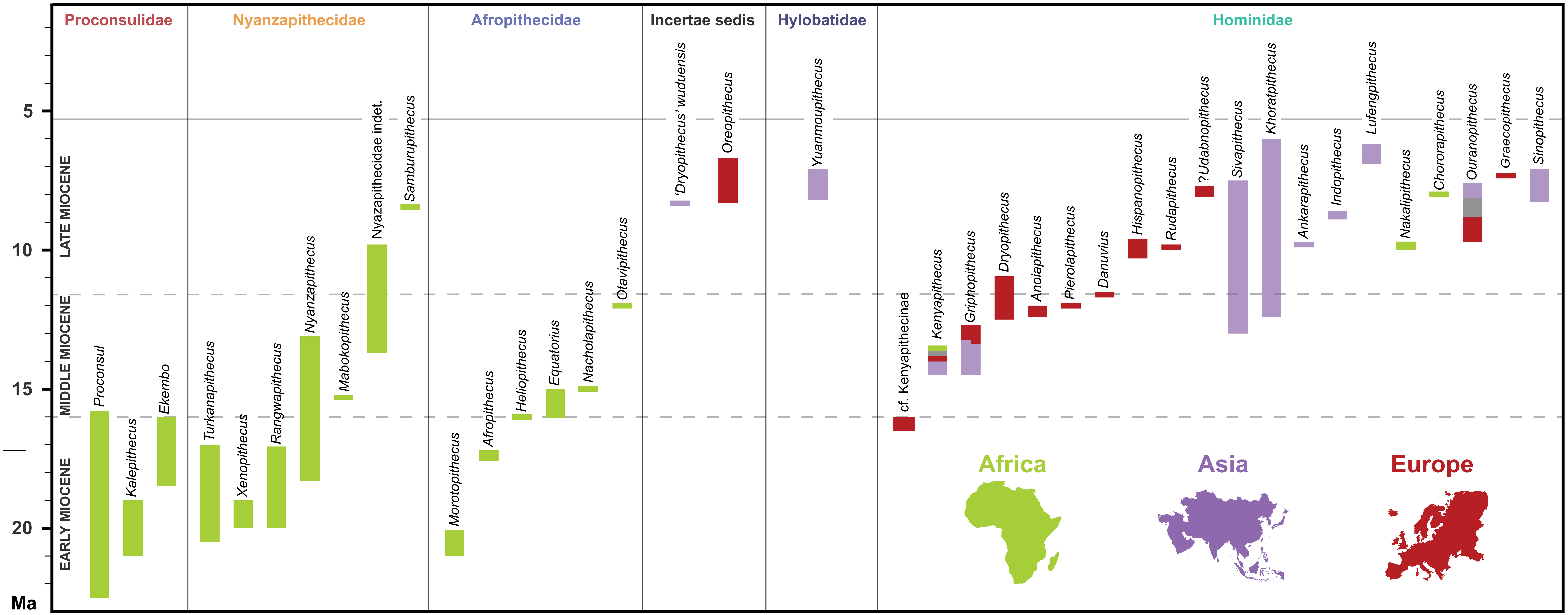
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EARLY MIOCENE
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Kalepithecus
Ekembo
Turkanapithecus
Xenopithecus
Rangwapithecus
Nyanzapithecus
Mabokopithecus
Nyazapithecidae indet.
Samburupithecus
Morotopithecus
Afropithecus
Heliopithecus
Equatorius
Nacholapithecus
Otavipithecus
'Dryopithecus' wuduensis
Oreopithecus
Yuanmoupithecus
cf. Kenyapithecinae
Kenyapithecus
Griphopithecus
Dryopithecus
Anoiapithecus
Pierolapithecus
Danuvius
Hispanopithecus
Rudapithecus
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Sivapithecus
Khoratpithecus
Ankarapithecus
Indopithecus
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Ouranopithecus
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Sinopithecus
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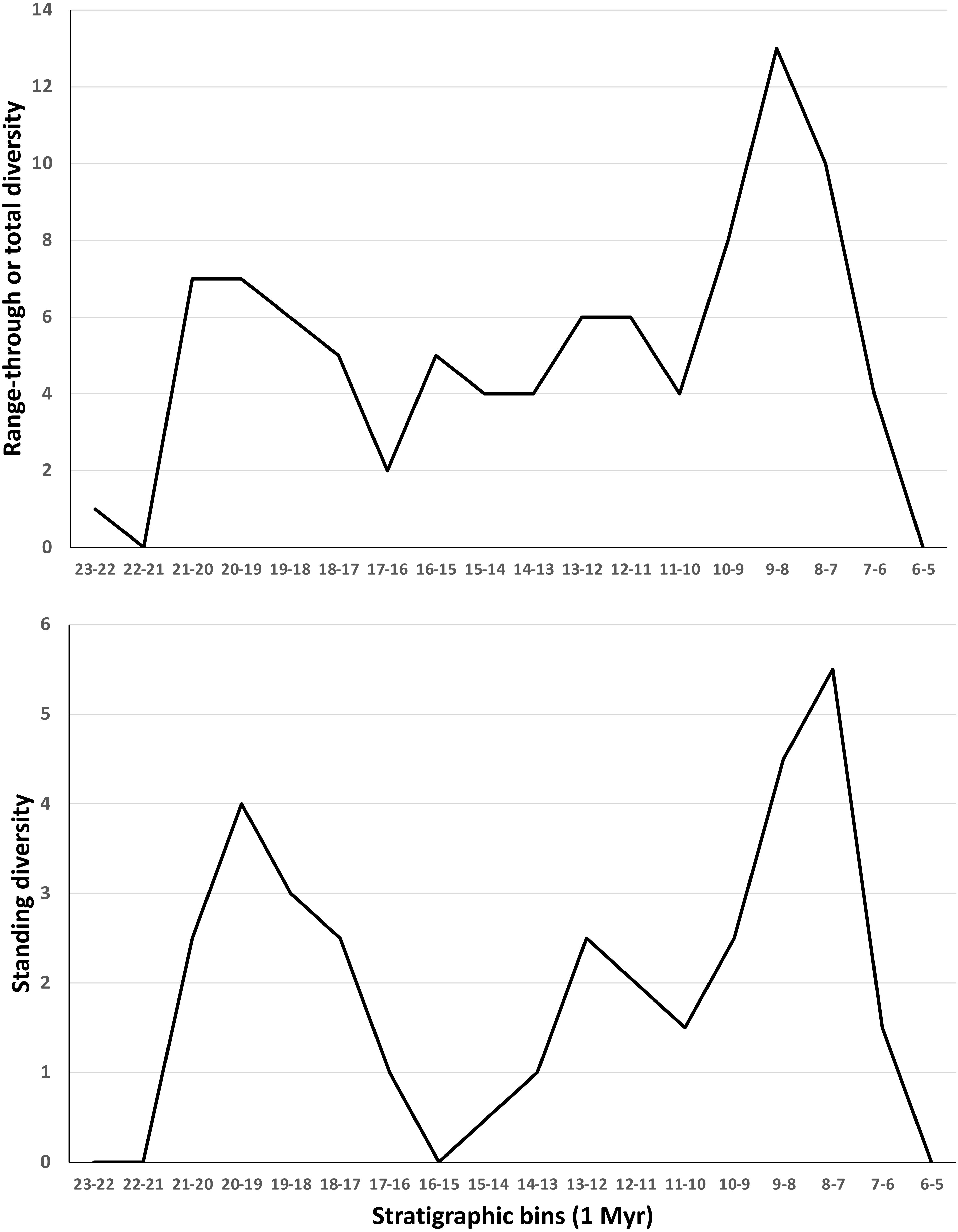
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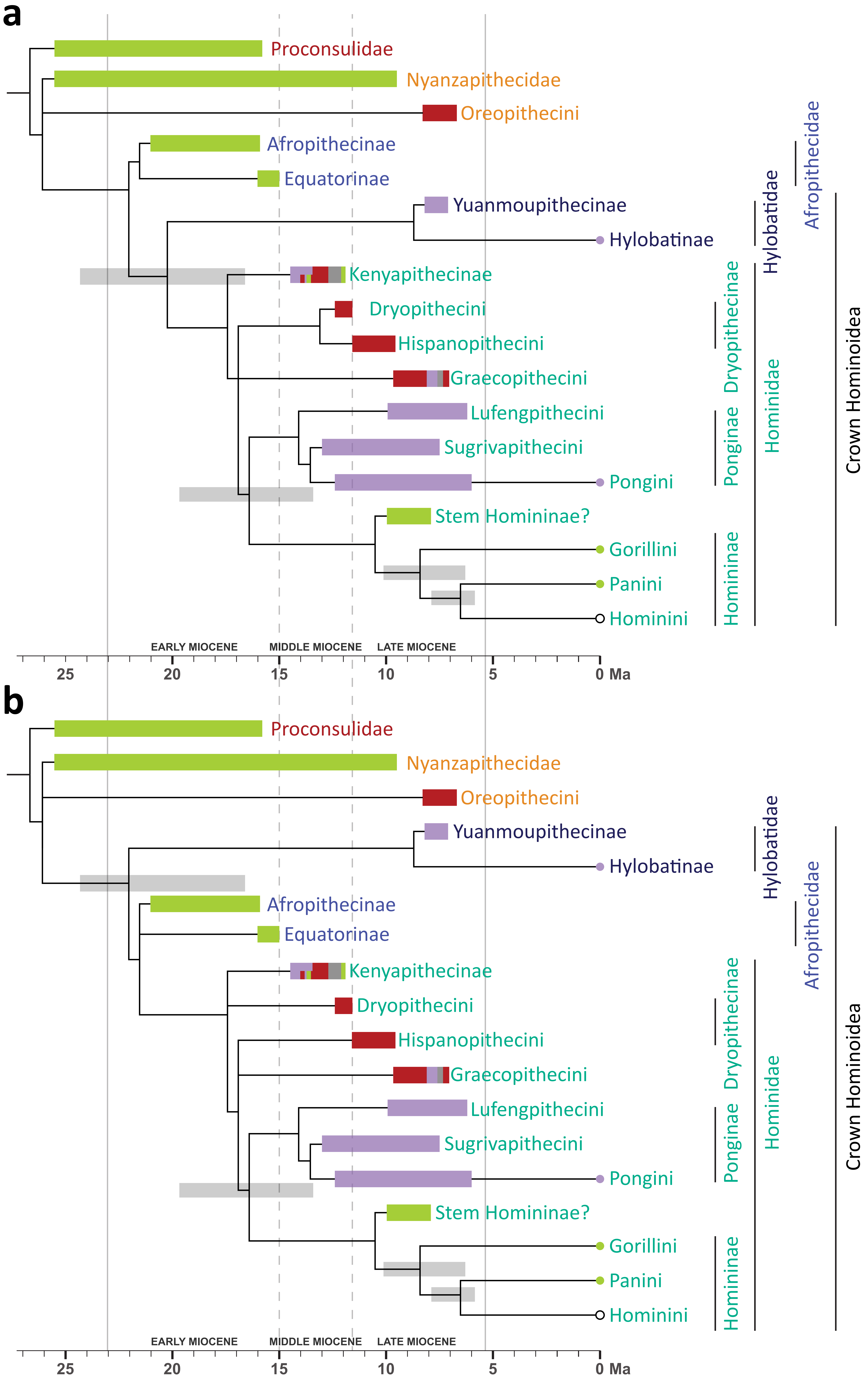
Stratigraphic bins (1 Myr)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Yuanmoupithecinae
Hylobatinae
Kenyapithecinae
Dryopithecini
Hispanopithecini
Graecopithecini
Lufengpithecini
Sugrivapithecini
Pongini
Stem Homininae?
Gorillini
Panini
Hominini
Afropithecidae
Hylobatidae
Dryopithecinae
Ponginae
Homininae
Hominidae
Crown Hominoidea
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Gorillini
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Ponginae
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Hominidae
Crown Hominoidea
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Table 1

A summary of the systematic classification of the Hominoidea followed in this paper down to tribe rank. A dagger denotes extinct taxa. See Table 2 for taxonomic authorities and a classification of Miocene ape genera and species.

Family	Subfamily	Tribe
Proconsulidae†	—	—
Nyanzapithecidae†	—	—
Afropithecidae†	Afropithecinae†	—
	Equatorinae†	—
Hylobatidae	Yuanmoupithecinae†	—
	Hylobatinae	—
Hominidae	Kenyapithecinae†	—
	Dryopithecinae†	Dryopithecini†
		Hispanopithecini†
	Ponginae	Pongini
		Lufengpithecini†
		Sugrivapithecini†
	Homininae	Gorillini
		Panini
		Hominini
	incertae sedis	Graecopithecini†
incertae sedis	incertae sedis	Oreopithecini†

Table 2

Systematics of Miocene apes including taxonomic rank, taxon name, and taxonomic authority[a]. A dagger denotes extinct taxa. Small-bodied catarrhines of uncertain systematic status (such as dendropithecids) are not included, whereas two species variously interpreted as hominoids or pliopithecoids depending on the authors are included as incertae sedis at superfamily rank.

Order Primates Linnaeus, 1758
Semiorder Euprimates Hoffstetter, 1977
Suborder Haplorrhini Pocock, 1918
Infraorder Anthropoidea Mivart, 1864
Parvorder Catarrhini É. Geoffroy Saint-Hilaire, 1812
Superfamily Hominoidea Gray, 1825
Family Proconsulidae Leakey, 1963†
Genus *Proconsul* Hopwood, 1933†
Proconsul africanus Hopwood, 1933†
Proconsul major Le Gros Clark and Leakey, 1950†
Proconsul gitongai (Pickford and Kunimatsu, 2005)†

Proconsul meswae Harrison and Andrews, 2009†

Proconsul legetetensis (Pickford et al., 2009a)†

Genus *Kalepithecus* Harrison, 1988†

Kalepithecus songhorensis (Andrews, 1978)†

Kalepithecus kogolensis Pickford et al., 2017†

Genus *Ekembo* McNulty et al., 2015†

Ekembo heseloni (Walker et al., 1993)†

Ekembo nyanzae (Le Gros Clark and Leakey, 1950)†

Family Afropithecidae Andrews, 1992†

Subfamily Afropithecinae Andrews, 1992†

Genus *Afropithecus* Leakey and Leakey, 1986a†

Afropithecus turkanensis Leakey and Leakey, 1986a†

Genus *Heliopithecus* Andrews and Martin, 1987b†

Heliopithecus leakeyi Andrews and Martin, 1987b†

Genus *Morotopithecus* Gebo et al., 1997†

Morotopithecus bishopi Gebo et al., 1997†

Subfamily Equatorinae Cameron, 2004†

Genus *Equatorius* Ward et al., 1999†

Equatorius africanus (Le Gros Clark and Leakey, 1950)†

Genus *Nacholapithecus* Ishida et al., 1999†

Nacholapithecus kerioi Ishida et al., 1999†

Subfamily incertae sedis

Genus *Otavipithecus* Conroy et al., 1992†

Otavipithecus namibiensis Conroy et al., 1992†

Family Nyanzapithecidae Harrison, 2002†

Genus *Xenopithecus* Hopwood, 1933†

Xenopithecus koruensis Hopwood, 1933†

Genus *Mabokopithecus* von Koenigswald, 1969†

Mabokopithecus clarki von Koenigswald, 1969†

Genus *Rangwapithecus* Andrews, 1974†

- *Rangwapithecus gordoni* (Andrews, 1974)†
- Genus *Nyanzapithecus* Harrison, 1986†
  - *Nyanzapithecus vancouveringorum* (Andrews, 1974)†
  - *Nyanzapithecus pickfordi* Harrison, 1986†
  - *Nyanzapithecus harrisoni* Kunimatsu, 1997†
  - *Nyanzapithecus alesi* Nengo et al., 2017†
- Genus *Turkanapithecus* Leakey and Leakey, 1986b†
  - *Turkanapithecus kalakolensis* Leakey and Leakey, 1986b†
  - *Turkanapithecus rusingensis* Pickford, 2010†
- Genus *Samburupithecus* Ishida and Pickford, 1997†
  - *Samburupithecus kiptalami* Ishida and Pickford, 1997†

Family Hylobatidae Gray, 1870

Subfamily Yuanmoupithecinae subfam. nov.†

- Genus *Yuanmoupithecus* Pan, 2006†
  - *Yuanmoupithecus xiaoyuan* Pan, 2006†

- Family Hominidae Gray, 1825
  - Subfamily Kenyapithecinae Andrews, 1992†
    - Genus *Griphopithecus* Abel, 1902†
      - *Griphopithecus suessi* Abel 1902†
      - *Griphopithecus alpani* (Tekkaya, 1974)†
    - Genus *Kenyapithecus* Leakey, 1961†
      - *Kenyapithecus wickeri* Leakey, 1961†
      - *Kenyapithecus kizili* Kelley et al., 2008†
  - Subfamily Dryopithecinae Gregory and Hellman, 1939†
    - Tribe Dryopithecini Gregory and Hellman, 1939†
      - Genus *Dryopithecus* Lartet, 1856†
        - *Dryopithecus fontani* Lartet, 1856†
      - Genus *Pierolapithecus* Moyà-Solà et al., 2004†
        - *Pierolapithecus catalaunicus* Moyà-Solà et al., 2004†
      - Genus *Anoiapithecus* Moyà-Solà et al., 2009b†

Anoiapithecus brevirostris Moyà-Solà et al., 2009b†

Genus incertae sedis

‘*Sivapithecus*’ *occidentalis* Villalta Comella and Crusafont Pairó, 1944 species inquirenda†

