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Miocene ape evolution: Where does *Oreopithecus* fit in?

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ABSTRACT - *Oreopithecus bambolii* Gervais, 1872, from the Late Miocene of Tusco-Sardinia, is the latest non-cercopithecoid catarrhine from Europe. Its geographic and phylogenetic origins remain uncertain despite being well known from craniodental and postcranial remains. Currently, there is a general agreement about its hominoid status (ape and human clade) but uncertainties persist regarding its specific relationships with other fossil and living apes. In the 1990s, *Oreopithecus* was considered a stem hominid (great ape and human clade) likely derived from dryopithecines (Middle to Late Miocene hominids from Europe). In contrast, recent cladistic analyses recovered *Oreopithecus* as a derived nyanzapithecoid (Early to Late Miocene putative stem hominoids from Africa). In turn, other studies hinted at a closer link with hylobatids (lesser apes). Given seemingly abundant homoplasy (false homology) in features related to orthogrady (upright body posture and locomotion), the *Oreopithecus* postcranium is compatible with being a stem or a crown hominoid. Craniodental evidence, in contrast, is at odds with a dryopithecine origin. A link with African nyanzapithecids seems more plausible based on dental morphology but hypothesized homologies deserve further investigation. In addition, preliminary analyses of tooth endostructure suggest similarities between *Oreopithecus* and pliopithecoids (putative stem catarrhines from the Miocene of Eurasia). The main branching topology of the hominoid total group (the divergence of hylobatids relative to putative stem hominoids from the Miocene of Africa) is far from being conclusively resolved due to abundant missing data and pervasive postcranial homoplasy between hylobatids and hominids, which might be causing a long-branch attraction problem. Hence, the hypothesized phylogenetic link between *Oreopithecus* and nyanzapithecids must not necessarily imply a stem hominoid status: given the long ghost lineage of hylobatids and the aforementioned long-branch attraction problem, a stem hylobatid status cannot be ruled out for nyanzapithecids. Previous difficulties to conclusively determine where *Oreopithecus* fits in hominoid phylogeny might simply stem from the need to shoehorn this taxon into broadly inaccurate Miocene ape phylogenetic schemes. Rather than considering *Oreopithecus* an oddball that deserves ad hoc explanations, this Late Miocene ape might be one of the key pieces needed to decipher the as yet unresolved puzzle of Miocene ape phylogeny.

INTRODUCTION

Hominoids are a clade of catarrhine primates that includes two extant lineages: hylobatids (lesser apes, including gibbons and siamangs) and hominids (great apes and humans). According to molecular data, these two families diverged in the Early Miocene ~20-17 Ma (Perelman et al., 2011; Springer et al., 2012). They differ in body size and craniodental morphology, while sharing a suite of postcranial features functionally related to orthograde (upright) behaviors, whose homology has been most debated (e.g., Larson, 1998). Many phylogenetic uncertainties persist regarding Miocene apes, for several reasons (for recent reviews, see Almécija et al., 2021; Urciuoli & Alba, 2023). First, hominoids are a currently decimated group that was much more taxonomically and morphologically diverse during the Miocene, when they were widely distributed across Eurasia and Africa. Second, fossil apes often display combinations of features that

are unknown among their extant counterparts and that do not fit well with the ancestral morphotypes that could be reconstructed exclusively on the basis of extant taxa, which appear notably autapomorphic (Harrison, 1991). Third, the fossil record of the group is very fragmentary (many species are still represented only by fragmentary dentognathic remains, while complete cranial specimens associated to postcrania are extremely rare), which hinders an unambiguous determination of the polarity of change (i.e., disentangling primitive from derived features). Finally, as for many other groups, there are strong indications of abundant homoplasy among various extant hominoid lineages, potentially affecting most of the postcranial features shared by hylobatids and hominids that are functionally related to orthograde positional behaviors (Larson, 1998; Moyà-Solà et al., 2004; Alba, 2012; Almécija et al., 2021).

The fossil record indicates that stem hominoids (i.e., those preceding the hylobatid-hominid split) are first

recorded during the Oligocene in Africa (Stevens et al., 2013; Hammond et al., 2019). Subsequently, hominoids experienced two major adaptive radiations during the Miocene (e.g., Almécija et al., 2021; Urciuoli & Alba, 2023): one during the Early Miocene in Afro-Arabia, including putative stem hominoids (proconsulids, afropithecids, and nyanzapithecids); and a second one during the Middle and Late Miocene, mainly (but not exclusively) in Eurasia and mostly including taxa customarily interpreted as either stem or crown members of the great ape and human clade (i.e., hominids; see Pugh, 2022, for a recent cladistic analysis of Middle to Late Miocene apes). Despite this general pattern, the systematic position and monophyly of most Miocene family-group taxa remains uncertain, as illustrated by the strong discrepancies among the cladistic analyses performed by different authors during the last decade (e.g., compare Rossie & Hill, 2018 with Nengo et al., 2017; Fig. 1).

The most vexing unresolved question in hominoid phylogenetics is probably the evolutionary origin of hylobatids. Although fossil hylobatids are recorded in Asia since at least the latest Miocene (Harrison, 2016; Ji et al., 2022), if not earlier (Gilbert et al., 2020a), the Early Miocene divergence supported by molecular data implies a long ghost lineage during which stem hylobatids must have existed, but we do not know what they looked like. Crown hylobatids might be a dwarfed lineage (Pilbeam, 1996; Reichard et al., 2016) that diverged from hominids in Eurasia after a transcontinental dispersal event ~16 Ma, or might have evolved from proconsulid or dendropithecoid ancestors that independently dispersed from Africa into Eurasia (Gilbert et al., 2020b). Although

this is seldom acknowledged, the latter possibility would imply that some of the groups of Miocene apes from Africa (nyanzapithecids and afropithecids), currently recovered as stem hominoids by cladistic analyses (Nengo et al., 2017; Gilbert et al., 2020a), might indeed be crown hominoids (Urciuoli & Alba, 2023).

Similarly embarrassing is the never-ending controversy surrounding the phylogenetic relationships of *Oreopithecus bambolii* Gervais, 1872 (established in Gervais, 1872a), despite (or maybe just because) its skeletal morphology is one of the most completely known among Miocene apes. *Oreopithecus* is recorded from several Late Miocene sites from the Maremma region in Tuscany and from Fiume Santo in Sardinia (Italy). These “Maremmian” faunas are considered to correspond to several successive faunal assemblages (V0 to V3, MN11 to MN13; Rook et al., 1999a, 2011; Bernor et al., 2001; Rook, 2016) that, except for the youngest one (V3), have a marked endemic component as a result of evolution under insularity conditions in the Late Miocene Tusco-Sardinian Paleobioprovince (Rook et al., 2006, 2011; Rook, 2016). *Oreopithecus* remains from both V1 (8.3-7.7 Ma) and V2 (7.1-6.7 Ma) assemblages from Tuscan localities are considered to belong to *O. bambolii* (Rook et al., 1996), whereas those from Sardinia (correlated to the V2 assemblage; Abbazzi et al., 2008; Casanovas-Vilar et al., 2011a) have tentatively been assigned to the same species (i.e., *O. cf. bambolii*; Cordy & Ginesu, 1994). The extinction of *Oreopithecus* slightly postdates that of other hominoids from the Miocene of mainland Europe (Casanovas-Vilar et al., 2011b). The extinction of most European hominoids has been related to paleoenvironmental changes driven