Tribe Hispanopithecini Cameron, 1997a†

Genus *Hispanopithecus* Villalta Comella and Crusafont Pairó, 1944†

Hispanopithecus laietanus Villalta Comella and Crusafont Pairó, 1944†

Hispanopithecus crusafonti (Begun, 1992b)†

Genus *Rudapithecus* Kretzoi, 1969†

Rudapithecus hungaricus Kretzoi, 1969†

Genus *Danuvius* Böhme et al., 2019†

Danuvius guggenmosi Böhme et al., 2019†

Tribe incertae sedis

Genus *Neopithecus* Abel, 1902 nomen dubium†

Neopithecus brancoi (Schlosser, 1901) nomen dubium†

Genus ?*Udabnopithecus* Burchak-Abramovich and Gabashvili, 1945†

?*Ubadnopithecus garedziensis* Burchak-Abramovich and Gabashvili, 1945

Subfamily Ponginae Elliot, 1913

Tribe Pongini Elliot, 1913

Genus *Khoratpithecus* Chaimanee et al., 2004†

Khoratpithecus chiangmuanensis (Chaimanee et al., 2003)†

Khoratpithecus piriyai Chaimanee et al., 2004†

Khorapithecus ayeyarwadyensis Jaeger et al., 2011†

Khoratpithecus magnus Chaimanee et al., 2022†

Tribe Sugrivapithecini Simonetta, 1958†

Genus *Sivapithecus* Pilgrim, 1910†

Sivapithecus sivalensis (Lydekker, 1879)†

Sivapithecus indicus Pilgrim, 1910†

Sivapithecus parvada Kelley, 1988†

Genus *Indopithecus* von Koenigswald, 1949†

Indopithecus giganteus (Pilgrim, 1915)†

Tribe Lufengpithecini Alba, 2012†

Genus *Ankarapithecus* Ozansoy, 1957†

Ankarapithecus meteai Ozansoy, 1957†

Genus *Lufengpithecus* Wu, 1987†

Lufengpithecus lufengensis (Xu et al., 1978)†

Subfamily Homininae Gray, 1825

Tribe incertae sedis

Genus *Chororapithecus* Suwa et al., 2007†

Chororapithecus abyssinicus Suwa et al., 2007†

Genus *Nakalipithecus* Kunimatsu et al., 2007†

Nakalipithecus nakayamai Kunimatsu et al., 2007†

Subfamily incertae sedis

Tribe Graecopithecini Cameron, 1997b†

Genus *Graecopithecus* von Koenigswald, 1972†

Graecopithecus freybergi von Koenigswald, 1972†

Genus *Ouranopithecus* de Bonis and Melentis, 1977†

Ouranopithecus macedoniensis (de Bonis et al., 1974)†

Ouranopithecus turkae Güleç et al., 2007†

Tribe incertae sedis

Genus *Sinopithecus* Zhang et al., 1990

Sinopithecus keiyuanensis (Woo, 1957)†

Sinopithecus hudienensis (Zhang et al., 1987)†

Family incertae sedis

Subfamily incertae sedis

Tribe Oreopithecini Schwalbe, 1915†

Genus *Oreopithecus* Gervais, 1872†

Oreopithecus bambolii Gervais, 1872†

Tribe incertae sedis

Genus incertae sedis

‘*Dryopithecus*’ *wuduensis* Xue and Delson, 1988†

[a] Taxonomic authority consists of the author(s) that originally described a given taxon followed by year of publication. Following the requirements of the Code (ICZN, 1999), taxonomic authorities are placed within parentheses only when a species was originally described within a different genus than the one in which it is included in this work.

Table 3

Chronostratigraphic range and geographic distribution of Miocene apes, synthesized from species-locality occurrences reported in SOM Table S2. The details for each locality are provided in SOM Table S1. Species of doubtful taxonomic validity and citations indeterminate to the species rank are excluded from this table; in contrast, tentative attributions to species (with 'cf.') are included.

Species	Family	Subfamily	Age	Subepoch	Distribution
Proconsul africanus	Proconsulidae	—	20.3–18.5	Early Miocene	Kenya, Uganda
Proconsul major	Proconsulidae	—	20.5–19.0	Early Miocene	Kenya, Uganda
Proconsul gitongai	Proconsulidae	—	15.8[a]	Early to Middle Miocene	Kenya, Uganda
Proconsul meswae	Proconsulidae	—	22.5	Early Miocene	Kenya
Proconsul legetetensis	Proconsulidae	—	20.5–19.0	Early Miocene	Uganda
Kalepithecus songhorensis	Proconsulidae	—	20.5–19.0	Early Miocene	Kenya, Uganda
Kalepithecus kogolensis	Proconsulidae	—	21.0–20.0	Early to Middle Miocene	Uganda
Ekembo heseloni	Proconsulidae	—	18.5–16.0	Early to Middle Miocene	Kenya
Ekembo nyanzae	Proconsulidae	—	18.5–16.0	Early to Middle Miocene	Kenya
Xenopithecus koruensis	Nyanzapithecidae	—	20.0–19.0	Early Miocene	Kenya

Mabokopithecus clarki	Nyanzapithecidae	—	15.3	Middle Miocene	Kenya
Rangwapithecus gordoni	Nyanzapithecidae	—	20.0–17.0	Early Miocene	Kenya
Nyanzapithecus pickfordi	Nyanzapithecidae	—	15.8–15.3	Middle Miocene	Kenya
Nyanzapithecus vancouveringorum	Nyanzapithecidae	—	18.3	Early Miocene	Kenya
Nyanzapithecus alesi	Nyanzapithecidae	—	13.3	Middle Miocene	Kenya
Nyanzapithecus harrisoni	Nyanzapithecidae	—	15.0	Middle Miocene	Kenya
Turkanapithecus kalakolensis	Nyanzapithecidae	—	17.5–17.0	Early Miocene	Kenya, Ethiopia
Turkanapithecus rusingensis	Nyanzapithecidae	—	20.5–18.3	Early Miocene	Kenya, Uganda
Samburupithecus kiptalami	Nyanzapithecidae	—	8.5	Late Miocene	Kenya
Afropithecus turkanensis	Afropithecidae	Afropithecinae	17.6–17.2[a]	Early to Middle Miocene	Kenya, Uganda
Heliopithecus leakeyi	Afropithecidae	Afropithecinae	16.0	Early Miocene	Saudi Arabia
Morotopithecus bishopi	Afropithecidae	Afropithecinae	21.0–20.0[b]	Early Miocene	Uganda
Equatorius africanus	Afropithecidae	Equatorinae	16.0–15.0	Middle Miocene	Kenya
Nacholapithecus kerioi	Afropithecidae	Equatorinae	15.0[a]	Early to Middle Miocene	Kenya, Uganda
Otavipithecus namibiensis	Afropithecidae	Incertae sedis	12.0	Middle Miocene	Namibia

Yuanmoupithecus xiaoyuan	Hylobatidae	Yuanmoupithecinae	8.2–7.1	Late Miocene	China
Griphopithecus suessi	Hominidae	Kenyapithecinae	13.8–12.7	Late Miocene	Austria, Slovakia
Griphopithecus alpani	Hominidae	Kenyapithecinae	14.5–13.4	Middle Miocene	Turkey
Kenyapithecus wickeri	Hominidae	Kenyapithecinae	13.8	Middle Miocene	Kenya
Kenyapithecus kizili	Hominidae	Kenyapithecinae	14.5–14.0	Middle Miocene	Turkey
Dryopithecus fontani	Hominidae	Dryopithecinae	12.5–11.0	Middle to Late Miocene	Austria, France, Spain
Pierolapithecus catalaunicus	Hominidae	Dryopithecinae	12.0	Middle Miocene	Spain
Anoiapithecus brevirostris	Hominidae	Dryopithecinae	12.4–12.0	Middle Miocene	Spain
Hispanopithecus laietanus	Hominidae	Dryopithecinae	10.0–9.6	Late Miocene	Spain
Hispanopithecus crusafonti	Hominidae	Dryopithecinae	10.3–10.0	Late Miocene	Spain
Rudapithecus hungaricus	Hominidae	Dryopithecinae	10.0–9.8	Late Miocene	Hungary
Danuvius guggenmosi	Hominidae	Dryopithecinae	11.6	Late Miocene	Germany
?*Udabnopithecus garedziensis*	Hominidae	Dryopithecinae	8.1–7.7	Late Miocene	Georgia
Khoratpithecus chiangmuanensis	Hominidae	Ponginae	12.4–12.2	Middle Miocene	Thailand
Khoratpithecus piriyai	Hominidae	Ponginae	9.0–6.0	Late Miocene	Thailand

Khorapithecus ayeyarwadyensis	Hominidae	Ponginae	10.4–8.0	Late Miocene	Myanmar
Khoratpithecus magnus	Hominidae	Ponginae	9.0–6.0	Late Miocene	Thailand
Ankarapithecus meteai	Hominidae	Ponginae	9.8	Late Miocene	Turkey
Lufengpithecus lufengensis	Hominidae	Ponginae	6.9–6.2	Late Miocene	China
Sivapithecus sivalensis	Hominidae	Ponginae	10.4–7.5	Late Miocene	India, Pakistan
Sivapithecus indicus	Hominidae	Ponginae	13.0–10.8[c]	Middle to Late Miocene	India, Pakistan
Sivapithecus parvada	Hominidae	Ponginae	10.1–10.0	Late Miocene	Pakistan
Indopithecus giganteus	Hominidae	Ponginae	8.9–8.6	Late Miocene	India, Pakistan
Chororapithecus abyssinicus	Hominidae	Homininae	8.0	Late Miocene	Ethiopia
Nakalipithecus nakayamai	Hominidae	Homininae	9.9–9.8	Late Miocene	Kenya
Graecopithecus freybergi	Hominidae	incertae sedis	7.2	Late Miocene	Greece
Ouranopithecus macedoniensis	Hominidae	incertae sedis	9.7–8.8	Late Miocene	Greece
Ouranopithecus turkae	Hominidae	incertae sedis	8.1–7.6	Late Miocene	Turkey
Sinopithecus keiyuanensis	Hominidae	incertae sedis	12.5–11.6	Middle Miocene	China
Sinopithecus hudienensis	Hominidae	incertae sedis	8.2–7.1	Late Miocene	China

Oreopithecus bambolii	incertae sedis	incertae sedis	8.3–6.7	Late Miocene	Italy
‘*Dryopithecus*’ *wuduensis*	incertae sedis	—	8.3	Late Miocene	China

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[a] Pickford et al. (2017) and Pickford (2021) identified *A. turkanensis*, *P. gitongai*, and *N. kerioi* at Moroto, whereas MacLatchy et al. (2019) recognized ?*M. bishopi* and Proconsulidae indet. and Jansma and MacLatchy (2015) further reported a nyanzapithecid. We have tentatively included cf. *P. gitongai* and cf. *N. kerioi* in SOM Table S1, but not considered them in the ranges of this table. If confirmed by subsequent studies, they would modify the chronostratigraphic ranges of these taxa, depending on the age attributed to Moroto (see next footnote).

[b] The age of Moroto localities has been much debated. It is noteworthy that some researchers (e.g., MacLatchy et al., 2019) favor the radiometric date of >20.6 Ma (Gebo et al., 1997) for Moroto, whereas Pickford and colleagues have favored younger ages of ~17.5–17.0 Ma (Pickford et al., 1986, 2003; Pickford and Mein, 2006) or even ~16.5–15.5 (Pickford et al., 2017) on biostratigraphic grounds. Most recently, Van Couvering and Delson’s (2020) provided a date of 19.3 Ma based on the redating of Bukwa at ~19 Ma (MacLatchy et al., 2006; Cote et al., 2018), which are somewhat older than Pickford’s (2017) radiometric dates for the same site (~18.0–17.5 Ma). Until new radiometric date for Moroto are published, we follow Cote (2018) in considering that biostratigraphic data support an older age for Moroto, tentatively around ~21.0–20.0 Ma.

[c] Kelley (2002) reported an approximate age range of ~12.5–10.5 Ma for *S. indicus*. The oldest citation from Pakistan would be 12.8–12.7 Ma according to Barry et al. (pers. comm. in SOM Table S1). Remains from Ramnagar in India (see SOM Table S1) might be older (13.8–12.5 Ma), probably close to ~13.0 Ma (Gilbert et al., 2020a), which is the maximum date considered here until the dates are clarified further.

Supplementary Online Material (SOM):

Systematics of Miocene apes: State of the art of a neverending controversy

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SOM S1

The principles of systematics and phylogenetic inference

1.1. Biological classifications as human constructs based on a natural system

Systematics aims to classify organisms according to a ‘natural’ (as opposed to ‘artificial’) system, which implies the existence of an external reality that needs to be discovered. Evolution, as the unifying paradigm for life sciences, provides such an objective basis for biological classification, and cladogenesis (beginning with speciation) further justifies the hierarchical structure of the system. Phylogenetic inference therefore plays a central role in the practice of systematics. However, besides cladogenesis, evolution further implies anagenesis, and there are different systematic approaches to reflect the patterns originated by these evolutionary processes—respectively, taxonomic diversity and morphological disparity (for a distinction between these concepts, see e.g., Briggs et al., 1992; Foote, 1994)—into classification, particularly given the double (both utilitarian and evolutionary) function of biological classifications (Benton, 2000). Despite the universal acceptance that systematics must reflect the evolutionary relationships among taxa, biological classifications are necessarily human constructs, so that there is no single true classification to be discovered in Nature (Benton, 2000). As a result, choosing among competing systematic classifications depends on both the systematic philosophy of each taxonomist and the phylogenetic hypotheses perceived by them as more accurate.

1.2. Monophyletic vs. paraphyletic groups

With the advent of phylogenetic systematics (Hennig, 1966), emphasis shifted from disparity to phylogeny (determined on the basis of synapomorphies), but the treatment of paraphyletic groups (i.e., those including taxa that share a common ancestor but that do not include all of its descendants) has proven controversial ever since. Phylogenetic systematics considers that only clades (i.e., strictly monophyletic groups) must be considered natural, such that paraphyletic groups should not be treated as taxa because they are based on the crossing of an arbitrary morphological threshold (or ‘grade’). Of course, paraphyletic groups can be inadvertently erected as presumed monophyletic taxa within a cladistic framework when most parsimonious cladograms do not reflect the true phylogeny of the group. Nevertheless, from an evolutionary viewpoint, the possibility that an originally monophyletic taxon becomes paraphyletic is contingent on it giving rise to a morphologically distinct subclade instead of becoming extinct (Carroll, 1988). Paraphyly is thus inescapable at the species and genus ranks because new species necessarily evolve from a pre-existing one and—unless we abandon

Linnean nomenclature—every species must belong to a genus (Sarmiento et al., 2002). This problem is often overlooked due to the cladistic convention that phylogenetic relationships must be depicted as dichotomic branching patterns, as if all species were monophyletic. This may generally hold true when only extant species are analyzed, but when applied to extinct species, sister-taxon relationships do not reflect the difference between sister species originated from a common ancestor and ancestor–descendant species pairs. In summary, paraphyly is an expected result of evolution (Carroll 1988) except when a lineage goes extinct. Therefore, some degree of tolerance toward paraphyly is advisable at lower taxonomic ranks. As noted by Sarmiento et al. (2002: 54), "Although at higher levels (above genus) a paraphyletic taxon is unacceptable, at lower levels it is inevitable".

To solve the purported problem of paraphyly, some authors have advocated the abandonment of binomial nomenclature and Linnean ranks altogether (de Queiroz and Gauthier, 1992; Cantino et al., 1999; de Queiroz and Cantino, 2001; Bryant and Cantino, 2002; Lee and Skinner, 2007). However, this proposal that has not been exempt of criticism (Benton, 2000; Forey, 2002) and has not gained wide acceptance. Adherence to the so-called phylogenetic nomenclature largely reflects a fundamental confusion about the difference between a phylogeny (which is real) and biological classification (which must be useful). Biological classifications must always be somewhat arbitrary: first, because they are conceived as practical means to efficiently transmit scientific knowledge; and second, because they cannot faithfully depict all the details of the continuum represented by the tree of life. Therefore, this work relies on the use of Linnean ranks—not because they have any intrinsic biological meaning, but rather because of their practical utility to simultaneously reflect (albeit imperfectly) both disparity and relatedness. Moreover, the use of Linnean ranks is not at all incompatible with trying to avoid paraphyly at suprageneric ranks—while recognizing that its avoidance at the genus and species-group levels is futile.

1.3. The epistemological basis of cladistics

Cladistics has been the predominant paradigm in morphology-based phylogenetic inference for several decades now. The word 'cladistics' may be employed as a synonym of 'phylogenetic systematics' or more specifically refer to a particular methodology of phylogenetic inference (i.e., cladistic analysis). Much has been written from the viewpoint of the philosophy of science about cladistic analysis, which is based on the main premise that only shared-derived features (synapomorphies) are phylogenetically informative (Hennig, 1966; Farris, 1983), as well as in the application of the principle of maximum parsimony. This principle, first introduced in phylogenetics as the ‘principle of minimum evolution’ (Edwards, 1996), stems from the assumption that homology must be presumed in the lack of evidence to the contrary (Hennig, 1966; Wiley, 1975), which is equivalent to assume that homoplasy must not be postulated beyond necessity a priori (Farris, 1983). In this sense, maximum parsimony is but the application in phylogenetic inference of an old and well-known epistemological approach that restricts inferential reasoning to the simplest theoretical framework necessary to account for the data (Kluge, 1984; Brower, 2000).

Following Wiley (1975) and Farris (1983), the scientific character of cladistic analysis based on maximum parsimony has generally been formulated as a refutationist (falsificationist) approach in terms of Popperian testability (Kluge, 1997, 1999, 2001). According to this interpretation, cladistic hypotheses (cladograms) would be composite explanations consisting of hypotheses of monophyly (cladogenetic events) and homology (character transformation events; Grant and Kluge, 2003), which are tested on the basis of the principle of parsimony. The latter emphasizes the degree of corroboration for deciding among competing hypotheses, so that the most parsimonious cladogram is the least disconfirmed and, hence, the most highly corroborated hypothesis (Kluge, 1999). Traditionally, it has been argued that parsimony maximizes explanatory power (presumed homologies) by minimizing the requirement for ad hoc hypotheses of homoplasy (Farris, 1983; Kluge, 1997). Subsequent reformulations have alluded to the ‘antisuperfluity principle,’ according to which explanatory power is maximized by minimizing the number of transformation events required as hypotheses of homology (Kluge and Grant, 2006).

From an operational viewpoint, similarity is only relevant for proposing hypotheses of primary homology based on similar traits shared by several taxa (Kluge, 1997). Hypotheses of primary homology, formalized as character statements, must be tested on the basis of the most parsimonious hypothesis (de Pinna, 1991), thus being corroborated (secondary homology) or refuted (homoplasy) a posteriori. Despite the claims to the contrary (Brower, 2000), cladistics must assume evolution (descent with modification) as background knowledge so as to interpret secondary homologies as such, as well as to interpret most parsimonious cladograms in terms of phylogenetic hypotheses. However, unless the most parsimonious hypothesis coincides with the true phylogeny, homoplasy as measured by cladistic analyses will always underestimate the true degree of homoplasy (Archie, 1996). In the lack of a better solution for the problem of homoplasy, a priori character weighting (Neff, 1986) might seem appealing. However, it is contrary to the epistemological basis of cladistics, according to which hypotheses of homology can only be corroborated or refuted a posteriori. Methods of character weighting a posteriori, such as successive weighting (Farris, 1969; Carpenter, 1988, 1994) or especially implied weighting (Goloboff, 1993, 1997) seem preferable, as the latter approach allows considering some character state transformations as more reliable than others as a consequence of the analysis, not as an assumption. Other alternative approaches include using a modified concept of parsimony (as in stratocladistics; see SOM S1.4) or probabilistic methods (such as Bayesian analyses; SOM S1.5).

Cladistics has been criticized by some researchers by arguing that it does not adhere to Popper's (1959, 1962) approach to the philosophy of science (e.g., Cartmill, 1981; Hull, 1988). Other authors have supported the scientific character of cladistics but questioned the interpretation of parsimony as a falsificationist method (Rieppel, 2003; Vogt, 2008; de Queiroz and Poe, 2001, 2003; de Santis, 2021). Some of the latter authors have argued that parsimony methods are only valid in Popperian terms if they incorporate probabilistic assumptions, with likelihood methods being considered the basis of Popper's degree of corroboration (de Queiroz and Poe, 2001, 2003; de Queiroz, 2004). This interpretation, which has been used to favor a unified and inclusive philosophy of phylogenetic inference (de Queiroz, 2004), has been criticized by others based on the contention that Popper's explanatory power is maximized deductively instead of inductively (Kluge and Grant, 2006). However, the latter position seems difficult to maintain and it is more reasonable to accept that testing among competing cladogram hypotheses cannot be based on Popperian falsificationism (Rieppel, 2003; Vogt, 2008, 2014).

We therefore concur with the views of Rieppel (2003) and Vogt (2008, 2014), according to whom: (1) cladistics is better interpreted as an inductive approach that is not based on Popperian falsificationism; (2) the hypothetico-deductive setting that constitutes the basis of Popperian falsificationism, developed for experimental sciences, must not necessarily be the only valid scientific approach, particularly for historical sciences such as phylogenetics; (3) hypothesis testing is not unique to Popperian falsificationism and plays a central role in phylogenetic inference by means of the application of general concepts that allow for hypothesis testing. Whether this means that cladograms are unfalsifiable (Vogt, 2008, 2014) or falsifiable (Crother and Murray, 2015) outside a Popperian philosophical framework is debatable—because a philosophy of phylogenetic inference independent from Popper's falsificationist approach would be necessary but is still a work in progress (Rieppel, 2003; de Queiroz, 2004; Helfenbein and DeSalle, 2005; Vogt, 2008; de Santis, 2021). However, this represents a rather semantical issue, as long as all methods of phylogenetic inference allow for testing among competing cladograms and potentially refuting them based on some general principle (such as maximum parsimony, among others). In any case, there can be little doubt that parsimony analysis differs epistemologically from probabilistic (likelihood and Bayesian) methods because the latter depend on specific evolutionary models (Huelsenbeck and Rannala, 1997; Goloboff et al., 2018), which arguably have some advantages and associated problems simultaneously, as explained in SOM S1.5.

1.4. Stratocladistics

Stratocladistics is a method of phylogenetic inference alternative to conventional cladistics that was developed during the 1990s to simultaneously consider morphological and chronostratigraphic data (Fisher, 1991, 1994, 2008). This method adheres to a similar epistemology to conventional cladistics (SOM S1.3) and is thus based on parsimony, but differs from conventional cladistics by minimizing ad hoc hypotheses of both character homoplasy and non-preservation in the fossil record (ghost lineages). Other differences of stratocladistics from conventional cladistics include taking into account autapomorphies and performing the analyses at the level of phylogenetic tree. This allows stratocladistic methods to infer ancestor–descendant relationships (Fisher, 2008), which are considered untestable under a strict cladistic paradigm. When stratocladistics was developed, several researchers warned against approaches incorporating stratigraphic data a priori because they would prevent using phylogeny as an independent test other temporal trends (Smith, 2000; Sumrall and Brochu, 2003), favoring instead the use of metrics measuring the congruence between cladograms and the stratigraphic record (e.g., Huelsenbeck, 1994; Hitchin and Benton, 1997).

Nevertheless, if it is conceded that stratigraphic data are relevant for inferring phylogeny, there is no reason to insist that they cannot in principle overturn parsimony considerations based on morphological data (Grantham, 2004). This contention fulfills the principle of total evidence—a basic maxim for non-deductive inference frequently advocated in cladistics—according to which “evidence must be considered if it has relevance to an inference” (Fitzhugh, 2006: 309). Stratocladistics thus minimizes the number of homoplasies and the number of ghost lineages simultaneously based on the concept of total parsimony debt (the sum of morphologic parsimony and stratigraphic parsimony debts) by assuming that an ad hoc hypothesis of preservation probability represents as much loss in explanatory power as an ad hoc hypothesis of homoplasy (Clyde and Fisher, 1997; Fisher, 1999, 2008). Despite criticisms, stratocladistic analyses with real data performed reasonably well, yielding cladograms with much lower stratigraphic parsimony debts than conventional cladistics at the expense only of slightly higher parsimony debts (Clyde and Fisher, 1997). Simulation studies further supported that stratocladistics outperforms the accuracy of conventional cladistics (Fox et al., 1999).

1.5. Bayesian analyses

Bayesian methods of phylogenetic inference using Markov chain Monte Carlo techniques developed two decades ago (Huelsenbeck et al., 2001; Holder and Lewis, 2003) can be applied to discrete morphological data and thus represent an alternative to parsimony analysis (Lewis, 2001a, 2001b; Nylander et al., 2004). Multiple simulation studies have shown that Bayesian methods outperform parsimony in terms of accuracy (Wiens, 2005; Wright and Hillis, 2014; O'Reilly et al., 2016, 2018; Puttick et al., 2019; Keating et al., 2020), particularly when homoplasy is high (Puttick et al., 2019), even if the former perform less efficiently in terms of node resolution (O'Reilly et al., 2016; Smith, 2019). Simulations further indicate that Bayesian analyses are less sensitive to long-branch attraction problems and that even very incompletely preserved extinct taxa can improve accuracy, unlike in parsimony analyses (Wright and Hillis, 2014). Moreover, Bayesian analyses allow for the simultaneous analysis of morphologic and molecular data, resulting (like stratocladistics) in time-calibrated phylogenies. Molecular evidence is customarily incorporated in parsimony analyses using a molecular backbone (e.g., Pugh, 2022) that does not inform about divergence times. In turn, fossil data are often included in molecular analyses to constrain the estimates of divergence times (e.g., Roos et al., 2019), an approach known as 'node dating'. In contrast, total-evidence analyses (combining morphologic and molecular data) based on Bayesian methods date divergence times by directly incorporating the age of the all the analyzed fossils, a procedure known as 'tip dating' or 'total-evidence dating' (e.g., Pyron, 2011; Ronquist et al., 2012, 2016; Donoghue and Yang, 2016). This approach has become more popular since the introduction of the fossilized birth–death process that models extant and fossil data as outcomes of the same macroevolutionary process (Heath et al., 2014; Zhang et al., 2016; King, 2021; Mongiardino Koch et al., 2021).

Tip dating differs from stratocladistics (see SOM S1.4) because topologies implying a higher stratigraphic debt are not explicitly penalized, although it has a similar result by making it more unlikely the grouping of morphologically similar but stratigraphically distant taxa (Hunt and Slater, 2016). Simulation studies have shown that tip-dated Bayesian analyses yield different topologies than both undated Bayesian and parsimony analyses, with the former having a better fit with stratigraphic data (King, 2021) and a greater accuracy (Mongiardino Koch et al., 2021), at least as long as fossil age uncertainties (Barido-Sottani et al., 2020) as well as fossilization and sampling biases (Zhang et al., 2016) are adequately modeled. Nevertheless, Bayesian methods had not been exempt from criticism, particularly regarding simulation results indicating that they have a lower resolution than parsimony methods (O'Reilly et al., 2016; Smith, 2019) or suggesting that the latter yield comparable, if not better, results as long as implied weighting is used (Goloboff, 2018; Smith, 2019; but see Keating et al., 2020). One of the caveats that currently apply to tip dating is that, unlike parsimony (Goloboff et al., 2006; Goloboff and Catalano, 2016), Bayesian methods do not permit the treatment of continuous morphological data as such, which is beneficial for reducing the subjectivity and potential loss of information implicit in the use of discrete characters (Parins-Fukichi, 2017), even if discretized using the gap-weighted method (Thiele, 1993). Nevertheless, recent developments of Bayesian methods are most promising in this regard (Álvarez-Carretero et al., 2017; Parins-Fukuchi, 2018). Even more important from an epistemological viewpoint is the fact that, unlike parsimony, Bayesian methods necessitate the a priori assumption of a particular evolutionary model of uncertain applicability to morphological data (Goloboff, 2018). On the other hand, this allows for further improvement in the future (as more realistic methods are developed) as well as the possibility to tackle potential problems of long-branch attraction (which parsimony cannot directly address because it does not take branch length or evolutionary rates into account; Pagel, 1999).

1.6. Apomorphy vs. clade-based definitions of taxa

Even if paraphyletic groups are avoided above the genus rank, not all clades can be erected as taxa. The advent of cladistics originally favored the use of apomorphy-based definitions of taxa, but subsequently phylogenetic nomenclature promoted instead clade-based definitions based on common ancestry (de Queiroz and Gauthier, 1990), which refer to a common ancestor of two taxa included in the taxon being defined. Two types of clade-based definitions of taxa are possible (de Queiroz and Gauthier 1992; Benton 2000): node-based definitions, which include all the descendants of the last common ancestor; and stem-based definitions, which further include those taxa more closely related to this last common ancestor than that of its closer formally-defined sister-taxon. The Code (ICZN, 1999) does not specify how taxa should be defined, so that Linnean ranks are not restricted to taxa defined on the basis of characters (Benton, 2000). Although both apomorphy-based and clade-based definitions may be useful, apomorphy-based definitions are the most problematic because they rely on an arbitrary selection of one or more synapomorphies that ultimately constitute a grade. Such a selection is particularly problematic when dealing with extinct taxa, due to the mosaic nature of evolution—the more basal is an extinct member of a clade, the more likely it will lack the synapomorphies of more advanced members of the same clade. Furthermore, some of the purported synapomorphies employed to define a particular group might eventually prove to be homoplastic. In contrast, clade-based definitions are more stable, and stem-based definitions are further favored here for groups with extant representatives.

1.7. Stem lineage vs. crown group

For an extant monophyletic group formally erected as a taxon, we can distinguish the crown group from the stem lineage (Jefferies, 1979; Ax, 1985; Smith, 1994; Benton, 2000), which together constitute the total group. The crown group is the clade that includes all the extant representatives of the taxon plus extinct representatives more closely related to some (but not all) of them. In contrast, the stem lineage is a paraphyletic assemblage of basal taxa that are more or less distantly (but equally) related to all crown group members, but more closely related to the latter than to its sister-group. Extinct representatives of the taxon's total group will be included into its crown group or stem lineage, depending on their particular phylogenetic relationships. Although supporters of node-based definitions of taxa have tended to restrict taxon names to the crown group (de Queiroz and Gauthier, 1992; Rowe and Gauthier, 1992), we prefer stem-based definitions, which apply to the whole community of descent (total group), because it may be difficult to determine whether a particular extinct species is a stem or a crown member of a particular clade. With a stem-based definition, the inclusion of this particular species into the taxon remains stable under both phylogenetic hypotheses. The crown group constitutes a clade and can be therefore formally erected as a taxon, whereas the stem lineage will rarely constitute a clade and, hence, it would constitute a paraphyletic taxon if formally designated. To avoid paraphyly, the use of several subtaxa (even if monotypic) for various subclades of the stem lineage (with the same rank as the crown group) is favored here—unless the current state of knowledge does not enable to discern whether the known members of the stem lineage constitute a monophyletic or paraphyletic assemblage.

SOM S2

Nomenclatural remarks

2.1. On the valid name for the family-group taxa including Kenyapithecus *and* Griphopithecus

Begun (2001, 2002) distinguished the family Griphopithecidae to include either *Griphopithecus* s.l. (including *Equatorius*) + *Afropithecus* (Begun, 2001) or *Griphopithecus* s.l. + *Kenyapithecus* (Begun, 2002), while Kelley (2002) distinguished a subfamily Griphopithecinae for *Griphopithecus* within the Afropithecidae. More recently, Begun (2010) distinguished a subfamily Griphopithecinae for these three genera plus *Nacholapithecus* within the Hominidae, while Andrews (2020) restricted the Griphopithecidae to *Griphopithecus*. Nevertheless, as remarked by previous authors (Moyà-Solà et al., 2009b; Harrison, 2010; Casanovas-Vilar et al., 2011), the tribes Afropithecini and Kenyapithecini erected by Andrews (1992) would have priority over family-group names derived from *Griphopithecus* if *Afropithecus* and/or *Kenyapithecus* are included. Furthermore, as noted by Casanovas-Vilar et al. (2011), Begun (2001, 2002) and Kelley (2002) did not fulfill the conditions of the Code (ICZN: Art. 16.1 and 16.2), according to which every new family-group name published after 1999 must be explicitly indicated as intentionally new and accompanied by citation of the name of the type genus; the same applies to Andrews (2020). None of these authors stated taxonomic authorities, so it is unclear if they attributed the taxon names to a previous author. Only Begun (2002) denoted both Griphopithecinae (for *Griphopithecus* s.l.) and Griphopithecidae (including Griphopithecinae + Kenyapithecinae) as 'new rank' but, to our knowledge, previous usage of this family-group taxon is restricted to Begun's (2001) Griphopithecidae. In any event, no family-group name derived from *Griphopithecus* is nomenclaturally available from these publications, irrespective of whether *Afropithecus* and *Kenyapithecus* are excluded, as in Kelley (2002) and Andrews (2020).

2.2. On the valid name for the European species of Griphopithecus

There are two species names available for the *Griphopithecus* species recorded in Germany and Slovakia, which were erected in the same publication based on material from the same locality: *Griphopithecus suessi* Abel, 1902 (the type species of the genus) and *Dryopithecus darwini* Abel, 2012. As noted by Simonetta (1958), Güleç and Begun (2003), and Casanovas-Vilar et al. (2011), either Remane (1921a) or Remane (1921b)—not Glaessner (1931), as argued by Holec and Emry (2003)—acted as the First Reviser (ICZN, 1999: Art. 24.2) by choosing *D. darwini* as the senior synonym. Following the resurrection of

Griphopithecus by Andrews et al. (1996), the combination *Griphopithecus darwini* has been frequently used (e.g., Begun, 2002, 2009; Kelley, 2002; Güleç and Begun, 2003). Nevertheless, *G. suessi* is the type species of *Griphopithecus* by monotypy (Holec and Emry, 2003; Casanovas-Vilar et al., 2011). A determination of precedence based on the Principle of the First Reviser is nullified if it can be subsequently shown that the precedence can be determined objectively. If it is interpreted that the designation of a type species fulfills the latter condition (Holec and Emry, 2003; Casanovas-Vilar et al., 2011), then the Principle of the First Reviser does not apply and the valid name for the species is *G. suessi*, with *G. darwini* being its junior subjective synonym.

2.3. On the valid name of the tribe including Sivapithecus

Although the intuitive name for a tribe including *Sivapithecus* would be Sivapithecini Pilbeam et al., 1977 (e.g., Andrews, 1992; Kelley, 2002), Bramapithecini Simonetta, 1958, Ramapithecini Simonetta, 1958, and Sugrivapithecini Simonetta, 1958 take precedence. Note that, although the publication year of these nominal taxa has generally been attributed to 1957 (e.g., Szalay and Delson, 1979), as noted by Ceccolini (2022) the publication was not issued until 1958—the date of the proofs stated in the last contribution of the same volume is February 4th, 1958, indicating that it could not have been issued before this date. Simonetta (1958) included these tribes within the Dryopithecinae, being based on genera erected by Lewis (1934), whereas *Sivapithecus* was included in the nominotypical tribe (Dryopithecini). Simonetta's (1958) spelling of Bramapithecini was Brahmapithecini, because he intentionally emended the spelling of *Bramapithecus* Lewis, 1934 into *Brahmapithecus*. However, although Lewis (1934) explicitly dedicated the genus to 'Brahma', the genus name was consistently written in Lewis (1934). Incorrect transliteration or latinization cannot be taken as an inadvertent error (ICZN, 1999: Art. 32.5), so that Simonetta's (1958) emendation of the genus name must be considered unjustified (ICZN, 1999: Art. 33.2). This means that *Brahmapithecus* Simonetta, 1958 is a junior objective synonym of *Bramapithecus* Lewis, 1934 and that the name of the tribe must be corrected as well (ICZN, 1999: Art. 35.4). Neither Simons and Pilbeam (1965) nor Szalay and Delson (1979) followed Simonetta's (1958) emendation of *Bramapithecus*, and Szalay and Delson (1979) apparently considered Brahmapithecini a lapsus, which was not.