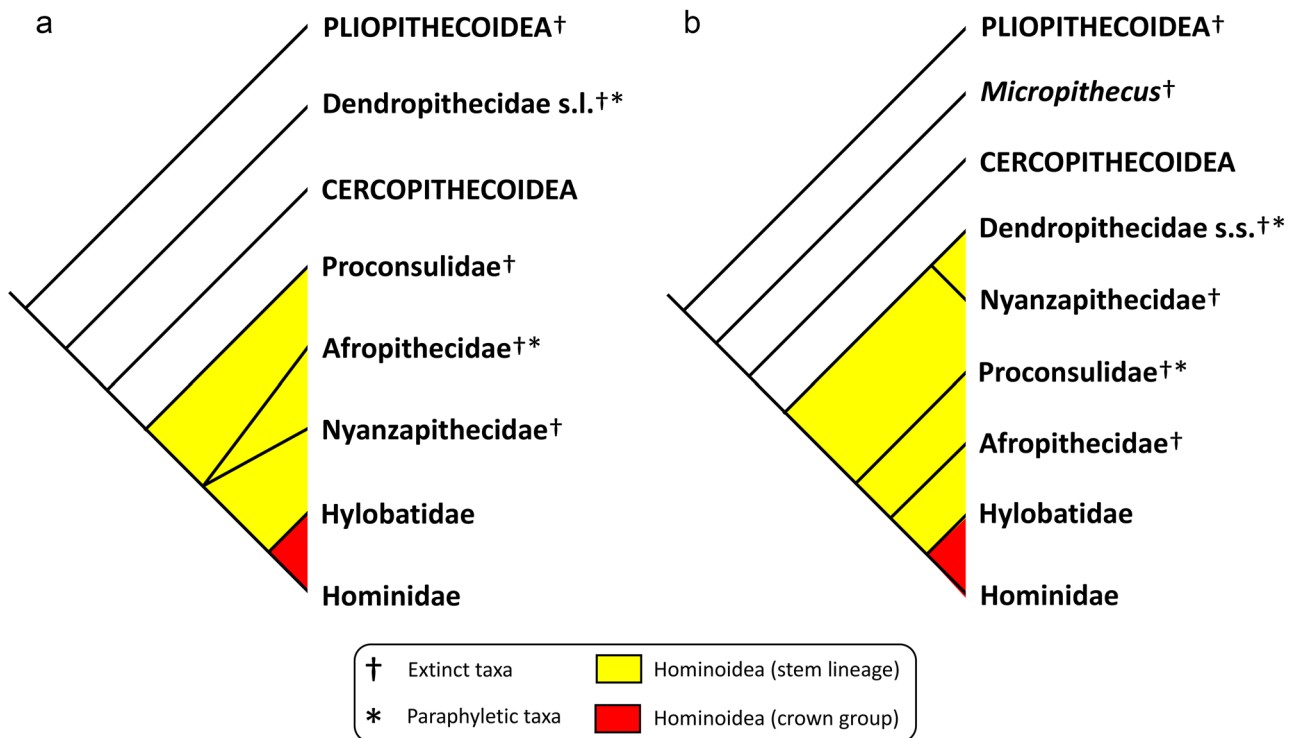


Fig. 1 - (color online) Schematic cladograms summarizing the phylogenetic relationships of extinct and extant hominoid families relative to cercopithecooids and the most derived purported stem catarrhines (pliopithecoids and dendropithecoids) according to the contrasting cladistic results of various authors: (a) based on Nengo et al. (2017) and Gilbert et al. (2020a); (b) based on Rossie & Hill (2018). Modified from Urciuoli & Alba (2023).

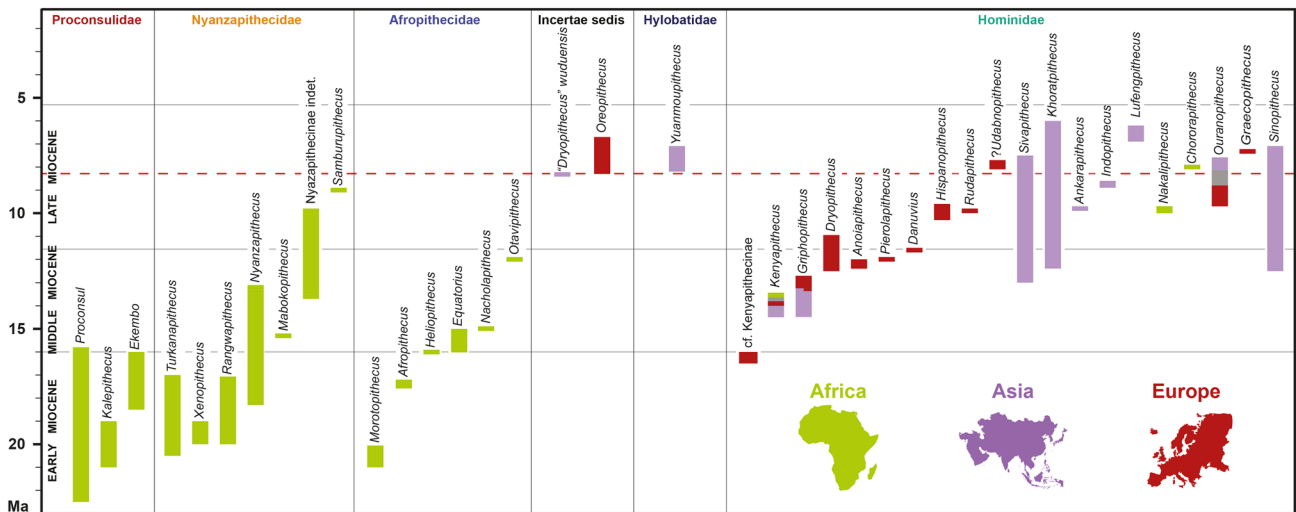


Fig. 2 - (color online) Chronostratigraphic ranges and broad geographic distribution of Miocene apes summarized at the genus level and organized according to the systematics of Urciuoli & Alba (2023). Chronostratigraphic ranges are organized from oldest to youngest (left to right) for each (sub)family 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 horizontal dashed red line corresponds to the first appearance datum of *Oreopithecus*, which slightly postdates that of African nyanzapithecids (including *Samburupithecus*, which has been placed at 9.6 Ma following Sawada et al., 2006) and European dryopithecines (except *?Udabnopithecus*). Modified from Urciuoli & Alba (2023).

by a longstanding trend toward cooling and increased seasonality (Agustí et al., 2003; Casanovas-Vilar et al., 2011b; Marmi et al., 2012; DeMiguel et al., 2014). In contrast, the extinction of *Oreopithecus* appears related to paleoecological changes caused by the entry of terrestrial predators and other vertebrates rather than any major climate shift (Matson et al., 2012; Nelson & Rook, 2016; Rook, 2016; DeMiguel & Rook, 2018). Such dispersals occurred when, as a consequence of the regional tectonism and paleogeographic changes that affected the northern Tyrrhenian regions in Late Miocene (latest Tortonian-Messinian) times, the Tusco-Sardinian Archipelago became connected to the mainland shortly after 7 Ma, as indicated by the composition of the V3 faunal assemblage (6.7-6.4 Ma; Rook et al., 2011).

Two main phylogenetic and paleobiogeographic hypotheses for the origin of *Oreopithecus* have been supported during the last couple of decades: 1) that it represents a derived nyanzapithecoid (stem hominoid) of African origin (Harrison, 1986b, 1987a; Benefit & McCrossin, 1997, 2001; Rossie & Cote, 2022); or 2) that it represents a derived dryopithecine (great ape) of European origin (Harrison & Rook, 1997; Moyà-Solà & Köhler, 1997). These two hypotheses are plausible on chronostratigraphic grounds (Fig. 2), given that *Oreopithecus* slightly postdates nyanzapithecids and most dryopithecines (except *?Udabnopithecus*; Urciuoli & Alba, 2023), but have opposite implications for its geographic origin (Fig. 3). Nevertheless, other possibilities, such as *Oreopithecus* being a stem hylobatid (Sarmiento, 1987; Hammond et al., 2020) or a derived pliopithecoid (Zanolli et al., 2022a, b), remain plausible given current uncertainties about Miocene ape evolution (Urciuoli & Alba, 2023). This review aims to: 1) recapitulate the different phylogenetic hypotheses put forward for *Oreopithecus* since its initial description more than 150 years ago; 2) discuss the pros and cons of the aforementioned main competing hypotheses based on current evidence for *Oreopithecus* and

other Miocene apes; and 3) frame the current debate about this taxon within standing uncertainties and prospects for the future regarding Miocene ape phylogenetics.

HISTORICAL BACKGROUND ON THE PHYLOGENY OF *OREOPITHECUS*

Early views

Oreopithecus bambolii was named by Gervais (1872a) based on a juvenile mandible from Montebamboli (Fig. 4). It entered in the collections of the “Regio Istituto di Studi Superiori e Pratici e di Perfezionamento” in 1862 and was entrusted to the French Paleontologist P. Gervais by I. Cocchi, at the time Director of the Florence Institute (Cocchi, 1872; Cioppi & Rook, 2010). Gervais then described in greater detail the specimen in another paper published the same year (Gervais, 1872b). The name of the genus (from the Greek *oros*, meaning “hill” or “mountain”) alluded to the protruding shape of its molar cusps (Gervais, 1872a). From the beginning, the dental morphology of *Oreopithecus* was rightfully perceived as unusual, leading to many divergent interpretations of its systematic affinities over the years. Originally, Gervais (1872a, b) noted some dental similarities with cercopithecoids (Old World monkeys) but considered *Oreopithecus* to be a fossil ape (hominoid). However, soon thereafter other researchers disagreed (for further details, see historical review in Delson, 1986). Rüttimeyer (1876) considered it a gibbon, Forsyth Major (1880) noted similarities with humans, Schlosser (1887) classified it as a cercopithecoid, and Ristori (1890) as somewhat intermediate between cercopithecoids and hominoids. The latter view was formalized by Schwalbe (1915), who erected the family Oreopithecidae on the basis of this genus, whereas Gregory (1920) considered *Oreopithecus* a cercopithecoid and noted similarities with *Apidium* (currently considered a stem anthropoid).

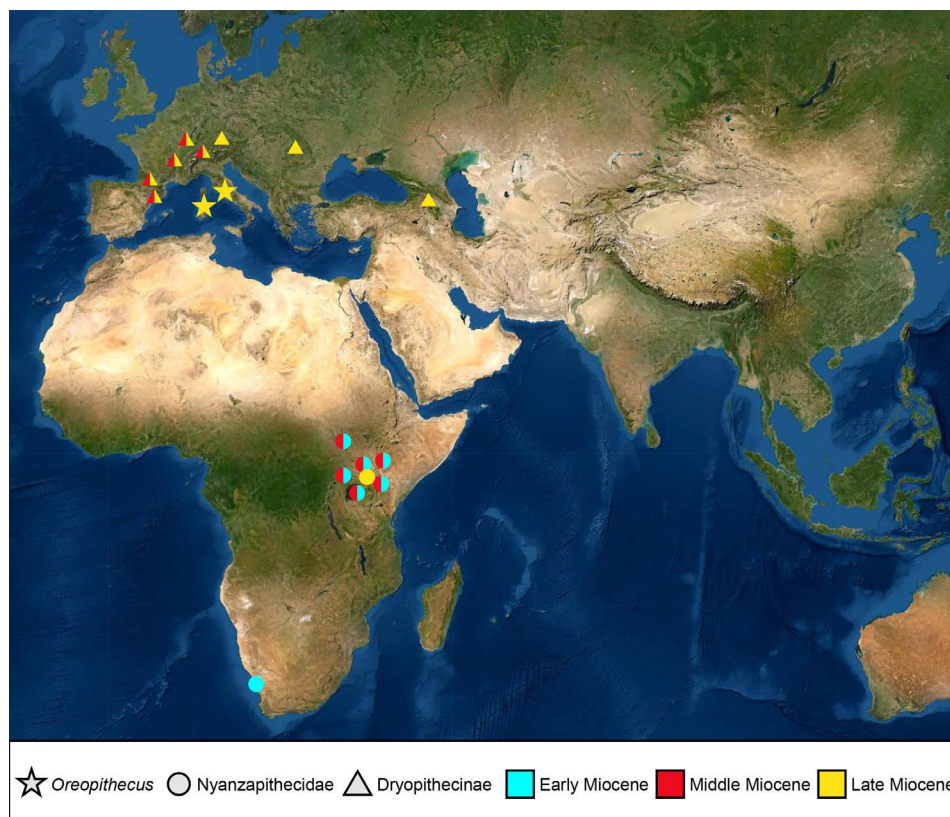


Fig. 3 - (color online) Geographic distribution of *Oreopithecus*, nyanzapithecids, and dryopithecine hominids during the Early, Middle, and Late Miocene on a map of the Old World based on the information summarized by Urciuoli & Alba (2023). Base map downloaded from ArcGIS Online (<https://www.esri.com/it-it/arcgis/products/arcgis-online/>); 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.

Schlosser (1887) and Gregory's (1920) views were still echoed by Simpson (1945), who included both *Oreopithecus* and *Apidium* in the Cercopithecoidea. Nevertheless, *Oreopithecus* was largely ignored for several decades, until Swiss paleontologist Johannes Hürzeler revitalized the study of this taxon and, ultimately, contributed to salvage the most complete individual available to date. Initially, Hürzeler (1949) redescribed the then available dentognathic remains of *Oreopithecus*, and favored affinities with hominoids rather than cercopithecoids. Similar views were expressed by Hürzeler (1951) when studying its dp4 morphology, further noting the bicuspid morphology of the p3, which he subsequently used (among other features) to support a phylogenetic link between *Oreopithecus* and the human lineage in multiple papers and conference proceedings (Hürzeler, 1954a, 1956a, b, 1958, 1959, 1960). From 1956 until 1958, Hürzeler actively contributed to the recovery of abundant fossil remains during mining works at Baccinello, which would otherwise have been destroyed (de Terra, 1956; Engesser, 2000). These works culminated with the recovery of a remarkably complete (albeit crushed) partial skeleton in 1958 (Straus, 1958a; Engesser, 2000), just after the publication of Hürzeler's main work on *Oreopithecus* (Hürzeler, 1958).

Hürzeler's views on *Oreopithecus* as an early member of the human lineage were received differently by other researchers (Trevor, 1961), being readily accepted by

some (Viret, 1955; Straus, 1957, 1958b, 1963; Crusafont Pairó, 1959) but rejected by others (Heberer, 1952; Remane, 1955; Von Koenigswald, 1955; Butler & Mills, 1959; Schultz, 1960). Some of the latter authors agreed on the hominoid status of *Oreopithecus* but considered it sufficiently distinct from both "pongids" (great apes) and "hominids" (currently hominins) to warrant classification in a distinct family (Butler & Mills, 1959; Schultz, 1960). Straus (1963) preliminarily reviewed the anatomical evidence, concluding that *Oreopithecus* was a hominoid, probably a stem "hominid", or else a member of its own family, the latter alternative being favored by Simpson (1963). In contrast, Simons (1960) revived Gregory's (1920) phylogenetic link with *Apidium* and, slightly later, the same author (Simons, 1961, 1964) supported instead the Miocene hominoid *Ramapithecus* as an alternate candidate for an early forerunner of the human lineage (following an earlier proposal by Lewis, 1934). By the same time, Leakey (1961) also favored as an early "hominid" the genus *Kenyapithecus* from Africa, which was subsequently synonymized with *Ramapithecus* by Simons & Pilbeam (1965), albeit not without criticism (Leakey, 1967). With several Miocene taxa contending for the role of an early member of the human lineage during the 1960s, Hürzeler's views on *Oreopithecus* received a lot of attention from the media (Engesser, 2000). They were also discussed by some of his peers (e.g., Simpson, 1963; Straus, 1963) but largely dismissed or even ignored