Pilbeam et al. (1977) distinguished the subfamilies Sivapithecinae and Ramapithecinae, but Szalay and Delson (1979) considered that Sivapithecini was a junior synonym of Sugrivapithecini. Following Simons and Pilbeam (1965), Szalay and Delson (1979) considered *Bramapithecus* a subjective synonym of *Ramapithecus* Lewis, 1934 (then included in the Hominidae), and hence listed both Ramapithecini and Bramapithecini as synonyms of this family. In contrast, following Simons and Pilbeam (1965), Szalay and Delson (1979) considered that *Sugrivapithecus* Lewis, 1934 was a junior subjective synonym of *Sivapithecus* Pilgrim, 1910, and hence considered that Sugrivapithecini had priority over Sivapithecini. Given that Lewis' (1934) genera are all currently considered junior subjective synonyms of *Sivapithecus*, the three tribes erected by Simonetta (1958) must be considered subjective synonym as well, but their priority cannot be objectively determined. Following Szalay and Delson (1979), Alba (2012) used Sugrivapithecini and noted it had priority over Sivapithecini, but failed to comment as to why Sugrivapithecini would have priority over Ramapithecini or Bramapithecini. According to the Principle of the First Reviser (ICZN, 1999: Art. 24.2), when the precedence between names cannot be objectively determined, the precedence is fixed by the action of the first author citing in a published work those names and selecting from them. Given that Szalay and Delson (1979) did not synonymize the three tribes erected by Simonetta's (1958) and that Alba (2012) did not cite two of the three available names, neither of them qualifies as First Reviser. As we have been unable to find another work where these family-group names are mentioned, the present paper should fulfill the requirements of the Principle of the First Reviewer by stating that, to preserve current usage (Szalay and Delson, 1977; Alba, 2012), we choose Sugrivapithecini over Ramapithecini and Bramapithecini as the valid name for the tribe including *Sivapithecus* and its junior subjective synonyms *Ramapithecus*, *Bramapithecus*, and *Sugrivapithecus*.

It is noteworthy that the name Gigantopithecinae von Koenigswald, 1958 might be available for any family-group taxon including *Gigantopithecus* von Koenigswald, 1935. Although von Koenigswald (1958) did not explicitly note his will to establish a new taxon or designate a type genus, these requirements were not mandatory at the time (ICZN, 1999: Art. 16). As we include *Gigantopithecus* in the same tribe as *Sivapithecus*, Gigantopithecini von Koenigswald becomes a synonym of Sugrivapithecini as used here. Although we have been unable to determine the exact publication date of von Koenigswald's (1958) contribution in a conference proceedings volume, it could not have appeared before May 23th, 1958, when the conference has held, while Simonetta (1958) likely appeared shortly after February 4th the same year (see above). As such, there is currently no reason to support the precedence of Gigantopithecini over Sugrivapithecini.

2.4. On the valid name of the tribe including Ouranopithecus *and* Graecopithecus

The tribe Graecopithecini was first used in two articles published in the same year (Cameron, 1997a, 1997b). Only Cameron (1997b) explicitly noted the intention to erect a new taxon but, as both articles were published before 2000, this requirement of the Code (ICZN, 1999: Art. 16.1) does not apply for the name to be valid. In any event, based on publication date, the authorship of the taxon must be attributed to Cameron (1997b)—unlike for Hispanopithecini, which was only mentioned by Cameron (1997a) and must be considered available from that publication despite the lack of explicit mention of the erection of a new taxon, for the reason outlined above. Both *Graecopithecus freybergi* and *Ouranopithecus macedoniensis* were included in the Graecopithecini by Cameron (1997b), although the latter species was included in *Graecopithecus* by this author. The different opinions about the synonymy between *Ouranopithecus* and *Graecopithecus* and the taxonomic validity of *G. freybergi* have caused some confusion as to the correct name for the tribe including these taxa, particularly since another family-group taxon, the subtribe Ouranopithecina Begun, 2009, was subsequently described to include both genera. Alba (2012) elevated the latter taxon to tribe rank (i.e., Ouranopithecini Begun, 2009) to refer exclusively for *Ouranopithecus*, implicitly considering that *Graecopithecus* and its type species were nomina vana (Casanovas-Vilar et al., 2011). The latter authors remarked that Graecopithecini Cameron, 1997b would take precedence to include *Ouranopithecus* if *Graecopithecus* was considered a taxonomically valid genus included in the same tribe. As this is the opinion followed in the present paper, Ouranopithecini Begun, 2009 must be considered a junior subjective synonym of Graecopithecini Cameron, 1997b, although the former remains available if *Ouranopithecus* and *Graecopithecus* were eventually classified in different family-group taxa of the same rank.

SOM S3

On the deformation of the *Pierolapithecus* cranium

Based on the distortion of the *Pierolapithecus* cranium, Begun (2009, 2010) casted doubts on Moyà-Solà et al.'s (2004) interpretation of its facial profile as more plesiomorphic than that of crown hominids. Begun (2015: 1302–1303) further considered that the face of *Anoiapithecus* is "distorted" and that of *Pierolapithecus* is "seriously damaged," but provided no further details in this regard. According to the more detailed account of the *Pierolapithecus* cranium preservation published by Pérez de los Ríos et al. (2012), the most serious issue relates to the missing contact between the premaxilla and the maxilla. Nevertheless, the study of Pérez de los Ríos et al. (2012), which was focused on internal cranial anatomy, failed to notice the difficulties in adequately orienting the lower face relative to the upper face. Based on our own evaluation of the original specimen, the distortion that affects the fossil in multiple areas is not caused by plastic deformation of the bone but by multiple cracks filled with matrix and the consequent displacement of some fragments from their original position, which can be reasonably corrected by means of virtual 3D reconstruction. The latter is currently underway—see preliminary results by Pugh et al. (2022), which are consistent with the stem hominid status originally favored by Moyà-Solà et al. (2004) and later supported by cladistic analyses (Alba et al., 2015; Pugh, 2022). Even if the reconstructed facial profile of *Pierolapithecus* is ultimately demonstrated to be more orthognathous than preserved, it will be difficult to reconcile with the much more orthognathous facial profile of *Anoiapithecus*, which further displays other important craniodental differences that justify their generic distinction (Moyà-Solà et al., 2009b; Pérez de los Ríos et al., 2012).

SOM S4

The phylogenetic relationships between *Ouranopithecus*, *Nakalipithecus*, and hominines

The cladistic analyses of Pugh (2022) supported a stem hominine status for *Ouranopithecus* and *Graecopithecus*, and further lent some support to the phylogenetic link between *Ouranopithecus* and *Nakalipithecus* (as previously hypothesized by Kunimatsu et al., 2007). We consider such phylogenetic links plausible but insufficiently supported. For this reason, we refrain from including *Nakalipithecus* into the tribe Graecopithecini and also from classifying the latter taxon within the Homininae. We provide some discussion below as to why we consider this link insufficiently supported.

First, as recognized by Pugh (2022), most of the purported hominine synapomorphies of graecopithecins are ambiguous because they are present in many other taxa (e.g., relatively broader P_3, inflated glabella, or square orbits). Second, other purported hominine synapomorphies can be easily explained by the overall cranial robusticity of *Ouranopithecus* (e.g., robust supraorbital 'torus' and broad nasal aperture). A geometric morphometric analysis of the *Ouranopithecus macedoniensis* face found closer similarities with gorillas among extant great apes (Ioannidou et al., 2019). This confirmed the previous morphometric results by McNulty (2005), which were based exclusively on the supraorbital region, thus apparently supporting phenetic affinities between *Ouranopithecus* and hominines. However, as recognized by Ioannidou et al. (2019), about half of the variance of the axis distinguishing gorillas from chimpanzees and orangutans was correlated with size, while a reconstruction of the *Hispanopithecus laietanus* face was also classified as gorilla despite occupying an intermediate position on the morphospace among the three great ape genera (Ioannidou et al., 2019). This suggests that the *Ouranopithecus* might resemble gorillas in facial morphology more closely than dryopithecines simply owing to size-scaling (allometric) effects.

Third, the definition and/or scoring of some of the characters mentioned above is debatable. For example, Pugh's (2022) scored the orbits of *Sivapithecus* and *Pongo* with the same state ('rounded') as those of *Ekembo* and hylobatids (among many other taxa). This arguably obscures the derived condition of the former in this regard and, in any event, according to Pugh (2022) the purportedly derived 'squared' state of *Ouranopithecus* is also present in the dryopithecine *Rudapithecus*. Regarding the supraorbital 'torus,' given previous controversies about the presence of supraorbital costae (Moyà-Solà and Köhler, 1995) vs. a supraorbital torus (Begun, 1994) in *Hispanopithecus*, *Rudapithecus*, and *Ouranopithecus*, Pugh (2022) explicitly refrained from coding this structure as such. Instead, she split it into five different characters to better capture the morphological variation in this area. Pugh (2022) noted similarities between *Ouranopithecus* and *Hispanopithecus* in the configuration of the temporal lines and supraglabellar region, but interpreted them as primitive retentions. Nevertheless, of the five characters used by Pugh (2022) to code the morphology this region, only three (orientation of temporal lines, presence of transverse supratoral sulcus, and glabellar development) show differences between orangutans and African apes and could potentially be phylogenetically informative for resolving the closer phylogenetic relationships of graecopithecins among crown hominids. For the first two features, *Ouranopithecus* shows the same condition as dryopithecines and pongines, so that *Ouranopithecus* only more closely resembles African apes regarding the development of the glabella. Nevertheless, the same character state is displayed by *Rudapithecus*, while the pronounced supraglabellar depression of *Ouranopithecus* is shared with *Hispanopithecus* and seems autapomorphically derived for these taxa (as opposed to the apparently plesiomorphic condition retained by extant hominids and other dryopithecines).

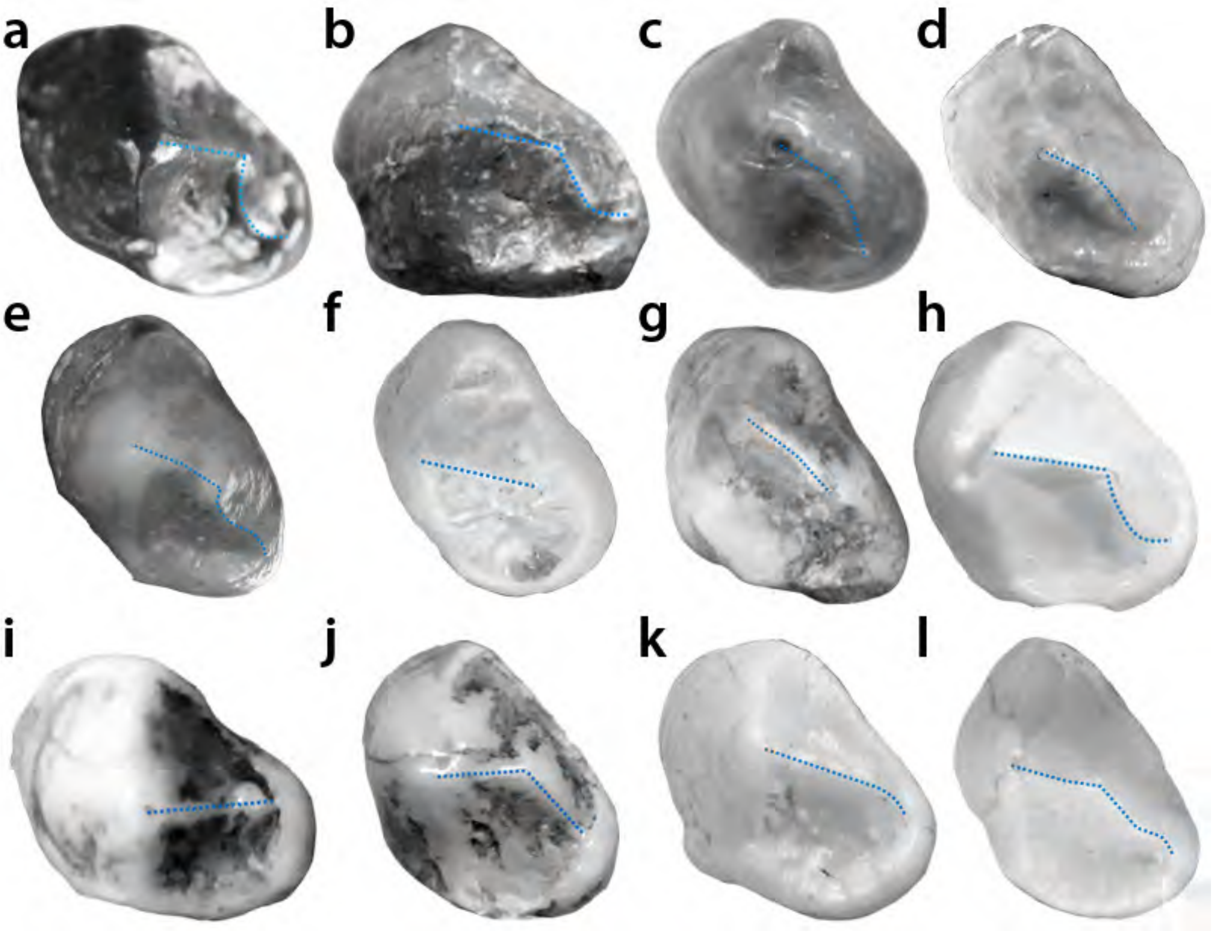
Finally, the interpretation of similarities in P_3 morphology between *Ouranopithecus*, *Nakalipithecus*, and gorillas (Pugh, 2022) is also debatable. Kunimatsu et al. (2007) noted similarities between *Nakalipithecus* and *Ouranopithecus* in the morphology of the P_3 (broader and with a more lingually oriented transverse cristid originating from the protoconid than in other Eurasian Miocene apes). Pugh (2022) elaborated further on these differences by noting that *Nakalipithecus* and *Ouranopithecus* uniquely share with gorillas (Delezene and Kimbel, 2011) a distal curvature of the P_3 transverse cristid. Nevertheless, according to Pugh's (2022) scorings, this cristid is more distally oriented in gorillas than in *Nakalipithecus* and *Ouranopithecus*; the latter genera rather resemble, in this regard, *Australopithecus*, *Indopithecus*, and *Gigantopithecus*—which might be related to the independent molarization of this tooth (Pugh, 2022, and references therein). In contrast, the distal curvature of the cristid, according to Pugh (2022), would only be present in gorillas, *Nakalipithecus*, and some specimens of *O. macedoniensis* (but not in other specimens of the latter or in *Ouranopithecus turkae*). However, we do not consider this configuration to be fundamentally different from that variably displayed by some dryopithecines (except by the more sectorial and buccolingually compressed crown of the latter), including the holotypes of *Dryopithecus fontani* and *H. laietanus* (SOM Fig. S1). Pugh (2022) argued that some chimpanzees display a distally curved cristid but considered this configuration to be different from that of gorillas, *Nakalipithecus*, and some specimens of *O. macedoniensis* in lacking a pronounced protrusion into the distal fovea. However, such a description might be applicable to the aforementioned dryopithecines and, even if the morphology of the cristid in considered most similar between the only available specimen of *Nakalipithecus* and some specimens of *Ouranopithecus* (something questionable in the light of the variability displayed by gorillas; SOM Fig. S1), the fact that this feature is variable in *Ouranopithecus* (Pugh, 2022) despite being dentally more derived than *Nakalipithecus* (Kunimatsu et al., 2007) renders its phylogenetic significance very tenuous. An alternative scoring of the P_3 transverse cristid in apes and humans based on enamel-dentine junction shape (Davies et al., 2019) reported that all the gorillas and chimpanzees investigated displayed a protoconid cristid that is either distally deflected or that flattens to the level of the surrounding fovea—these taxa only differing by the more distal origin of the cristid (relative to the protoconid dentine horn) in most chimpanzees. The configuration of African apes regarding the orientation of the cristid is shared with hylobatids but not with orangutans, which like most hominins display a more transversely oriented cristid originating at or near the apex of the protoconid dentine horn (Davies et al., 2019). On this basis, the distal deflection of the cristid in *Nakalipithecus*, *Ouranopithecus*, dryopithecines, and hominines, with its multiple variants, might be more plausibly interpreted as a hominoid symplesiomorphy.

SOM S5

Paleobiodiversity dynamics

To estimate Miocene ape paleobiodiversity through time, we divided the Miocene into equal-duration stratigraphic bins of 1 Myr (e.g., the bin 19–18 corresponds to 19.0–18.1 Ma), except for the most recent bin, which was restricted to 6.0–5.3 Ma (in agreement with the Miocene/Pliocene boundary). The maximum and minimum age for the ranges of each species were attributed to their respective bins, and a range-through approach was followed to compute diversity. Ranges that include a single dating ending in .0 Ma (e.g., 19.0 Ma) were thus assigned to the 19–18 bin, but ranges that include two datings ending in .0 Ma (e.g., 19.0–18.0 Ma) were assigned to a single bin (the 19–18 bin, as in the previous example), so as not to artifactually increase diversity counts.