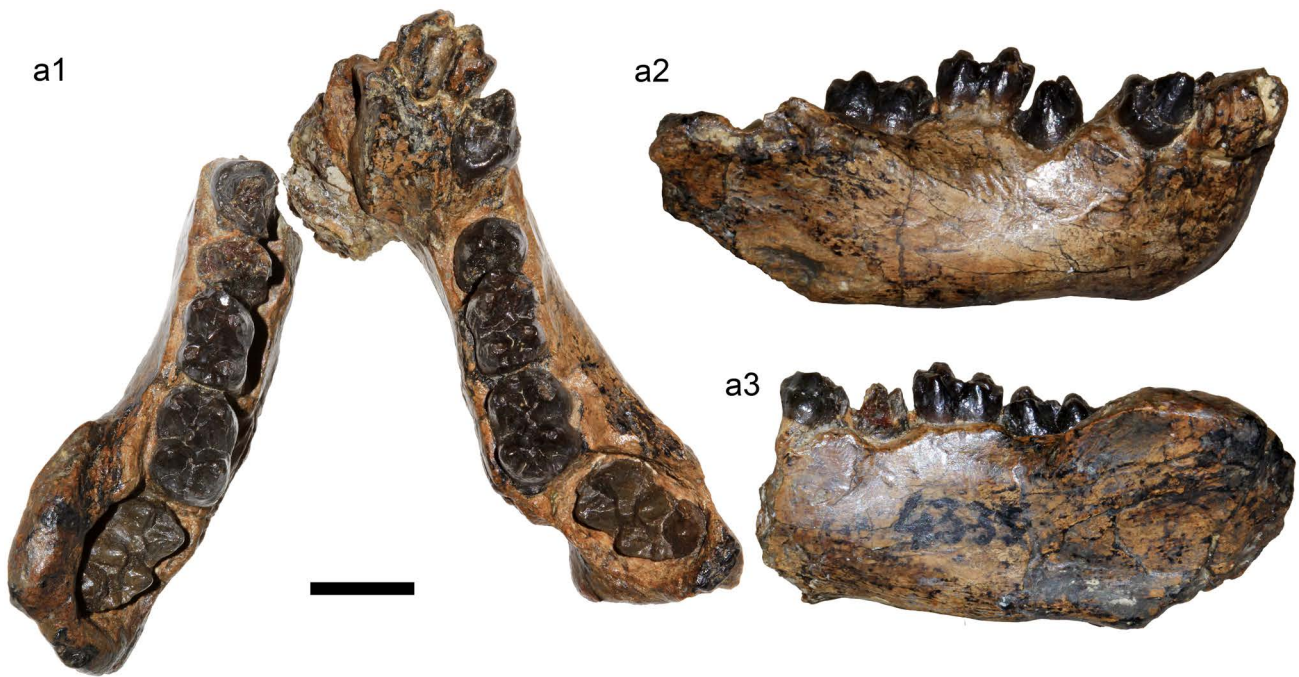


Fig. 4 - (color online) Mandible of *Oreopithecus bambolii* Gervais, 1872 (IGF 4335, holotype) from Montebamboli, housed in the Museo di Storia Naturale dell'Università degli Studi di Firenze. a1) Left corpus and right corpus with symphysis in occlusal view. a2) Right corpus and symphysis in lateral view. a3) Left corpus in lateral view. The mandible belongs to a juvenile specimen whose m3s were originally inside their crypts. Photographs kindly provided by S. Bartolini-Lucenti. Scale bar equals 1 cm.

by others (Simons, 1964; Simons & Pilbeam, 1965), such that they never gained general acceptance. Disappointed by this fact, Hürzeler ultimately refrained from publishing the more detailed monograph on *Oreopithecus* that he had planned for years (Engesser, 2000).

Hürzeler's last paper on the subject (Hürzeler, 1968) is indeed a review on ape evolution, where he extensively delved into the *Oreopithecus* question. He proposed a subdivision between apes and humans at the superfamily rank (Pongoidea vs Hominoidea, respectively), with *Oreopithecus* occupying a more basal position within the human clade than australopiths, as previously argued by him (Hürzeler, 1960, fig. 2). Hürzeler (1960) hypothesized a divergence between *Oreopithecus* and other "hominids" well within the Miocene, and a divergence between apes and humans in the Oligocene. Hürzeler (1968, fig. 27) went even further, by hypothesizing an early divergence of *Oreopithecus* from the human lineage as far back as the Eocene (~40 Ma), and a divergence between apes and humans during the Paleocene (~60 Ma). During the first two-thirds of the 20th century, most authors favored an early divergence between apes (or at least great apes) and humans well within the Miocene or even earlier (e.g., Le Gros Clark, 1959; see review in Lewin, 1987). However, Hürzeler's (1968) views in this regard are extreme in chronological terms and certainly outdated for the late 1960s. By then, serological analyses already supported a close relationship between African apes and humans (Zuckerkandl et al., 1960; Goodman, 1963) and protein data had started to hint at a much more recent divergence between them than previously assumed (Sarich & Wilson, 1967). Hürzeler (1968) also ignored several relevant discoveries in the African Miocene that took place in the 1960s and are relevant for later debates

on the phylogenetic relationships of *Oreopithecus*. In particular, teeth resembling those of *Oreopithecus* were reported from Middle Miocene sites of Kenya: those from Fort Ternan (13.8 Ma; Van Couvering & Delson, 2020) were tentatively assigned to cf. *Oreopithecus* (Leakey, 1968; Simons, 1969), whereas an m3 from Maboko (15.3 Ma; Van Couvering & Delson, 2020) was used by Von Koenigswald (1969) to erect a new genus and species, *Mabokopithecus clarki* Von Koenigswald, 1969, who considered it an "oreopithecoid".

Modern views

The 1970s were largely focused on the *Ramapithecus* debate, which was not settled until the early 1980s, fueled by the find and reinterpretation of fossil remains but also deeply influenced by molecular results (Lewin, 1987; Pilbeam, 1997). The 1970s also witnessed the spread of cladistics in paleoanthropology (see review in Cartmill, 2018), largely thanks to the efforts by Delson and colleagues (Delson & Andrews, 1975; Delson, 1977; Delson et al., 1977). Initially, they considered *Oreopithecus* to be a stem catarrhine more derived than *Parapithecus* and *Apidium*, but more basal than taxa currently considered stem catarrhines (such as propliopithecoids, pliopithecoids, and dendropithecids), which at the time were considered stem hominoids (Delson & Andrews, 1975; Delson, 1977). Shortly thereafter, in their seminal book, Szalay & Delson (1979) further dismissed the link with *Apidium* previously proposed by Simons (1960) but favored the classification of *Oreopithecus* as a distinct family within the cercopithecoid stem lineage, as previously supported by Szalay (1975) and Delson (1979).

Szalay & Delson's (1979) was probably the last significant contribution about *Oreopithecus* before the

resolution of the *Ramapithecus* debate, which undoubtedly contributed to sideline the importance of *Oreopithecus* for ape and human evolution. Once the debate was settled with the recognition that *Ramapithecus* is but a junior synonym of *Sivapithecus*, which in turn is a member of the *Pongo* clade (Andrews & Cronin, 1982; Pilbeam, 1982) — something of utmost significance for the controversies that were about to unfold during the following decade — a renewed interest in *Oreopithecus* followed, again thanks to the efforts of Delson. In 1983, the specimens of the skeleton found in 1958 were moved to the USA for preparation and study. They were made available to various researchers in 1984, and a symposium on this taxon was celebrated in 1985 (Delson, 1986). Several contributions to meetings (Delson & Szalay, 1985; Grine et al., 1985; Rosenberger & Delson, 1985; Stern & Jungers, 1985; Susman, 1985; Harrison, 1986a) and papers (Harrison, 1986b, 1987a; Szalay & Langdon, 1986; Jungers, 1987; Sarmiento, 1987) followed, covering multiple aspects of *Oreopithecus* anatomy, functional morphology, and phylogeny. Rosenberger & Delson (1985) restated the possession of putative cercopithecoïd synapomorphies in *Oreopithecus*, but the more detailed comparisons by Harrison (1986b) with African taxa supported instead close phylogenetic affinities with members of the clade currently known as nyanzapithecids (e.g., Urciuoli & Alba, 2023).

As the application of a cladistic way of thinking in paleoanthropology progressed further during the 1980s, several researchers highlighted the usefulness and importance of postcranial features. In the case of *Oreopithecus*, both Sarmiento (1983, 1987) and Harrison (1986a, b, 1987a) stressed the possession by *Oreopithecus* of multiple postcranial features, functionally related to orthograde behaviors, supporting its hominoid status. Based on his comparisons with extant and some fossil taxa, Sarmiento (1987) classified *Oreopithecus* in a family of its own and concluded that it was either a “pongid”-“hominid” ancestor (i.e., a stem hominid in current terminology) or a giant hylobatid. In turn, Harrison’s (1986a, b, 1987a) more detailed comparisons with East African taxa favored close phylogenetic links suggesting that *Oreopithecus* was a derived member of a hominoid lineage originated in the Early Miocene of Africa. Harrison (1986b), in particular, erected the genus *Nyanzapithecus* and included it, together with the previously described *Rangwapithecus* from Africa and *Oreopithecus*, into the Oreopithecidae. Harrison (1986b) further confirmed the presence of a large oreopithecid (attributed to *Oreopithecus* sp. at the time) in the Middle Miocene of Kenya, including material from both Fort Ternan and Kapsibor (see also Harrison, 1992, 2010), which probably belongs to a new genus, larger and more derived than *Nyanzapithecus* (Harrison, 2010). Harrison (1986b, p. 279) remarked that “the degree of similarity of the molars and premolars of *Nyanzapithecus* and *Oreopithecus* is so marked, and the specializations they share so distinctive, that there can be little doubt that the two taxa are closely phyletically related”.

In a subsequent paper focused on *Oreopithecus*, Harrison (1987a) better substantiated the hominoid affinities of this taxon (Fig. 5a). According to this author, most of the craniodental features of *Oreopithecus*

would not be phylogenetically informative, being either catarrhine symplesiomorphies or autapomorphies of this taxon. In contrast, its multiple postcranial similarities with crown hominoids would unambiguously support its hominoid status: “*Oreopithecus* shares with the living hominoids a unique range of derived catarrhine features of the postcranium that are so detailed that there seems little possibility that they could have been developed independently in the two taxa” (Harrison, 1987a, p. 541). Harrison (1987a) noted closest postcranial similarities with hominids (e.g., in the proximal ulna and distal humerus) but considered the possibility that these were simply attributable to functional convergence owing to large body size, as further noted by Sarmiento (1987). Therefore, Harrison (1987a) entertained the possibility that *Oreopithecus* is no more closely related to hominids than to hylobatids (i.e., a stem hominoid) and favored its inclusion into a distinct family Oreopithecidae, together with the East African taxa currently included in the Nyanzapithecidae. Indeed, as remarked by Sarmiento (1987), *Oreopithecus* displays a mixture of great ape-like and hylobatid-like features (e.g., overall cranial morphology and some features of the wrist joint). Such similarities with hylobatids are not attributable to large body size but may be interpreted as either hominoid symplesiomorphies or hylobatid synapomorphies.

In the 1990s, the discovery of some new remains of *Oreopithecus* (Rook, 1993; Rook et al., 1996) was accompanied by new ideas about its phylogenetic relationships. Thus, Harrison (1991) took a slightly different stance than before, by arguing that *Oreopithecus* was craniodentally very derived but that, postcranially, it was a good proxy for the “ancestral large hominoid morphotype” because previous studies had established its hominid (great ape) status. To support the latter, Harrison (1991) cited previous studies summarized above (Harrison, 1987a; Sarmiento, 1987) that in fact supported *Oreopithecus* being a hominoid, but not necessarily a great ape. Andrews (1992) further classified *Oreopithecus* as incertae sedis within the Hominidae without much justification, and slightly later Andrews et al. (1996) included *Oreopithecus* in subfamily Oreopithecinae within the Hominidae, mostly on the basis of postcranial similarities with extant and fossil great apes such as dryopithecines, which are currently best interpreted as stem hominids (Alba et al., 2015; Pugh, 2022; Pugh et al., 2023). This argument was elaborated further by Harrison & Rook (1997), who dismissed as merely homoplastic the dental similarities between *Oreopithecus* and nyanzapithecids that had been previously considered homologous by Harrison (1986b, 1987a). These authors further emphasized the significance of a few cranial similarities with great apes (such as the lack of subarcuate fossa) to conclude that *Oreopithecus* is likely a derived dryopithecine of European origin that evolved under insularity conditions (Fig. 5b). Accordingly, Harrison & Rook (1997) considered *Oreopithecus* to be a stem hominid, including it in a tribe of its own (Oreopithecini) within subfamily Dryopithecinae. Similar views were simultaneously favored by Moyà-Solà & Köhler (1997) — see also Alba et al. (2001a, b), Bernor et al. (2001), Köhler & Moyà-Solà (2003) and Moyà-Solà & Köhler (2003) — who considered *Oreopithecus* to be an insular