The sample is too small to undertake a rigorous study of diversity dynamics (including the computation of origination and extinction rates), but two different metrics of diversity were computed: range-through or total diversity (N_{tot}) and standing diversity (N_{st}). The former is the most standard measure of diversity and is computed as follows (Foote, 2000): $N_{tot} = N_{bt} + N_{bL} + N_{Ft} + N_{FL}$, where N_{bt} is the number of range-through taxa (those found before and after the interval considered), N_{bL} is the number of bottom-only boundary crossers (those found before but not after the interval considered), N_{Ft} is the number of top-only boundary crossers (those found after but not before the interval considered), and N_{FL} is the number of singletons (single-interval taxa). Given that N_{tot} includes singletons, this metric is particularly sensitive to variation in preservation rates (Foote, 2000). In contrast, N_{st} ignores single-interval taxa because it is computed as the average of two successive (bottom and top) boundary crossers, thereby being a more robust estimate of standing diversity at a point in time within the interval (Foote, 2000); it is computed as follows: $N_{st} = (N_{bL} + N_{Ft} + 2N_{bt}) / 2 = N_{rt} - N_{FL} - ½ (N_{bL} + N_{Ft})$. The ranges for Miocene apes and per-bin metrics are shown in SOM Table S3. It should be taken into account that such metrics are seriously affected by multiple biases of the fossil record and can lead to misleading conclusions when interpreted literally (e.g., see discussion in Casanovas-Vilar et al., 2014). Nevertheless, they provide a rough idea of ape diversity changes throughout the Miocene.



SOM Figure S1. P_3 morphology in extant great apes and a selected sample of Miocene apes, in occlusal view. The approximate course of the transverse cristid originating from the protoconid is outlined by a dotted blue line. All specimens are depicted as from the left side (mirrored when necessary), with the mesial and distal cristids oriented to define an arbitrary mesiodistal axis (with mesial on top), and not to scale. a) *Nakalipithecus nakayamai*, KNM-NA 46423. b) *Ouranopithecus macedoniensis*, KNM-NA 46423. c) IPS1803, *Hispanopithecus laietanus* (holotype, mirrored). d) IPS1764, *H. laietanus* (mirrored). e) HGP2, *Dryopithecus fontani* (holotype, mirrored). f) AMNH-M 80008, *Pongo* sp. g) AMNH-M 28253, *Pongo pygmaeus* (mirrored). h) *Gorilla gorilla*, AMNH-M 167340. i) *Pan troglodytes*, AMNH-M 90292 (mirrored). j) *P. troglodytes*, AMNH-M 89406. k) *P. troglodytes*, AMNH-M 89351 (mirrored). l) *Pan paniscus*, AMNH-M 86857 (mirrored). Panels a–b, h–j, and k reproduced from Pugh (2022).

SOM Table S1

Miocene ape species-locality occurrences, including classification to family and subfamily ranks (see Table 2), subepoch, locality and site, country, age range, and citations of primary literature.[a] For further details on each locality, see SOM Table S2. (Provided separately as an Excel file.)

[a] When indicated as "Barry et al. (pers. comm.)", identifications of Siwalik hominoid remains checked or updated based on data kindly provided by John Barry, Larry Flynn, Jay Kelley, Michèle Morgan, and David Pilbeam on September 2022.

SOM Table S2

Miocene ape-bearing localities (in alphabetical order), including site/geographic area, country, age range, subepoch, and citations for the age.[a] (Provided separately as an Excel file.)

[a] When indicated as "Barry et al. (pers. comm.)", age of Siwalik localities checked or updated based on unpublished data kindly provided by John Barry, Larry Flynn, Jay Kelley, Michèle Morgan, and David Pilbeam on September 2022.

SOM Table S3

Chronostratigraphic ranges of Miocene apes divided by 1 Myr-duration bins and the corresponding diversity metrics. (Provided separately as an Excel file.)

SOM References

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SOM Table S1

Miocene ape species-locality occurrences, including classification to family and subfamily ranks (see Table 2), subepoch, locality and site, country, age range, and citations of primary literature. For further details on each locality, see SOM Table S2.