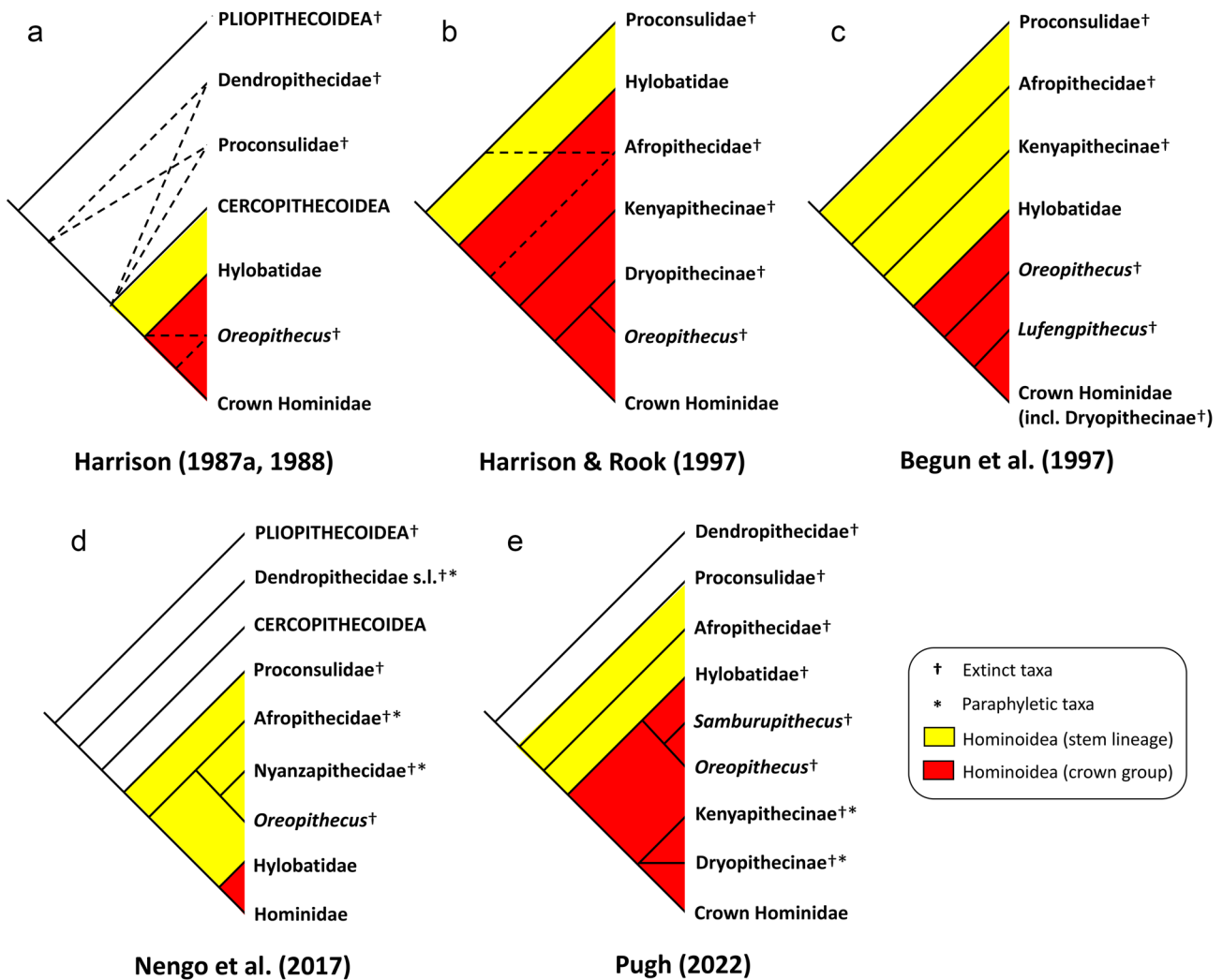


Fig. 5 - (color online) Simplified cladograms depicting the alternative phylogenetic hypotheses proposed by various authors for *Oreopithecus* in relation to extant and extinct catarrhines: (a) Harrison (1987a, fig. 8; 1988, fig. 10); (b) Harrison & Rook (1997, fig. 2); (c) Begun et al. (1997, fig. 1); (d) Nengo et al. (2017, fig. 5); (e) Pugh (2022, fig. 3b). Systematics for hominoid (sub)families follows Urciuoli & Alba (2023).

descendant of *Dryopithecus* s.l. (i.e., currently including, besides *Dryopithecus* s.s., the genera *Hispanopithecus* and *Rudapithecus*).

The conclusions by the authors cited in the preceding paragraph were greatly influenced by the discovery of a partial skeleton of *Hispanopithecus laietanus* Villalta Comella & Crusafont Pairó, 1944 (then in *Dryopithecus*), which shows an orthograde body plan with suspensory adaptations and is thus more similar to modern hominoids than previously known Miocene apes (Moyà-Solà & Köhler, 1996). At the time, Moyà-Solà and colleagues (Moyà-Solà & Köhler, 1993, 1995, 1996; Agustí et al., 1996; Köhler et al., 2001) considered that all Eurasian great apes (such as *Dryopithecus* s.l., *Ouranopithecus*, and *Sivapithecus*) were members of the *Pongo* clade. In that context, and given some cranial indications of a great ape status for *Oreopithecus*, it made sense from a paleobiogeographic viewpoint to consider that this genus was but another member of the same radiation. The same applies to later works that considered different alternative hypotheses for dryopithecines, such as Alba (2012), who left the Oreopithecini as subfamily incertae sedis within the

Hominidae. Nevertheless, a nyanzapithecid origin is also consistent with paleobiogeographic evidence, given that a Late Miocene intermittent connection between northern Africa and the Tusco-Sardinian Paleobioprovince is indeed supported by multiple lines of evidence, including other faunal elements of clear African origin (Hürzeler, 1983; Thomas, 1984; Azzaroli et al., 1986; Rook et al., 2011). Not surprisingly, thus, the phylogenetic link between *Oreopithecus* and nyanzapithecids continued to be supported throughout the 1990s and early 2000s by some authors based on craniodental features, mostly by focusing on the Maboko material. Unfortunately, most of these comparisons were only reported in conference presentations (Benefit & McCrossin, 1997, 2001; Jansma, 2011) and the Maboko collection remains to be described in detail.

Cladistic analyses

The discussion of the phylogenetic affinities of *Oreopithecus* during the 1980s and 1990s, particularly those provided by Harrison and colleagues (Harrison, 1986b, 1987a; Harrison & Rook, 1997), was framed

within a cladistic mindset. However, formal cladistic analyses including *Oreopithecus* were not performed until the late 1990s (Begun et al., 1997). Their analyses, like those of others using a modified version of the same matrix (Finarelli & Clyde, 2004; Begun et al., 2012), recovered *Oreopithecus* as a very basal stem hominid postdating the divergence of hylobatids but preceding that of crown hominids and some other putative stem hominids, such as *Kenyapithecus* (Fig. 5c). In parallel, the cladistic analyses performed by other authors recovered a nyanzapithecoid clade including *Turkanapithecus*, *Rangwapithecus*, and *Nyanzapithecus* spp. (Rossie & MacLachy, 2006; see also Rossie & Hill, 2018), to which the Oligocene *Rukwapithecus* was subsequently added (Stevens et al., 2013), but *Oreopithecus* was not included in the analyses. This situation changed with the publication of a more thorough cladistic analysis by Nengo et al. (2017), which recovered *Oreopithecus* as deeply embedded within the nyanzapithecoid clade, as sister to *Rukwapithecus* and forming with *Nyanzapithecus* spp. a subclade more derived than *Rangwapithecus* and *Turkanapithecus* (Fig. 5d). A more recent analysis based on a further development of the same matrix (Gilbert et al., 2020a) yielded similar results, recovering *Oreopithecus* in a polytomy with *Rukwapithecus* and *Nyanzapithecus* spp.

A sister-taxon relationship between *Oreopithecus* and *Rukwapithecus* is quite unlikely on chronological grounds, as these taxa are separated by ~17 Myr. However, taken overall, these cladistic results support Harrison's (1986a, b, 1987a) former views that *Oreopithecus* and nyanzapithecoids are closely related. It is noteworthy that family-group taxa based on *Oreopithecus*, such as family Oreopithecidae, were erected by Schwalbe (1915) and therefore take precedence over Nyanzapithecidae, first erected (at the tribe rank) by Harrison (2002). This implies that, if *Oreopithecus* is included in the same family-group taxon as *Nyanzapithecus*, the correct name for this family must be Oreopithecidae. Nevertheless, given the phylogenetic uncertainties that still surround *Oreopithecus*, Urciuoli & Alba (2023) opted to leave *Oreopithecus* in a tribe of its own as incertae sedis at the family rank. Thus far, cladistic analyses of nyanzapithecoids (Rossie & MacLachy, 2006; Nengo et al., 2017; Rossie & Hill, 2018; Gilbert et al., 2020a) have only included the genera *Turkanapithecus*, *Rangwapithecus*, and *Nyanzapithecus*, but not *Mabokopithecus* (which displays greater dental similarities with *Oreopithecus*), the larger-bodied unnamed nyanzapithecoid from Fort Ternan and Kapsobir (Harrison, 1986b, 2010), or the late occurring nyanzapithecoid from the Late Miocene (10.0–9.8 Ma) of Nakali, Kenya (Kunimatsu et al., 2017). These analyses have neither included *Samburupithecus* from the Late Miocene, dated to 9.6 Ma according to Sawada et al. (2006) and ~8.5 Ma according to Van Couvering & Delson (2020) of Kenya, previously considered a hominine (Ishida & Pickford, 1997; Pickford & Ishida, 1998) or a late surviving stem hominoid (Begun, 2001, 2015; Almécija et al., 2021), and most recently considered to display nyanzapithecoid affinities (Pugh, 2022). Indeed, some previous authors already noted similarities with *Rangwapithecus* (Ishida & Pickford, 1997) and nyanzapithecoids more generally (Harrison, 2010), but a close phylogenetic link was not advocated.