Family	Subfamily	Species	Locality (Site)	Country	Subepoch	Maximum age (Ma)	Minimum age (Ma)
Proconsulidae	-	*Proconsul africanus*	Chamtwara Member (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Proconsulidae	-	*Proconsul africanus*	Kapurtay (Kapurtay)	Kenya	Early Miocene	20,0	18,5
Proconsulidae	-	*Proconsul africanus*	Koru Fm. (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Proconsulidae	-	*Proconsul africanus*	Legetet Fm. (Koru-Muhoroni area)	Kenya	Early Miocene	20,0	19,0
Proconsulidae	-	*Proconsul africanus*	Songhor (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Proconsulidae	-	*Proconsul major*	Chamtwara Member (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Proconsulidae	-	*Proconsul major*	Koru Fm. (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Proconsulidae	-	*Proconsul major*	Legetet Fm. (Koru-Muhoroni area)	Kenya	Early Miocene	20,0	19,0
Proconsulidae	-	*Proconsul major*	Locality 14 - Maize Crib (Koru-Muhoroni area)	Kenya	Early Miocene	20,0	19,0
Proconsulidae	-	*Proconsul major*	Locality 34 - Maize Crib (Koru-Muhoroni area)	Kenya	Early Miocene	20,0	19,0
Proconsulidae	-	*Proconsul major*	Napak I (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul major*	Napak IV (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul major*	Napak V (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul major*	Napak IX (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul major*	Napak XIII (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul major*	Napak XV (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul major*	Napak XXVI (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul major*	Napak XXX (Akisim)	Uganda	Early Miocene	20,5	20,5
Proconsulidae	-	*Proconsul major*	Napak XXXI (Akisim)	Uganda	Early Miocene	20,5	20,5
Proconsulidae	-	*Proconsul major*	Napak CC (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul major*	Songhor (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Proconsulidae	-	*Proconsul gitongai*	BPRP K089A (Baringo)	Kenya	Middle Miocene	15,8	15,8
Proconsulidae	-	*Proconsul gitongai*	BPRP K091 (Baringo)	Kenya	Middle Miocene	15,8	15,8
Proconsulidae	-	*Proconsul gitongai*	Muruyur Fm. (Cheparawa)	Kenya	Middle Miocene	15,8	15,8
Proconsulidae	-	cf. *Proconsul gitongai*	Moroto II (Karamoja)	Uganda	Early Miocene	21,0	20,0
Proconsulidae	-	*Proconsul meswae*	Locality 36 - Meswa Bridge (Koru-Muhoroni area)	Kenya	Early Miocene	22,5	22,5
Proconsulidae	-	*Proconsul legetetensis*	Napak CC (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul legetetensis*	Napak I (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul legetetensis*	Napak IV (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul legetetensis*	Napak V (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul legetetensis*	Napak IX (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul legetetensis*	Napak V (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul legetetensis*	Napak XII (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul legetetensis*	Napak XIII (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul legetetensis*	Napak XV (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Proconsul legetetensis*	Napak XVIII (Akisim)	Uganda	Early Miocene	20,5	20,5
Proconsulidae	-	*Proconsul legetetensis*	Napak XXX (Akisim)	Uganda	Early Miocene	20,5	20,5
Proconsulidae	-	*Proconsul legetetensis*	Napak XXXI (Akisim)	Uganda	Early Miocene	20,5	20,5
Proconsulidae	-	*Proconsul* sp.	Fort Ternan (Fort Ternan)	Kenya	Middle Miocene	13,7	13,7
Proconsulidae	-	*Kalepithecus songhorensis*	Chamtwara Member (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Proconsulidae	-	*Kalepithecus songhorensis*	Koru Fm. (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Proconsulidae	-	*Kalepithecus songhorensis*	Napak IV (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Kalepithecus songhorensis*	Napak V (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Kalepithecus songhorensis*	Napak XV (Akisim)	Uganda	Early Miocene	20,5	19,0
Proconsulidae	-	*Kalepithecus songhorensis*	Napak XXXI (Akisim)	Uganda	Early Miocene	20,5	20,5
Proconsulidae	-	*Kalepithecus songhorensis*	Songhor (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Proconsulidae	-	*Kalepithecus kogolensis*	Moroto II (Karamoja)	Uganda	Early Miocene	21,0	20,0
Proconsulidae	-	*Ekembo heseloni*	Hiwegi Fm. (Rusinga Island)	Kenya	Early Miocene	18,3	18,3
Proconsulidae	-	*Ekembo heseloni*	Kulu Fm. (Rusinga Island)	Kenya	Early Miocene	16,0	16,0
Proconsulidae	-	*Ekembo heseloni*	Mfangano Island (Mfangano Island)	Kenya	Early Miocene	18,3	18,3
Proconsulidae	-	*Ekembo heseloni*	Kiahera Fm. (Rusinga Island)	Kenya	Early Miocene	18,5	18,5
Proconsulidae	-	*Ekembo nyanzae*	Kiahera Fm. (Rusinga Island)	Kenya	Early Miocene	18,5	18,5
Proconsulidae	-	*Ekembo nyanzae*	Hiwegi Fm. (Rusinga Island)	Kenya	Early Miocene	18,3	18,3
Proconsulidae	-	*Ekembo nyanzae*	Kulu Fm. (Rusinga Island)	Kenya	Early Miocene	16,0	16,0
Proconsulidae	-	*Ekembo nyanzae*	Mfangano Island (Mfangano Island)	Kenya	Early Miocene	18,3	18,3
Proconsulidae	-	Proconsulidae indet.	Bukwa II (Bukwa)	Uganda	Early Miocene	19,5	19,1
Nyanzapithecidae	-	*Xenopithecus koruensis*	Locality 14 - Maize Crib (Koru-Muhoroni area)	Kenya	Early Miocene	20,0	19,0
Nyanzapithecidae	-	*Mabokopithecus clarki*	Bed 3 (Maboko Island)	Kenya	Middle Miocene	15,3	15,3
Nyanzapithecidae	-	*Rangwapithecus gordoni*	Redbed Member Unit 5 (Koru-Muhoroni area - Songhor)	Kenya	Early Miocene	20,0	18,5
Nyanzapithecidae	-	*Rangwapithecus gordoni*	Redbed Member Unit 6 (Koru-Muhoroni area - Songhor)	Kenya	Early Miocene	20,0	18,5
Nyanzapithecidae	-	*Rangwapithecus gordoni*	Calcified Tuff Member (Lower Kapurtay)	Kenya	Early Miocene	20,0	18,5
Nyanzapithecidae	-	*Rangwapithecus gordoni*	LpM4 (Loperot)	Kenya	Early Miocene	17,0	17,0
Nyanzapithecidae	-	*Nyanzapithecus pickfordi*	Bed 3 (Maboko Island)	Kenya	Middle Miocene	15,3	15,3
Nyanzapithecidae	-	*Nyanzapithecus* cf. *pickfordi*	Muruyur - Kipsaraman (Baringo)	Kenya	Middle Miocene	15,8	15,8
Nyanzapithecidae	-	*Nyanzapithecus vancouveringorum*	Hiwegi Fm. (Rusinga Island)	Kenya	Early Miocene	18,3	18,3
Nyanzapithecidae	-	*Nyanzapithecus vancouveringorum*	Mfangano Island (Mfangano Island)	Kenya	Early Miocene	18,3	18,3
Nyanzapithecidae	-	*Nyanzapithecus vancouveringorum*	Magare (Uyoma Peninsula)	Kenya	Early Miocene	18,3	18,3
Nyanzapithecidae	-	*Nyanzapithecus alesi*	North Napudet (Napudet)	Kenya	Middle Miocene	13,3	13,3
Nyanzapithecidae	-	*Nyanzapithecus harrisoni*	BG-X (Nachola)	Kenya	Middle Miocene	15,0	15,0
Nyanzapithecidae	-	*Turkanopithecus kalakolensis*	FJ-18 (Fejej)	Ethiopia	Early Miocene	17,5	17,0
Nyanzapithecidae	-	*Turkanopithecus kalakolensis*	Kalodirr Member (Losodok)	Kenya	Early Miocene	17,5	17,5
Nyanzapithecidae	-	*Turkanopithecus rusingensis*	Hiwegi Fm. (Rusinga Island)	Kenya	Early Miocene	18,3	18,3
Nyanzapithecidae	-	*Turkanopithecus rusingensis*	Mfangano Island (Mfangano Island)	Kenya	Early Miocene	18,3	18,3
Nyanzapithecidae	-	*Turkanopithecus rusingensis*	Napak V (Akisim)	Uganda	Early Miocene	20,5	19,0
Nyanzapithecidae	-	*Turkanopithecus rusingensis*	Songhor (Koru-Muhoroni area)	Kenya	Early Miocene	20,3	20,3
Nyanzapithecidae	-	*Samburupithecus kiptalami*	Namurungule Fm. (Samburu Hills)	Kenya	Late Miocene	8,5	8,5
Nyanzapithecidae	-	Nyanzapithecidae indet.	Ryskop (Ryskop)	South Africa	Early Miocene	16,0	16,0
Nyanzapithecidae	-	Nyanzapithecidae indet.	Nakali (Nakali)	Kenya	Late Miocene	9,9	9,8
Nyanzapithecidae	-	Nyanzapithecidae indet.	Fort Ternan (Fort Ternan)	Kenya	Middle Miocene	13,7	13,7
Nyanzapithecidae	-	Nyanzapithecidae indet.	Kapsibor (Kapsibor)	Kenya	Middle Miocene	13,7	13,7
Nyanzapithecidae	-	Nyanzapithecidae indet.	Moroto II (Karamoja)	Uganda	Early Miocene	21,0	20,0
Afropithecidae	Afropithecinae	*Afropithecus turkanensis*	Buluk Member (Bakate Fm.)	Kenya	Early Miocene	17,2	17,2
Afropithecidae	Afropithecinae	*Afropithecus turkanensis*	Kalodirr Member (Losodok)	Kenya	Early Miocene	17,5	17,5
Afropithecidae	Afropithecinae	*Afropithecus turkanensis*	Locherangan (Locherangan)	Kenya	Early Miocene	17,6	17,6
Afropithecidae	Afropithecinae	*Afropithecus turkanensis*	Moruorot (Losodok)	Kenya	Early Miocene	17,5	17,5
Afropithecidae	Afropithecinae	*Heliopithecus leakeyi*	Ad Dabtiyah (Ad Dabtiyah)	Saudi Arabia	Early Miocene	16,0	16,0
Afropithecidae	Afropithecinae	*Morotopithecus bishopi*	Moroto I (Karamoja)	Uganda	Early Miocene	21,0	20,0
Afropithecidae	Afropithecinae	*Morotopithecus bishopi*	Moroto II (Karamoja)	Uganda	Early Miocene	21,0	20,0
Afropithecidae	Afropithecinae	cf. Afropithecinae	Napak XXXII (Akisim)	Uganda	Early Miocene	20,1	20,1
Afropithecidae	Equatorinae	*Equatorius africanus*	Ombo (Ombo)	Kenya	Early Miocene	16,0	16,0
Afropithecidae	Equatorinae	*Equatorius africanus*	Bed 3 (Maboko Island)	Kenya	Middle Miocene	15,3	15,3
Afropithecidae	Equatorinae	*Equatorius africanus*	BPRP 122 (Baringo)	Kenya	Middle Miocene	15,8	15,8
Afropithecidae	Equatorinae	*Equatorius africanus*	Kaloma (Kaloma)	Kenya	Middle Miocene	15,3	15,3
Afropithecidae	Equatorinae	*Equatorius africanus*	Majiwa (Majiwa)	Kenya	Middle Miocene	15,3	15,3
Afropithecidae	Equatorinae	*Equatorius africanus*	Muruyur Fm. (Cheparawa)	Kenya	Middle Miocene	15,8	15,8
Afropithecidae	Equatorinae	*Equatorius africanus*	Nyakach (Nyakach)	Kenya	Middle Miocene	15,0	15,0
Afropithecidae	Equatorinae	*Nacholapithecus kerioi*	BG-I (Nachola)	Kenya	Middle Miocene	15,0	15,0
Afropithecidae	Equatorinae	*Nacholapithecus kerioi*	BG-K (Nachola)	Kenya	Middle Miocene	15,0	15,0
Afropithecidae	Equatorinae	*Nacholapithecus kerioi*	BG-X (Nachola)	Kenya	Middle Miocene	15,0	15,0
Afropithecidae	Equatorinae	cf. *Nacholapithecus kerioi*	Moroto I (Karamoja)	Uganda	Early Miocene	21,0	20,0
Afropithecidae	Equatorinae	cf. *Nacholapithecus kerioi*	Moroto II (Karamoja)	Uganda	Early Miocene	21,0	20,0
Afropithecidae	Incertae sedis	*Otavipithecus namibiensis*	Berg Aukas (Berg Aukas)	Namibia	Middle Miocene	12,0	12,0
Hylobatidae	Yuanmoupithecinae	*Yuanmoupithecus xiaoyuan*	Leilao (Xiaohe Fm.)	China	Late Miocene	8,2	7,1
Hominidae	Kenyapithecinae	*Griphopithecus suessi*	Kleinhadersdorf (Vienna Basin)	Austria	Middle Miocene	13,8	12,7
Hominidae	Kenyapithecinae	*Griphopithecus suessi*	Devínska Nová Ves – Sandberg (Devínska Nová Ves –Sandberg (+	Slovakia	Middle Miocene	13,6	13,1
Hominidae	Kenyapithecinae	*Griphopithecus alpani*	Çandir (Çandir)	Turkey	Middle Miocene	14,1	13,4
Hominidae	Kenyapithecinae	*Griphopithecus alpani*	Paşalar (Paşalar)	Turkey	Middle Miocene	14,5	14,0
Hominidae	Kenyapithecinae	*Kenyapithecus wickeri*	Fort Ternan (Fort Ternan)	Kenya	Middle Miocene	13,8	13,8
Hominidae	Kenyapithecinae	*Kenyapithecus kizili*	Paşalar (Paşalar)	Turkey	Middle Miocene	14,5	14,0
Hominidae	Kenyapithecinae	cf. *Kenyapithecus* sp.	Berg Aukas (Berg Aukas)	Namibia	Middle miocene	12,0	12,0
Hominidae	Kenyapithecinae	Kenyapithecinae indet.	Thannhausen (Thannhausen)	Germany	Middle Miocene	14,0	14,0
Hominidae	Kenyapithecinae	cf. Kenyapithecinae	Engelwiess (Engelswies)	Germany	Early Miocene	16,5	16,0
Hominidae	Dryopithecinae	*Dryopithecus fontani*	ACM/C3-Ae (ACM)	Spain	Middle Miocene	11,9	11,9
Hominidae	Dryopithecinae	*Dryopithecus fontani*	ACM/C4-Ap (ACM)	Spain	Middle Miocene	11,9	11,9
Hominidae	Dryopithecinae	*Dryopithecus fontani*	La Grive Saint-Alban M (Isère)	France	Middle Miocene	12,5	11,9
Hominidae	Dryopithecinae	*Dryopithecus fontani*	St. Stefan im Lavanttal (Gratkorn Basin)	Austria	Middle Miocene	12,2	12,0
Hominidae	Dryopithecinae	*Dryopithecus fontani*	Can Mata s.l. (Can Mata)	Spain	Middle-Late Miocene	12,0	11,0
Hominidae	Dryopithecinae	*Dryopithecus fontani*	La Grive Saint-Alban L3/La Grive Saint-Alban L5? (Isère)	France	Middle-Late Miocene	11,9	11,2
Hominidae	Dryopithecinae	*Dryopithecus fontani*	St. Gaudens (Haute-Garonne)	France	Middle-Late Miocene	12,5	11,2
Hominidae	Dryopithecinae	*Dryopithecus* cf. *fontani*	ACM/C3-Az (ACM)	Spain	Middle Miocene	11,9	11,9
Hominidae	Dryopithecinae	*Pierolapithecus catalaunicus*	ACM/BCV1 (ACM)	Spain	Middle Miocene	12,0	12,0
Hominidae	Dryopithecinae	*Anoiapithecus brevirostris*	ACM/C1-E* (ACM)	Spain	Middle Miocene	12,4	12,3
Hominidae	Dryopithecinae	*Anoiapithecus brevirostris*	ACM/C3-Aj (ACM)	Spain	Middle Miocene	12,0	12,0
Hominidae	Dryopithecinae	*Anoiapithecus brevirostris*	ACM/C4-Cp (ACM)	Spain	Middle Miocene	12,0	12,0
Hominidae	Dryopithecinae	*Hispanopithecus laietanus*	Can Llobateres 1 (Can Llobateres)	Spain	Late Miocene	9,8	9,8
Hominidae	Dryopithecinae	*Hispanopithecus laietanus*	Can Llobateres 2 (Can Llobateres)	Spain	Late Miocene	9,6	9,6
Hominidae	Dryopithecinae	*Hispanopithecus laietanus*	La Tarumba 1 (La Tarumba)	Spain	Late Miocene	9,6	9,6
Hominidae	Dryopithecinae	*Hispanopithecus laietanus*	Can Feu 1 (Can Feu)	Spain	Late Miocene	10,0	9,7
Hominidae	Dryopithecinae	*Hispanopithecus* cf. *laietanus*	Can Pallars i Llobateres (Can Pallars i Llobateres)	Spain	Late Miocene	10,0	9,7
Hominidae	Dryopithecinae	*Hispanopithecus crusafonti*	Can Poncic 1 (Can Poncic)	Spain	Late Miocene	10,3	10,0
Hominidae	Dryopithecinae	*Hispanopithecus crusafonti*	Teuleria del Firal (Teuleria del Firal)	Spain	Late Miocene	10,3	10,0
Hominidae	Dryopithecinae	*Hispanopithecus* sp.	EDAR13 (EDAR)	Spain	Late Miocene	10,3	10,0
Hominidae	Dryopithecinae	*Hispanopithecus* sp.	Polinyà 2 (Polinyà)	Spain	Late Miocene	11,6	9,7
Hominidae	Dryopithecinae	*Rudapithecus hungaricus*	Rudabánya 2 (Pannonian Basin)	Hungary	Late Miocene	10,0	9,8
Hominidae	Dryopithecinae	*Danuvius guggenmosi*	Hammerschmiede 5 (Pforzen)	Germany	Late Miocene	11,6	11,6
Hominidae	Dryopithecinae	*?Udabnopithecus garedziensis*	Udabno 1 (Udabno)	Georgia	Late Miocene	8,1	7,7
Hominidae	Dryopithecinae	Dryopithecinae indet.	Castell de Barberà (Castell de Barberà)	Spain	Late Miocene	11,2	11,1
Hominidae	Dryopithecinae	Dryopithecinae indet.	Can Mata 1 (Can Mata)	Spain	Late Miocene	11,6	11,2
Hominidae	Dryopithecinae	Dryopithecinae indet.	Ebingen (Swabian Alb)	Germany	Late Miocene	11,0	9,0
Hominidae	Dryopithecinae	Dryopithecinae indet.	Melchingen (Swabian Alb)	Germany	Late Miocene	11,2	7,5
Hominidae	Dryopithecinae	Dryopithecinae indet.	Melchingen (Swabian Alb)	Germany	Late Miocene	11,2	7,5
Hominidae	Dryopithecinae	Dryopithecinae indet.	Neuhausen (Swabian Alb)	Germany	Late Miocene	11,0	9,0
Hominidae	Dryopithecinae	Dryopithecinae indet.	Neuhausen (Swabian Alb)	Germany	Late Miocene	11,0	9,0
Hominidae	Dryopithecinae	Dryopithecinae indet.	Neuhausen (Swabian Alb)	Germany	Late Miocene	11,0	9,0
Hominidae	Dryopithecinae	Dryopithecinae indet.	Trochtelfingen (Swabian Alb)	Germany	Late Miocene	11,0	9,0
Hominidae	Dryopithecinae	Dryopithecinae indet.	ACM/C5-C3 (ACM)	Spain	Middle Miocene	11,9	11,9
Hominidae	Dryopithecinae	Dryopithecinae indet.	ACM/C5-D1 (ACM)	Spain	Middle Miocene	11,7	11,7
Hominidae	Dryopithecinae	Dryopithecinae indet.	ACM/C8-B* (ACM)	Spain	Middle Miocene	11,9	11,9
Hominidae	Dryopithecinae	Dryopithecinae indet.	Wissberg (Gau-Weinheim)	Germany	Middle-Late Miocene	13,7	7,5
Hominidae	Dryopithecinae	*Neopithecus brancoi* nomem dubium	Salmendingen (Swabian Alb)	Germany	Late Miocene	11,6	7,5
Hominidae	Dryopithecinae	'*Sivapithecus*' *occidentalis* species inquirenda	ACM/BCV4 (ACM)	Spain	Middle Miocene	11,9	11,9
Hominidae	Dryopithecinae	'*Sivapithecus*' *occidentalis* species inquirenda	Can Vila (Can Vila)	Spain	Middle Miocene	12,0	12,0
Hominidae	Ponginae	*Khoratpithecus chiangmuanensis*	Chiang Muan - Upper Lignite (Nakhon Ratchasima Province, Kho	Thailand	Middle Miocene	12,4	12,2
Hominidae	Ponginae	*Khoratpithecus piriyai*	Somsak (Nakhon Ratchasima Province, Khorat)	Thailand	Late Miocene	9,0	6,0
Hominidae	Ponginae	*Khoratpithecus piriyai*	Lower Sand Unit (Nakhon Ratchasima Province, Khorat)	Thailand	Late Miocene	9,0	6,0
Hominidae	Ponginae	*Khoratpithecus* cf. *piriyai*	YS1 (Irrawaddy Fm.)	Myanmar	Late Miocene	9,0	6,0
Hominidae	Ponginae	*Khoratpithecus ayeyarwadyensis*	YS1 ? (Irrawaddy Fm.)	Myanmar	Late Miocene	10,4	8,8
Hominidae	Ponginae	*Khoratpithecus* cf. *ayeyarwadyensis*	SMG1 (Irrawaddy Fm.)	Myanmar	Late Miocene	10,0	8,0
Hominidae	Ponginae	*Khoratpithecus magnus*	Lower Sand Unit (Nakhon Ratchasima Province, Khorat)	Thailand	Late Miocene	9,0	6,0
Hominidae	Ponginae	*Ankarapithecus meteai*	Sinap Locality 12 (Sinap Formation)	Turkey	Late Miocene	9,8	9,8
Hominidae	Ponginae	*Lufengpithecus lufengensis*	Shihuiba 75033 D2-6 (Lufeng)	China	Late Miocene	6,9	6,2
Hominidae	Ponginae	*Lufengpithecus* cf. *lufengensis*	Shuitangba (Shuitangba)	China	Late Miocene	6,2	6,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Jabbi (Potwar Plateau)	Pakistan	Late Miocene	10,4	8,5
Hominidae	Ponginae	*Sivapithecus sivalensis*	Potwar Plateau [Dhok Pathan] (Potwar Plateau)	Pakistan	Late Miocene	9,8	8,5
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0182 (Gandakas)	Pakistan	Late Miocene	9,3	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0224 (Dinga Kas)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0226 (Dinga Kas)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0260 (Kaulial Kas)	Pakistan	Late Miocene	9,2	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0317 (Choutriwali Kas)	Pakistan	Late Miocene	9,3	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0350 (269 Section)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0409 (Kaulial Kas)	Pakistan	Late Miocene	9,3	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0410 (Kaulial Kas)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0463 (Kaulial Kas)	Pakistan	Late Miocene	9,3	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0137 (Gandakas Road)	Pakistan	Late Miocene	9,3	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0191 (Gandakas)	Pakistan	Late Miocene	9,4	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0207 (Malhuwala Kas)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0211 (Dinga Kas)	Pakistan	Late Miocene	9,3	9,3
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0221 (Dinga Kas)	Pakistan	Late Miocene	9,4	9,3
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0227 (227 Section)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0230 (227 Section)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0309 (Dhok Mila, Khaur Kas)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0310 (Dhok Mila, Khaur Kas)	Pakistan	Late Miocene	9,4	9,3
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0314 (Dhok Mila, Khaur Kas)	Pakistan	Late Miocene	9,3	9,3
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0327 (Kot Maliaran)	Pakistan	Late Miocene	9,3	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0414 (Kaulial Kas)	Pakistan	Late Miocene	9,3	9,3
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0416 (Kaulial Kas)	Pakistan	Late Miocene	9,4	9,3
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0442 (Kaulial Kas)	Pakistan	Late Miocene	8,6	8,5
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0604 (Kaulial Kas)	Pakistan	Late Miocene	8,6	8,5
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0328 (Hasal Kas, Bora Kas)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0885 (?)	Pakistan	-	?	?
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0891 (Kaulial Kas)	Pakistan	Late Miocene	8,8	8,7
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0990 (?)	Pakistan	-	?	?
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0997 (Kaulial Kas)	Pakistan	Late Miocene	9,3	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y1002 (Kaulial Kas)	Pakistan	Late Miocene	9,4	9,4
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y1004 (Kaulial Kas)	Pakistan	Late Miocene	9,4	9,3
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0261 (Kaulial Kas)	Pakistan	Late Miocene	9,6	9,6
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0251 (Ratha Kas)	Pakistan	Late Miocene	10,0	10,0
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks L0094 (Dhala Nala)	Pakistan	Late Miocene	10,3	10,1
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks KL0001 (Kaulial Kas)	Pakistan	Late Miocene	9,3	9,2
Hominidae	Ponginae	*Sivapithecus sivalensis*	Siwaliks Y0158 (=Y0388) (Malhuwala Kas)	Pakistan	Late Miocene	8,8	8,7
Hominidae	Ponginae	*Sivapithecus* cf. *sivalensis*	Haritalyangar (Haritalyangar)	India	Late Miocene	9,2	8,1
Hominidae	Ponginae	*Sivapithecus* cf. *sivalensis*	Chakrana (Haritalyangar)	India	Late Miocene	9,2	8,1
Hominidae	Ponginae	*Sivapithecus* cf. *sivalensis*	Bandal [Nagri Beds] (Bandal)	India	Late Miocene	10,1	8,6
Hominidae	Ponginae	*Sivapithecus* cf. *sivalensis*	Bharari (Haritalyangar)	India	Late Miocene	8,1	7,5
Hominidae	Ponginae	*Sivapithecus* cf. *sivalensis*	VPL-1 (Hari Mandar Dhar)	India	Late Miocene	9,0	9,0
Hominidae	Ponginae	*Sivapithecus* cf. *sivalensis*	Hari Devi 1 (HD1) (Haritalyangar)	India	Late Miocene	8,9	8,9
Hominidae	Ponginae	*Sivapithecus indicus*	Rashole 3 (Ramnagar)	India	Middle Miocene	13,8	12,5
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0083 (Hutch Nala)	Pakistan	Late Miocene	11,6	11,6
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0499 (Kanatti Upper)	Pakistan	Middle Miocene	12,1	12,1
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0500 (Kanatti Upper)	Pakistan	Late Miocene	12,1	12,1
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0663 (Parrawali)	Pakistan	Late Miocene	11,6	11,6
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0076 (Gambhir Section)	Pakistan	Late Miocene	11,5	11,4
Hominidae	Ponginae	*Sivapithecus indicus*	Potwar Plateau [Chinji] (Potwar Plateau)	Pakistan	Middle-Late Miocene	12,7	11,2
Hominidae	Ponginae	*Sivapithecus indicus*	Ramnagar (Ramnagar)	India	Middle Miocene	13,8	12,5
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0494 (Gambhir Section)	Pakistan	Middle Miocene	12,4	12,4
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0495 (Gambhir Section)	Pakistan	Late Miocene	11,6	11,6
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0496 (Gambhir Section)	Pakistan	Middle Miocene	12,4	12,4
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0498 (Hutch Nala)	Pakistan	Middle Miocene	11,7	11,7
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0647 (Gambhir Section)	Pakistan	Middle Miocene	12,4	12,4
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0750 (Samriala Nala)	Pakistan	Middle Miocene	12,8	12,7
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0767 (Gambhir Section)	Pakistan	Middle Miocene	12,4	12,3
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0775 (Rata Dala Nala)	Pakistan	Middle Miocene	12,4	12,2
Hominidae	Ponginae	*Sivapithecus indicus*	Dalsar (Ramnagar)	India	Middle Miocene	13,8	12,5
Hominidae	Ponginae	*Sivapithecus indicus*	Kundal Nala [Chinji] (Potwar Plateau)	Pakistan	Late Miocene	11,5	11,4
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks L0021 (Hutch Nala)	Pakistan	Late Miocene	11,4	11,4
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0829 (Samriala Nala)	Pakistan	Middle-Late Miocene	11,9	11,1
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks L0024 (Hutch Nala)	Pakistan	Middle Miocene	12,4	12,2
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks Y0502 (Hutch Nala)	Pakistan	Middle Miocene	12,0	12,0
Hominidae	Ponginae	*Sivapithecus indicus*	Siwaliks B0145 (?)	Pakistan	-	?	?
Hominidae	Ponginae	*Sivapithecus* cf. *indicus*	Siwaliks L0081 (Andar Kas)	Pakistan	Late Miocene	11,2	10,8
Hominidae	Ponginae	*Sivapithecus parvada*	Siwaliks Y0311 (Gambhir Section)	Pakistan	Late Miocene	10,1	10,0
Hominidae	Ponginae	*Sivapithecus* sp.	Siwaliks B0009 (Hasnot)	Pakistan	Late Miocene	11,2	10,8
Hominidae	Ponginae	*Sivapithecus* sp.	Dhara Reserve (Uttar Pradesh)	India	Middle-Late Miocene	12,7	11,2
Hominidae	Ponginae	*Sivapithecus* sp.	Siwaliks L0035 (Haritalyangar)	India	Late Miocene	?	?
Hominidae	Ponginae	*Sivapithecus* sp.	Tinau Khola (Dang Valley)	Nepal	Late Miocene	9,5	9,0
Hominidae	Ponginae	*Sivapithecus* sp.	Tapar (Kutch)	India	Late Miocene	10,8	10,0
Hominidae	Ponginae	*Sivapithecus* sp.	Siwaliks Y0259 (Kaulial Kas)	Pakistan	Late Miocene	10,5	10,4
Hominidae	Ponginae	*Sivapithecus* sp.	Dera Gopipur (Himachal Pradesh)	India	-	?	?
Hominidae	Ponginae	*Sivapithecus* sp.	Domeli (Potwar Plateau)	Pakistan	Late Miocene	11,5	9,0
Hominidae	Ponginae	*Sivapithecus* sp.	Siwaliks L0039 (Haritalyangar)	India	-	?	?
Hominidae	Ponginae	*Sivapithecus* sp.	Siwaliks L0040 (Haritalyangar)	India	-	?	?
Hominidae	Ponginae	*Sivapithecus* sp.	Siwaliks S0008 (?)	Pakistan	-	?	?
Hominidae	Ponginae	*Indopithecus giganteus*	Chandigarh (Haritalyangar)	India	Late Miocene	8,6	8,6
Hominidae	Ponginae	*Indopithecus giganteus*	HD1 (Haritalyangar)	India	Late Miocene	8,9	8,9
Hominidae	Ponginae	*Indopithecus giganteus*	Alipur (Alipur)	India	Late Miocene	8,6	8,6
Hominidae	Homininae	*Chororapithecus abyssinicus*	Chorora Fm. (Beticha)	Ethiopia	Late Miocene	8,0	8,0
Hominidae	Homininae	*Nakalipithecus nakayamai*	Nakali (Nakali)	Kenya	Late Miocene	9,9	9,8
Hominidae	Homininae	Homininae indet.	Kapsomin (Lukeino)	Kenya	Late Miocene	6,2	5,7
Hominidae	Homininae	Homininae indet.	Cheboit (Lukeino)	Kenya	Late Miocene	6,2	5,7
Hominidae	Incertae sedis	*Graecopithecus freybergi*	Pikermi Fm. - Red Conglomerate Member (Pyrgos)	Greece	Late Miocene	7,2	7,2
Hominidae	Incertae sedis	*Ouranopithecus macedoniensis*	Nikiti 1 (Chalkidiki Peninsula)	Greece	Late Miocene	9,7	8,8
Hominidae	Incertae sedis	*Ouranopithecus macedoniensis*	Ravin de la Pluie (Axios Valley)	Greece	Late Miocene	9,4	9,3
Hominidae	Incertae sedis	*Ouranopithecus macedoniensis*	Xirochori 1 (Axios Valley)	Greece	Late Miocene	9,7	9,7
Hominidae	Incertae sedis	*Ouranopithecus turkae*	Çorakyerle (Çorakyerle)	Turkey	Late Miocene	8,1	7,6
Hominidae	Incertae sedis	Graecopithecini indet.	Azmaka 6 (Azmaka)	Bulgaria	Late Miocene	7,2	7,2
Hominidae	Incertae sedis	*Sinopithecus keiyuanensis*	Xiaolungtan (Kaiyuan)	China	Middle-Late Miocene	12,5	11,6
Hominidae	Incertae sedis	*Sinopithecus hudienensis*	Baozidongqing (Xiaohe Fm.)	China	Late Miocene	8,2	8,1
Hominidae	Incertae sedis	*Sinopithecus hudienensis*	Fangbeiliangzi (Xiaohe Fm.)	China	Late Miocene	8,2	8,1
Hominidae	Incertae sedis	*Sinopithecus hudienensis*	Hudieliangzi (Xiaohe Fm.)	China	Late Miocene	8,2	8,1
Hominidae	Incertae sedis	*Sinopithecus hudienensis*	Leilao (Xiaohe Fm.)	China	Late Miocene	8,2	7,1
Hominidae	Incertae sedis	*Sinopithecus hudienensis*	Zhupeng (Xiaohe Fm.)	China	Late Miocene	7,4	7,2
Hominidae	-	Hominidae indet.	Maragheh - Middle Pumice (Maragheh)	Iran	Late Miocene	7,5	7,5
Hominidae	-	Hominidae indet.	BPRP 38 (Ngorora)	Kenya	Middle Miocene	12,8	12,8
Hominidae	-	Hominidae indet.	BPRP 60 (Ngorora)	Kenya	Middle Miocene	12,0	12,0
Hominidae	-	Hominidae indet.	BPRP 65 (Ngorora)	Kenya	Middle Miocene	12,8	12,8
Incertae sedis	-	*Oreopithecus bambolii*	Fiume Santo (Fiume Santo)	Italy	Late Miocene	8,1	6,7
Incertae sedis	-	*Oreopithecus bambolii*	V1 (Baccinello)	Italy	Late Miocene	8,3	8,1
Incertae sedis	-	*Oreopithecus bambolii*	V2 (Baccinello)	Italy	Late Miocene	8,1	6,7
Incertae sedis	-	'*Dryopithecus*' *wuduensis*	Wudu (Gansu)	China	Late Miocene	8,3	8,3
-	-	Hominoidea indet.	Moruorot (Losodok)	Kenya	Early Miocene	17,5	17,5
-	-	Hominoidea indet.	N 885 (N 885)	Niger	Late Miocene	11,0	8,0