Most recently, Pugh's (2020) cladistic analyses, including *Samburupithecus* (but no other nyanzapithecoids), recovered *Oreopithecus* + *Samburupithecus* as a stem hylobatid clade (Fig. 5e). Unfortunately, these results cannot be directly compared with those of Nengo et al. (2017) and Gilbert et al. (2020a) because nyanzapithecoids (other than *Samburupithecus*) are missing from Pugh's (2022) analysis.

Taken literally, Pugh's (2022) results would simultaneously support the phylogenetic link between African nyanzapithecoids and *Oreopithecus* (as formerly advocated by many previous studies; e.g., Harrison, 1986b) and the hypothesis that the latter taxon is a stem hylobatid (as originally proposed by Rüttimeyer, 1876 and subsequently discussed by Sarmiento, 1987). Nevertheless, while Pugh (2022) supported the "oreopithecoid" hypothesis, she dismissed a possible link between *Oreopithecus* and hylobatids by considering that it is likely an artifact caused by the lack of additional nyanzapithecoids in her analyses, coupled with the largely plesiomorphic cranial morphology of *Oreopithecus* and hylobatids, as well as the possession of suspensory adaptations convergently evolved with those of crown hominoids. On this basis, Pugh (2022) concluded that her results for *Oreopithecus* were not conclusive, merely supporting a stem hominoid rather than a stem hominid status for this taxon. Nevertheless, Pugh's (2022) interpretation that cranial similarities between *Oreopithecus* and hylobatids are largely plesiomorphic is questionable based on her own cladistic analyses of craniodental and postcranial datasets separately. Based exclusively on postcranial features, Pugh (2022) recovered *Oreopithecus* as a stem hominid (not as a hylobatid) — as in the previous analyses by Begun et al. (1997) that did not include nyanzapithecoids, and in further agreement with Harrison's (1987a) assessment that *Oreopithecus* displayed greater similarities with great apes (even if potentially related to its large body size). In contrast, Pugh's (2022) analysis of craniodental features recovered *Oreopithecus* + *Samburupithecus* as a stem hylobatid clade, thus suggesting that at least some cranial similarities between *Oreopithecus* and hylobatids might be synapomorphic instead of symplesiomorphic.

MAIN COMPETING HYPOTHESES IN LIGHT OF CURRENT EVIDENCE

The postcranium

Since Hürzeler (1958, 1968), many papers have focused on various aspects the postcranial morphology of *Oreopithecus*, either from a morphofunctional and/or a phylogenetic perspective (Schultz, 1960; Straus, 1962, 1963; Knußmann, 1967; Riesenfeld, 1975; Stern & Jungers, 1985; Szalay & Langdon, 1986; Harrison, 1987a, 1991; Jungers, 1987; Senut, 1989; Rose, 1993; Harrison & Rook, 1997; Köhler & Moyà-Solà, 1997, 2003; Rook et al., 1999b; Sarmiento & Marcus, 2000; Moyà-Solà & Köhler, 2003; Susman, 2004, 2005; Moyà-Solà et al., 2005; Russo & Shapiro, 2013; Almécija et al., 2014; Hammond et al., 2020). This is not surprising given that *Oreopithecus* is known from multiple postcranial remains, including the aforementioned skeleton recovered in 1958 (Fig. 6). The

“orthodox” interpretation of its overall total morphological pattern, characterized by a high intermembral index, a broad and shallow thorax, and numerous similarities with extant hominoids (e.g., in the distal humerus and proximal ulna) is that *Oreopithecus* would have displayed an orthograde body plan adapted to a forelimb-dominated arboreal positional repertoire mostly consisting of vertical climbing, clambering, and suspensory behaviors (Harrison, 1987a, 1991; Jungers, 1987; Rose, 1993, 1997). Admittedly, inferences about the emphasis put on climbing (Sarmiento, 1987) vs suspension (Wunderlich et al., 1999) widely differ among authors. However, an alternative hypothesis, already put forward in the 1960s (Straus, 1962, 1963; Hürzeler, 1968) and subsequently elaborated further on the morphology and internal structure of the knee, the pelvis, and the hand, argues that *Oreopithecus* would have mainly been a terrestrial biped (Köhler & Moyà-Solà, 1997, 2003; Moyà-Solà et al., 1999; Rook et al., 1999b; Alba et al., 2001b; Moyà-Solà & Köhler, 2003; Moyà-Solà, 2010). Such interpretation has been further supported based on the fact that insular mammals display peculiar adaptations (e.g., Sondaar, 1977; Köhler & Moyà-Solà, 2003; Moyà-Solà & Köhler, 2003), which owing to the lack of predators often imply (among others) a slower and more secure type of locomotion.

The diverging hypotheses about the main locomotor mode of *Oreopithecus* rely in part on different interpretations of the foot anatomy of this taxon, characterized by a widely diverging hallux (Köhler & Moyà-Solà, 1997, 2003; Sarmiento & Marcus, 2000), but overall most similar to that of hylobatids (Sarmiento, 1987). The foot of *Oreopithecus* has been interpreted as either suitable for slow arboreal climbing (Szalay & Langdon, 1986; Sarmiento, 1987; Sarmiento & Marcus, 2000) or as autapomorphically adapted for a type of terrestrial bipedalism different from that of humans (Köhler & Moyà-Solà, 1997, 2003; Moyà-Solà & Köhler, 2003). Even greater disagreements exist about the interpretation of hand proportions and distal thumb phalanx morphology in *Oreopithecus*, with some authors arguing that it displayed a relatively long hand suitable for arboreality, including suspensory behaviors (Susman, 1985, 2004, 2005), while the proponents of the bipedal hypothesis interpreted instead that *Oreopithecus* displayed a short frail hand with a relatively long thumb and a distal pollical phalanx morphology indicating precision grasping capabilities (Moyà-Solà et al., 1999, 2005; Köhler & Moyà-Solà, 2003; Moyà-Solà & Köhler, 2003). The more detailed analyses of the *Oreopithecus* thumb by Almécija et al. (2014) concluded that, in terms