* When indicated as 'Barry et al. (pers. comm.)', identifications of Siwalik hominoid remains checked or updated based on data kindly provided by John Barry, Larry Flynn, Jay Kelley, Michèle Morgan, and David Pilbeam on September 2022.

SOM Table S2

Miocene ape-bearing localities (in alphabetical order), including site/geographic area, country, age range, subepoch, and citations for the age.[a]

Locality	Site	Continent	Country	Maximum age (Ma)	Minimum age (Ma)	Subepoch	Citations
ACM/BCV1	ACM	Europe	Spain	12,0	12,0	Middle Miocene	Alba et al. (2017)
ACM/BCV4	ACM	Europe	Spain	11,9	11,9	Middle Miocene	Alba et al. (2017)
ACM/C1-E*	ACM	Europe	Spain	12,3	12,4	Middle Miocene	Alba et al. (2017)
ACM/C3-Ae	ACM	Europe	Spain	11,9	11,9	Middle Miocene	Alba et al. (2017)
ACM/C3-Aj	ACM	Europe	Spain	12,0	12,0	Middle Miocene	Alba et al. (2017)
ACM/C3-Az	ACM	Europe	Spain	11,9	11,9	Middle Miocene	Alba et al. (2017)
ACM/C4-Ap	ACM	Europe	Spain	11,9	11,9	Middle Miocene	Alba et al. (2017)
ACM/C4-Cp	ACM	Europe	Spain	12,0	12,0	Middle Miocene	Alba et al. (2017)
ACM/C5-C3	ACM	Europe	Spain	11,9	11,9	Middle Miocene	Alba et al. (2017)
ACM/C5-D1	ACM	Europe	Spain	11,6	11,6	Late Miocene	Alba et al. (2017)
ACM/C8-B*	ACM	Europe	Spain	11,7	11,7	Middle Miocene	Alba et al. (2017)
Ad Dabtiyah	Ad Dabtiyah	Africa	Saudi Arabia	16,0	16,0	Early Miocene	Van Couvering and Delson (2020)
Alipur	Alipur	Asia	India	8,6	8,6	Late Miocene	Pillans et al. (2005)
Azmaka 6	Azmaka	Europe	Bulgaria	7,2	7,2	Late Miocene	Böhme et al. (2017)
Bandal	Bandal	Asia	India	10,1	8,6	Late Miocene	Pickford (2010)
Baozidongqing	Xiaohe Fm.	Asia	China	8,2	8,1	Late Miocene	Woodburne et al. (2013)
Bed 3	Maboko Island	Africa	Kenya	15,3	15,3	Middle Miocene	Van Couvering and Delson (2020)
Berg Aukas	Berg Aukas	Africa	Namibia	12,0	12,0	Middle Miocene	Conroy et al. (1992)
BG-I	Nachola	Africa	Kenya	15,0	15,0	Middle Miocene	Van Couvering and Delson (2020)
BG-K	Nachola	Africa	Kenya	15,0	15,0	Middle Miocene	Van Couvering and Delson (2020)
BG-X	Nachola	Africa	Kenya	15,0	15,0	Middle Miocene	Van Couvering and Delson (2020)
Bharari	Haritalyangar	Asia	India	8,1	7,5	Late Miocene	Pillans et al. (2005); Pickford and Tiwari (2010)
BPRP 122	Baringo	Africa	Kenya	15,8	15,8	Middle Miocene	Van Couvering and Delson (2020)
BPRP 38	Ngorora	Africa	Kenya	12,8	12,8	Middle Miocene	Van Couvering and Delson (2020)
BPRP 60	Ngorora	Africa	Kenya	12,0	12,0	Middle Miocene	Van Couvering and Delson (2020)
BPRP 65	Ngorora	Africa	Kenya	12,8	12,8	Middle Miocene	Van Couvering and Delson (2020)
BPRP K089A	Baringo	Africa	Kenya	15,8	15,8	Middle Miocene	Van Couvering and Delson (2020)
BPRP K091	Baringo	Africa	Kenya	15,8	15,8	Middle Miocene	Van Couvering and Delson (2020)
Bukwa II	Bukwa	Africa	Uganda	19,5	19,1	Early Miocene	MacLatchy et al. (2006); Cote et al. (2018) [contra Pickford (2017)]
Buluk Member	Bakate Fm.	Africa	Kenya	17,2	17,2	Early Miocene	McDougall and Watkins (1985)
Calcified Tuff Member	Lower Kapurtay	Africa	Kenya	20,0	18,5	Early Miocene	Bishop et al. (1969)
Can Feu 1	Can Feu	Europe	Spain	10,0	9,7	Late Miocene	Casanovas-Vilar et al. (2016)
Can Llobateres 1	Can Llobateres	Europe	Spain	9,8	9,8	Late Miocene	Casanovas-Vilar et al. (2016)
Can Llobateres 2	Can Llobateres	Europe	Spain	9,6	9,6	Late Miocene	Casanovas-Vilar et al. (2016)
Can Mata 1	Can Mata	Europe	Spain	11,6	11,2	Late Miocene	Casanovas-Vilar et al. (2011)
Can Mata s.l.	Can Mata	Europe	Spain	11,3	11,0	Late Miocene	Alba et al. (2022)
Can Pallars i Llobateres	Can Pallars i Llobateres	Europe	Spain	10,0	9,7	Late Miocene	Alba et al. (2018)
Can Poncic 1	Can Poncic	Europe	Spain	10,3	10,0	Late Miocene	Casanovas-Vilar et al. (2011)
Can Vila	Can Vila	Europe	Spain	12,0	12,0	Middle Miocene	Casanovas-Vilar et al. (2011)
Çandir	Çandir	Asia	Turkey	14,1	13,4	Middle Miocene	Casanovas-Vilar et al. (2011)
Castell de Barberà	Castell de Barberà	Europe	Spain	11,2	11,2	Late Miocene	Casanovas-Vilar et al. (2011)
Chakrana	Haritalyangar	Asia	India	9,2	8,1	Late Miocene	Patnaik (2013)
Chamtwara member	Koru-Muhoroni area	Africa	Kenya	20,3	20,3	Early Miocene	Van Couvering and Delson (2020)
Cheboit	Lukeino	Africa	Kenya	6,2	5,7	Late Miocene	Pickford and Senut (2001)
Chorora Fm.	Beticha	Africa	Ethiopia	8,0	8,0	Late Miocene	Katoh et al. (2016)
Çorakyerle	Çorakyerle	Asia	Turkey	8,1	7,6	Late Miocene	Kaya et al. (2015)
Dalsar	Ramnagar	Asia	India	13,8	12,5	Middle Miocene	Sehgal and Patnaik (2012); Gilbert et al. (2020)
Dera Gopipur	Himachal Pradesh	Asia	India	?	?	-	Pickford and Tiwari (2010)
Devínska Nová Ves –Sandberg (= Neudorf Sandberg)	Devínska Nová Ves –Sandberg (= Neudorf Sandberg)	Europe	Slovakia	13,6	13,1	Middle Miocene	Březina et al. (2021); Sabol et al. (2021)
Dhara Reserve	Uttar Pradesh	Asia	India	11,0	10,0	Late Miocene	Johnson et al. (1983); Cameron et al. (1999)
Domeli	Potwar Plateau	Asia	Pakistan	11,5	9,0	Late Miocene	Barry et al. (2013)
Ebingen	Swabian Alb	Europe	Germany	11,0	9,0	Late Miocene	Pickford (2012)
EDAR13	EDAR	Europe	Spain	10,3	10,0	Late Miocene	Casanovas-Vilar et al. (2011)
Engelwies	Engelswies	Europe	Germany	16,5	16,0	Early Miocene	Casanovas-Vilar et al. (2011)
Fangbeiliangzi	Xiaohe Fm.	Asia	China	8,2	8,1	Late Miocene	Woodburne et al. (2013)
Fiume Santo	Fiume Santo	Europe	Italy	8,1	6,7	Late Miocene	Rook et al. (2011)
FJ-18	Fejej	Africa	Ethiopia	16,2	16,2	Early Miocene	Richmond et al. (1998)
Fort Ternan	Fort Ternan	Africa	Kenya	13,8	13,8	Middle Miocene	Van Couvering and Delson (2020)
Hammerschmiede 5	Pforzen	Europe	Germany	11,6	11,6	Late Miocene	Böhme et al. (2019)
Hari Devi 1 (HD1)	Haritalyangar	Asia	India	8,9	8,9	Late Miocene	Pillans et al. (2005)
Haritalyangar	Haritalyangar	Asia	India	9,2	8,1	Late Miocene	Patnaik (2013)
Hiwegi Fm.	Rusinga Island	Africa	Kenya	18,3	18,3	Early Miocene	Van Couvering and Delson (2020)
Hudieliangzi	Xiaohe Fm.	Asia	China	8,2	8,1	Late Miocene	Woodburne et al. (2013)
Jabbi	Potwar Plateau	Asia	Pakistan	10,4	8,5	Late Miocene	Lydekker (1879); Kelley (2005a)
Kalodirr Member	Losodok (=Lothidok, Losidok)	Africa	Kenya	17,5	17,5	Early Miocene	Van Couvering and Delson (2020)
Kaloma	Kaloma	Africa	Kenya	15,3	15,3	Middle Miocene	Van Couvering and Delson (2020)
Kapsibor	Kapsibor	Africa	Kenya	13,7	13,7	Middle Miocene	Harrison (1986)
Kapsomin	Lukeino	Africa	Kenya	6,2	5,7	Late Miocene	Pickford and Senut (2001)
Kapurtay	Kapurtay	Africa	Kenya	20,0	18,5	Early Miocene	Bishop et al. (1969)
Kiahera Fm.	Rusinga Island	Africa	Kenya	18,5	18,5	Early Miocene	Van Couvering and Delson (2020)
Kleinshadersdorf (= Klein Hadersdorf)	Vienna Basin	Europe	Austria	13,8	12,7	Middle Miocene	Steininger (1986), Kováč et al. (2018) y Březina et al. (2021)
Koru Fm.	Koru-Muhoroni area	Africa	Kenya	20,3	20,3	Early Miocene	Van Couvering and Delson (2020)
Kulu Fm.	Rusinga Island	Africa	Kenya	16,0	16,0	Early Miocene	Van Couvering and Delson (2020)
Kundal Nala [Chinji]	Potwar Plateau	Asia	Pakistan	11,5	11,4	Late Miocene	Barry et al. (2013)
La Grive Saint-Alban L3/La Grive Saint-Alban L5?	Isère	Europe	France	11,9	11,2	Middle-Late Miocene	Casanovas-Vilar et al. (2011)
La Grive Saint-Alban M	Isère	Europe	France	13,0	11,9	Middle Miocene	Casanovas-Vilar et al. (2011)
La Tarumba 1	La Tarumba	Europe	Spain	9,6	9,6	Late Miocene	Casanovas-Vilar et al. (2016)
Legetet Fm.	Koru-Muhoroni area	Africa	Kenya	20,0	19,0	Early Miocene	McCollum et al. (2013)
Leilao	Xiaohe Fm.	Asia	China	8,2	7,1	Late Miocene	Woodburne et al. (2013)
Locality 14 (Maize Crib)	Koru-Muhoroni area (Koru)	Africa	Kenya	20,0	19,0	Early Miocene	Pickford (1986)
Locality 34 (Maize Crib)	Koru-Muhoroni area (Koru)	Africa	Kenya	20,0	19,0	Early Miocene	Pickford (1986)
Locherangan	Locherangan	Africa	Kenya	17,6	17,6	Early Miocene	Van Couvering and Delson (2020)
Lower Sand Unit	Nakhon Ratchasima Province (Khorat)	Asia	Thailand	9,0	6,0	Late Miocene	Chaimanee et al. (2006)
LpM4	Loperot	Africa	Kenya	17,0	17,0	Early Miocene	Liutkus-Pierce et al. (2019)
Magare	Uyoma Peninsula	Africa	Kenya	18,3	18,3	Early Miocene	Drake et al. (1988); Van Couvering and Delson (2020)
Majiwa	Majiwa	Africa	Kenya	15,3	15,3	Middle Miocene	Van Couvering and Delson (2020)
Maragheh (Middle Pumice)	Maragheh	Asia	Iran	7,5	7,5	Late Miocene	Suwa et al. (2016)
Melchingen	Swabian Alb	Europe	Germany	11,2	7,5	Late Miocene	Casanovas-Vilar et al. (2011)
Meswa Bridge (Locality 36)	Koru-Muhoroni area	Africa	Kenya	22,5	22,5	Early Miocene	Van Couvering and Delson (2020)
Mfangano Island	Mfangano Island	Africa	Kenya	18,3	18,3	Early Miocene	Van Couvering and Delson (2020)
Moroto I	Karamoja	Africa	Uganda	21,0	20,0	Early Miocene	Cote et al. (2018)
Moroto II	Karamoja	Africa	Uganda	21,0	20,0	Early Miocene	Cote et al. (2018)
Moruorot	Losodok (=Lothidok, Losidok)	Africa	Kenya	17,5	17,5	Early Miocene	Boschetto et al. (1992)
Muruyur	Cheparawa	Africa	Kenya	15,8	15,8	Middle Miocene	Van Couvering and Delson (2020)
Muruyur - Kipsaraman	Baringo	Africa	Kenya	15,8	15,8	Middle Miocene	Van Couvering and Delson (2020)
N 885	N 885	Africa	Niger	11,0	8,0	Late Miocene	Mocke et al. (2022)
Nakali	Nakali	Africa	Kenya	9,9	9,8	Late Miocene	Kunimatsu et al. (2007)
Namurungule Fm.	Samburu Hills	Africa	Kenya	8,5	8,5	Late Miocene	Van Couvering and Delson (2020)
Napak CC	Akisim	Africa	Uganda	20,5	19,0	Early Miocene	Pickford et al. (2020)
Napak I	Akisim	Africa	Uganda	20,5	19,0	Early Miocene	Pickford et al. (2020)
Napak IV	Akisim	Africa	Uganda	20,5	19,0	Early Miocene	Pickford et al. (2020)
Napak IX	Akisim	Africa	Uganda	20,5	19,0	Early Miocene	Pickford et al. (2020)
Napak V	Akisim	Africa	Uganda	20,5	19,0	Early Miocene	Pickford et al. (2020)
Napak XII	Akisim	Africa	Uganda	20,5	19,0	Early Miocene	Pickford et al. (2020)
Napak XIII	Akisim	Africa	Uganda	20,5	19,0	Early Miocene	Pickford et al. (2020)
Napak XV	Akisim	Africa	Uganda	20,5	19,0	Early Miocene	Pickford et al. (2020)
Napak XVIII	Akisim	Africa	Uganda	20,5	20,5	Early Miocene	Pickford et al. (2020)
Napak XXVI	Akisim	Africa	Uganda	20,5	19,0	Early Miocene	Pickford et al. (2020)
Napak XXX	Akisim	Africa	Uganda	20,5	20,5	Early Miocene	Pickford et al. (2020)
Napak XXXI	Akisim	Africa	Uganda	20,5	20,5	Early Miocene	Pickford et al. (2020)
Napak XXXII	Akisim	Africa	Uganda	20,1	20,1	Early Miocene	Van Couvering and Delson (2020)
Neuhausen	Swabian Alb	Europe	Germany	11,0	9,0	Late Miocene	Pickford (2012)
Nikiti 1	Chalkidiki Peninsula	Europe	Greece	9,7	8,8	Late Miocene	Casanovas-Vilar et al. (2011)
North Napudet	Napudet	Africa	Kenya	13,3	13,3	Middle Miocene	Nengo et al. (2017)
Nyakach	Nyakach	Africa	Kenya	15,0	15,0	Middle Miocene	Van Couvering and Delson (2020)
Ombo	Ombo	Africa	Kenya	16,0	16,0	Early Miocene	Van Couvering and Delson (2020)
Paşalar	Paşalar	Asia	Turkey	14,5	14,0	Middle Miocene	Casanovas-Vilar et al. (2011)
Pikermi Fm. (Red Conglomerate Member)	Pyrgos	Europe	Greece	7,2	7,2	Late Miocene	Böhme et al. (2017)
Polinyà 2	Polinyà	Europe	Spain	11,6	9,7	Late Miocene	Casanovas-Vilar et al. (2011)
Potwar Plateau [Chinji]	Potwar Plateau	Asia	Pakistan	12,7	11,2	Middle-Late Miocene	Barry et al. (2002); Kelley (2005b) [used for specimens collected in early 20th century]
Potwar Plateau [Dhok Pathan]	Potwar Plateau	Asia	Pakistan	9,8	8,5	Late Miocene	Barry et al. (2002); Kelley (2005b) [used for specimens collected in early 20th century]
Ramnagar	Ramnagar	Asia	India	13,8	12,5	Middle Miocene	Pillans et al. (2005); Gilbert et al. (2020)
Rashole 3	Ramnagar	Asia	India	13,8	12,5	Middle Miocene	Gilbert et al. (2020)
Ravin de la Pluie	Axios Valley	Europe	Greece	9,4	9,3	Late Miocene	Casanovas-Vilar et al. (2011)
Redbed Member Unit 5	Koru-Muhoroni area (Songhor)	Africa	Kenya	20,0	18,5	Early Miocene	Bishop et al. (1969)
Redbed Member Unit 6	Koru-Muhoroni area (Songhor)	Africa	Kenya	20,0	18,5	Early Miocene	Bishop et al. (1969)
Rudabánya 2	Pannonian Basin	Europe	Hungary	10,0	9,7	Late Miocene	Casanovas-Vilar et al. (2011)
Ryskop	Ryskop	Africa	South Africa	16,0	16,0	Early Miocene	Van Couvering and Delson (2020)
Salmendingen	Swabian Alb	Europe	Germany	11,6	7,5	Late Miocene	Casanovas-Vilar et al. (2011)
Shihuiba 75033 D2-6	Lufeng	Asia	China	6,9	6,2	Late Miocene	Yue and Zhang (2006)
Shuitangba	Shuitangba	Asia	China	6,2	6,2	Late Miocene	Jablonski et al. (2014)
Sinap Locality 12	Sinap Formation	Asia	Turkey	9,8	9,8	Late Miocene	Kappelman et al. (2003)
Siwaliks B0009	Hasnot (Nagri Fm. - Siwalik Group)	Asia	Pakistan	11,2	10,8	Late Miocene	Brown et al. (1924); Barry et al. (2002); Barry et al. (pers. comm.)
Siwaliks B0145	? (Chinji Fm. - Siwalik Group)	Asia	Pakistan	?	?	-	Barry et al. (pers. comm.)
Siwaliks KL0001	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,2	Late Miocene	Barry et al. (pers. comm.)
Siwaliks L0021	Hutch Nala (Chinji Fm. - Siwalik Group)	Asia	Pakistan	11,4	11,4	Late Miocene	Barry (1986); Barry et al. (pers. comm.)
Siwaliks L0024	Hutch Nala (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,4	12,2	Middle Miocene	Barry et al. (pers. comm.)
Siwaliks L0035	Haritalyangar	Asia	India	?	?	-	Barry (1986); Barry et al. (pers. comm.)
Siwaliks L0039	Haritalyangar	Asia	India	?	?	-	Barry et al. (pers. comm.)
Siwaliks L0040	Haritalyangar	Asia	India	?	?	-	Barry et al. (pers. comm.)
Siwaliks L0081	Andar Kas (Chinji Fm. - Siwalik Group)	Asia	Pakistan	11,2	10,8	Late Miocene	Barry (1986); Barry et al. (pers. comm.)
Siwaliks L0094	Dhala Nala (Lower) (Nagri Fm. - Siwalik Group)	Asia	Pakistan	10,3	10,1	Late Miocene	Barry et al. (pers. comm.)
Siwaliks S0008	? (Manchar Fm. - Siwalik Group)	Asia	Pakistan	?	?	-	Khan et al. (1984); Raza et al. (1984); Barry et al. (pers. comm.)
Siwaliks Y0076	Gambhir Section (Chinji Fm. - Siwalik Group)	Asia	Pakistan	11,5	11,4	Late Miocene	Kappelman et al. (1991); Barry et al. (2002, pers. comm.); Flynn et al. (2020)
Siwaliks Y0083	Hutch Nala (Chinji Fm. - Siwalik Group)	Asia	Pakistan	11,6	11,6	Late Miocene	Flynn et al. (2020); Barry et al. (pers. comm.)
Siwaliks Y0137	Gandakas Road (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,2	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0158 (=Y0388)	Malhuwala Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	8,8	8,7	Late Miocene	Barry et al. (pers. comm.)
Siwaliks Y0182	Gandakas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,2	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0191	Gandakas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,2	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0207	Malhuwala Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0211	Dinga Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,3	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0221	Dinga Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,3	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0224	Dinga Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0226	Dinga Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0227	227 Section	Asia	Pakistan	9,4	9,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0230	227 Section	Asia	Pakistan	9,4	9,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0251	Ratha Kas (Nagri Fm. - Siwalik Group)	Asia	Pakistan	10,0	10,0	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0259	Kaulial Kas (Nagri Fm. - Siwalik Group)	Asia	Pakistan	10,5	10,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0260	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,3	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0261	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,7	9,7	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0309	Dhok Mila, Khaur Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0310	Dhok Mila, Khaur Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,3	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0311	Gambhir Section (Nagri Fm. - Siwalik Group)	Asia	Pakistan	10,1	10,0	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0314	Dhok Mila, Khaur Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,3	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0317	Choutriwali Kas (Nagri Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,2	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0327	Kot Maliaran (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,2	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0328	Hasal Kas, Bora Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0350	269 Section (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0409	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,2	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0410	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,4	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0414	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,3	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0416	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,3	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0442	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	8,6	8,5	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0463	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,2	Late Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0494	Gambhir Section (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,4	12,4	Middle Miocene	Barry (1986); Barry et al. (2002, pers. comm.)
Siwaliks Y0495	Gambhir Section (Chinji Fm. - Siwalik Group)	Asia	Pakistan	11,6	11,6	Late Miocene	Barry (1986); Kappelman et al. (1991); Barry et al. (pers. comm.)
Siwaliks Y0496	Gambhir Section (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,4	12,4	Middle Miocene	Barry (1986); Kappelman et al. (1991); Barry et al. (pers. comm.)
Siwaliks Y0498	Hutch Nala (Chinji Fm. - Siwalik Group)	Asia	Pakistan	11,7	11,7	Middle Miocene	Barry (1986); Kappelman et al. (1991); Barry et al. (pers. comm.)
Siwaliks Y0499	Kanatti Upper (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,1	12,1	Middle Miocene	Barry (1986); Kappelman et al. (1991); Barry et al. (pers. comm.)
Siwaliks Y0500	Kanatti Upper (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,1	12,1	Middle Miocene	Barry (1986); Kappelman et al. (1991); Barry et al. (pers. comm.)
Siwaliks Y0502	Hutch Nala (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,0	12,0	Middle Miocene	Barry et al. (pers. comm.)
Siwaliks Y0604	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	8,6	8,5	Late Miocene	Barry (1986); Barry et al. (pers. comm.)
Siwaliks Y0647	Gambhir Section (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,4	12,4	Middle Miocene	Morgan et al (2015); Barry et al. (pers. comm.)
Siwaliks Y0663	Parrawali (Chinji Fm. - Siwalik Group)	Asia	Pakistan	11,6	11,6	Late Miocene	Barry (1986); Kappelman et al. (1991); Barry et al. (pers. comm.)
Siwaliks Y0750	Samriala Nala (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,8	12,7	Middle Miocene	Kappelman et al. (1991); Barry et al. (pers. comm.)
Siwaliks Y0767	Gambhir Section (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,4	12,3	Middle Miocene	Kappelman et al. (1991); Barry et al. (pers. comm.)
Siwaliks Y0775	Rata Dala Nala (Chinji Fm. - Siwalik Group)	Asia	Pakistan	12,4	12,2	Middle Miocene	Kappelman et al. (1991); Barry et al. (pers. comm.)
Siwaliks Y0829	Samriala Nala (Chinji Fm. - Siwalik Group)	Asia	Pakistan	11,9	11,1	Middle-Late Miocene	Barry et al. (pers. comm.)
Siwaliks Y0885	? (Siwalik Group)	Asia	Pakistan	?	?	-	Barry et al. (pers. comm.)
Siwaliks Y0891	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	8,8	8,7	Late Miocene	Barry et al. (pers. comm.)
Siwaliks Y0990	? (Chinji Fm. - Siwalik Group)	Asia	Pakistan	?	?	-	Barry et al. (pers. comm.)
Siwaliks Y0997	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,3	9,2	Late Miocene	Barry et al. (pers. comm.)
Siwaliks Y1002	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,4	Late Miocene	Barry et al. (pers. comm.)
Siwaliks Y1004	Kaulial Kas (Dhok Pathan Fm. - Siwalik Group)	Asia	Pakistan	9,4	9,3	Late Miocene	Barry et al. (pers. comm.)
SMG1	Irrawaddy Fm.	Asia	Myanmar	10,0	8,0	Late Miocene	Takai et al. (2021)
Somsak	Nakhon Ratchasima Province (Khorat)	Asia	Thailand	9,0	6,0	Late Miocene	Chaimanee et al. (2006)
Songhor	Koru-Muhoroni area	Africa	Kenya	20,3	20,3	Early Miocene	Van Couvering and Delson (2020)
St. Gaudens	Haute-Garonne	Europe	France	12,5	11,2	Middle-Late Miocene	Casanovas-Vilar et al. (2011)
St. Stefan im Lavanttal	Gratkonr Basin	Europe	Austria	12,2	12,0	Middle Miocene	Casanovas-Vilar et al. (2011)
Sunetar 2	Lower Siwalik	Asia	India	13,8	12,5	Middle Miocene	Gilbert et al. (2020)
Tapar	Kutch	Asia	India	10,8	10,0	Late Miocene	Flynn et al. (2013); Patnaik et al. (2022)
Teuleria del Firal	Teuleria del Firal	Europe	Spain	10,3	10,0	Late Miocene	Casanovas-Vilar et al. (2011)
Thannhausen	Thannhausen	Europe	Germany	14,0	14,0	Middle Miocene	Pickford (2013)
Tinau Khola	Dang Valley	Asia	Nepal	9,5	9,0	Late Miocene	Munthe et al. (1983); West et al. (1991)
Tinau Khola	Dang Valley	Asia	Nepal	9,5	9,0	Late Miocene	Munthe et al. (1983)
Trochtelfingen	Swabian Alb	Europe	Germany	11,0	9,0	Late Miocene	Pickford (2012)
Udabno 1	Udabno	Asia	Georgia	8,1	7,7	Late Miocene	Agustí et al. (2020)
V1	Baccinello	Europe	Italy	8,3	8,1	Late Miocene	Rook et al. (2011)
V2	Baccinello	Europe	Italy	8,1	6,7	Late Miocene	Rook et al. (2011)
VPL-1	Hari Mandar Dhar	Asia	India	9,0	9,0	Late Miocene	Pillans et al. (2005)
Wissberg	Gau-Weinheim	Europe	Germany	13,7	7,5	Middle-Late Miocene	Casanovas-Vilar et al. (2011)
Wudu	Gansu	Asia	China	8,3	8,3	Late Miocene	Woodburne et al. (2013)
Xiaolungtan	Kaiyuan	Asia	China	12,5	11,6	Middle-Late Miocene	Li et al. (2015)
Xirochori 1	Axios Valley	Europe	Greece	9,7	9,7	Late Miocene	Casanovas-Vilar et al. (2011)
YS1	Irrawaddy Fm.	Asia	Myanmar	10,4	8,8	Late Miocene	Jaeger et al. (2011)
Zhupeng	Xiaohe Fm.	Asia	China	7,4	7,2	Late Miocene	Zhu et al. (2005)

[a] When indicated as 'Barry et al. (pers. comm.)", age of Siwalik localities checked or updated based on unpublished data kindly provided by John Barry, Larry Flynn, Jay Kelley, Michèle Morgan, and David Pilbeam on September 2022.

SOM Table S3

Chronostratigraphic ranges of Miocene apes divided by 1 Myr-duration bins and the corresponding diversity metrics.

Miocene ape species	Range / Bin	23-22	22-21	21-20	20-19	19-18	18-17	17-16	16-15	15-14	14-13	13-12	12-11	11-10	10-9	9-8	8-7	7-6	6-5
Proconsul africanus	20.3–18.5			x	x	x													
Proconsul major	20.5–19			x	x														
Proconsul gitongai	15.8								x										
Proconsul meswae	22.5	x																	
Proconsul legetetensis	20.5–19.0			x	x														
Kalepithecus songhorensis	20.5–19.0			x	x														
Kalepithecus kogolensis	21.0-20.0			x															
Ekembo heseloni	18.5–16.0					x	x	x											
Ekembo nyanzae	18.5–16.0					x	x	x											
Xenopithecus koruensis	20.0–19.0				x														
Mabokopithecus clarki	15.3								x										
Rangwapithecus gordoni	20.0–17.0				x	x	x												
Nyanzapithecus pickfordi	15.8–15.3								x										
Nyanzapithecus vancouveringorum	18.3					x													
Nyanzapithecus alesi	13.3										x								
Nyanzapithecus harrisoni	15.0									x									
Turkanapithecus kalakolensis	17.5–17.0						x												
Turkanapithecus rusingensis	20.5–18.3			x	x	x													
Samburupithecus kiptalami	8.5															x			
Afropithecus turkanensis	17.6–17.2						x												
Heliopithecus leakeyi	16.0								x										
Morotopithecus bishopi	21-20			x															
Equatorius africanus	16.0–15.0								x										
Nacholapithecus kerioi	15.0									x									
Otavipithecus namibiensis	12.0												x						
Yuanmoupithecus xiaoyuan	8.2–7.1															x	x		
Griphopithecus suessi	13.8–12.7										x	x							
Griphopithecus alpani	14.5–13.4									x	x								
Kenyapithecus wickeri	13.8										x								
Kenyapithecus kizili	14.5–14.0									x									
Dryopithecus fontani	12.5–11.0											x	x						
Pierolapithecus catalaunicus	12.0												x						
Anoiapithecus brevirostris	12.4–12.0											x							
Hispanopithecus laietanus	10.0–9.6														x				
Hispanopithecus crusafonti	10.3–10.0													x					
Rudapithecus hungaricus	10.0–9.8														x				
Danuvius guggenmosi	11.6												x						
?*Udabnopithecus garedziensis*	8.1–7.7															x	x		
Khoratpithecus chiangmuaneneis	12.4–12.2											x							
Khoratpithecus piriyai	9.0–6.0															x	x	x	
Khorapithecus ayeyarwadyenis	10.4–8.0													x	x	x			
Khoratpithecus magnus	9.0–6.0															x	x	x	
Ankarapithecus meteai	9.8														x				
Lufengpithecus lufengensis	6.9–6.2																	x	
Sivapithecus sivalensis	10.4–7.5													x	x	x	x		
Sivapithecus indicus	13.0–10.8											x	x	x					
Sivapithecus parvada	10.1–10.0														x				
Indopithecus giganteus	8.9–8.6															x			
Chororapithecus abyssinicus	8.0																x		
Nakalipithecus nakayamai	9.9–9.8														x				
Graecopithecus freybergi	7.2																x		
Ouranopithecus macedoniensis	9.7–8.8														x	x			
Ouranopithecus turkae	8.1–7.6															x	x		
Sinopithecus keiyuanensis	12.5–11.6											x	x						
Sinopithecus hudienensis	8.2–7.1															x	x		
Oreopithecus bambolii	8.3–6.7															x	x	x	
‘Dryopithecus’ wuduensis	8.3															x			
Variable		23-22	22-21	21-20	20-19	19-18	18-17	17-16	16-15	15-14	14-13	13-12	12-11	11-10	10-9	9-8	8-7	7-6	6-5
Nbt		0	0	0	1	1	2	0	0	0	0	0	1	0	2	0	3	0	0
NbL		0	0	0	4	2	1	2	0	0	1	1	2	1	0	2	5	3	0
NFt		0	0	5	2	2	0	0	0	1	1	4	0	2	1	7	0	0	0
NFL		1	0	2	0	1	2	0	5	3	2	1	3	1	5	4	2	1	0
Ntot = Nbt + NbL + NFt + NFL		1	0	7	7	6	5	2	5	4	4	6	6	4	8	13	10	4	0
Nst = (NbL + NFt + 2Nbt) / 2		0	0	2,5	4	3	2,5	1	0	0,5	1	2,5	2	1,5	2,5	4,5	5,5	1,5	0

Abbreviations: Nbt = range-through taxa; NbL = bottom-only boundary crossers; NFt = top-only boundary crossers; NFL = single-interval taxa; Ntot = range-through or total diversity; Nst = standing diversity.