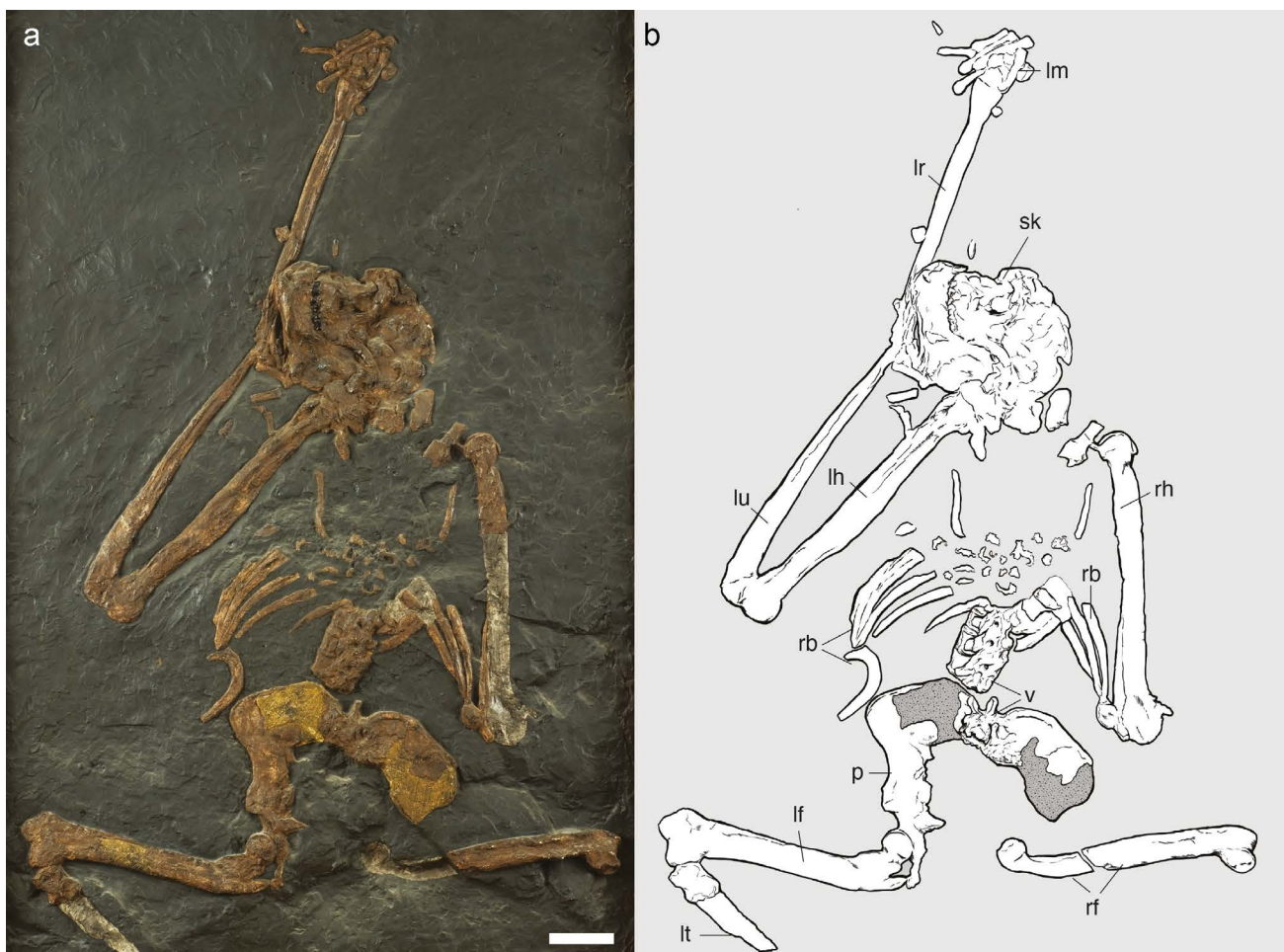


Fig. 6 - (color online) Partial skeleton of *Oreopithecus bambolii* Gervais, 1872 (IGF 11778) discovered in 1958 at Baccinello and housed in the Museo di Storia Naturale dell'Università degli Studi di Firenze (a), and schematic line drawing indicating the anatomical areas preserved (b). Scale bar equals 5 cm. Abbreviations: lf, left femur; lh, left humerus; lm, left manus; lt, left tibia; lr, left radius; lu, left ulna; p, pelvis; rb, ribs; rh, right humerus; rf, right femur; sk, skull; v, vertebrae. Reproduced from Hammond et al. (2020, fig. 1), with permission.

of proportions and shape of the distal pollical phalanx, it reflects enhanced manipulative abilities compared with extant apes. However, it is largely plesiomorphic, similar to other fossil hominoids that lack specific suspensory adaptations. In this regard, *Oreopithecus* differs from the (likely independently) derived condition of the extant ape lineages specialized in suspension, characterized by different degrees of digital elongation relative to their seemingly shorter thumbs (Almécija et al., 2015). With regard to the evidence from the pelvis and lumbosacral region of the vertebral column, which has been used by some authors to criticize the bipedal hypothesis (Russo & Shapiro, 2013), the more thorough analysis provided by Hammond et al. (2020) concluded that *Oreopithecus* lacks the lower torso features related to habitual and committed bipedalism in hominins (e.g., projecting anterior inferior iliac spine, a short lower ilium, sagittally-oriented iliac blades). On the other hand, these authors showed that *Oreopithecus* lacks the extreme torso stiffness characteristic of great apes and very likely possesses (like hylobatids but unlike hominids) ischial callosities (Hammond et al., 2020; contra Schultz, 1960; Sarmiento, 1987; Rose, 1993). Coupled with the moderate (plesiomorphic) thumb/digit ratio (Moyà-Solà et al., 1999; Almécija et al., 2014), which denotes no suspensory specialization (not the lack of suspensory capabilities altogether), currently available evidence favors the interpretation that the positional repertoire of *Oreopithecus* emphasized arboreal climbing, even if it would have been more capable of bipedalism and refined manipulatory behaviors than extant great apes (Hammond et al., 2020).

As explained above, from a phylogenetic viewpoint both Harrison (1987a, 1991) and Sarmiento (1987) interpreted the crown hominoid-like postcranial features of *Oreopithecus* as indicative of an unambiguous hominoid status close to the ancestral morphotype from which hylobatids and hominids evolved — albeit Harrison (1987a) noted that some features, such as the high intermembral index, might have been independently acquired as a result of large body size and Sarmiento (1987) further considered that the postcranium of *Oreopithecus* is compatible with that expected for a large-bodied hylobatid. Based on available evidence from extant forms, the modern but generalized hominoid-like postcranial morphology of *Oreopithecus* would indeed be compatible with that of a derived stem hominoid slightly preceding the hylobatid-hominid split. However, such a consideration largely relies on the assumption that the postcranial similarities between extant hylobatids and hominids are homologous. This was advocated by some researchers during the 1980s and 1990s (Harrison, 1987a, 1991; Benefit & McCrossin, 1995; Pilbeam, 1996, 1997) but has been disputed by other authors during the last couple of decades (e.g., Larson, 1998; Moyà-Solà et al., 2004; Alba, 2012). The latter contention stems from the recognition that the pongine *Sivapithecus* displays a much more primitive postcranial skeleton than expected for a crown hominid (Pilbeam et al., 1990; Madar et al., 2002; Morgan et al., 2015). The same holds for putative stem hominids such as the dryopithecine *Pierolapithecus*, which despite the possession of an orthograde body plan lack of specific suspensory adaptations (Moyà-Solà et al.,

2004; Almécija et al., 2009; Alba et al., 2010a). These and other sources of evidence have led to an increased suspicion, during the last decade, that many of the postcranial similarities shared between extant ape lineages likely evolved in parallel as an adaptation for orthograde behaviors (Alba, 2012; Almécija et al., 2015, 2021; Ward, 2015). As a result, the phylogenetic interpretation of the *Oreopithecus* postcranium becomes ambiguous, being compatible with both a stem hominoid, a stem hylobatid, or a stem hominid systematic position (Hammond et al., 2020).

Nevertheless, the apparent possession of ischial callosities in *Oreopithecus* (Hammond et al., 2020) deserves particular mention. This feature — present in cercopithecoids and hylobatids but lacking in great apes and humans (Schultz, 1936; Washburn, 1957; Rose, 1974; McCrossin & Benefit, 1992; Ward et al., 1993) — is unrelated to orthograde and has been interpreted as an adaptation for stable sitting postures above terminal branches (Vilensky, 1978; McGraw & Sciulli, 2011). Some authors have advocated an independent origin of ischial callosities in cercopithecoids and hylobatids (McCrossin & Benefit, 1992), as further supported by their apparent lack (the ischial tuberosity is not adequately preserved) in the stem hominoid *Ekembo* (Ward et al., 1993), thereby supporting a stem hylobatid status for *Oreopithecus*. However, it is generally assumed that the possession of ischial callosities is just symplesiomorphic for crown catarrhines and that their loss is a synapomorphy of great apes and humans likely related to the adoption of nest-building behaviors (Washburn, 1957). According to this interpretation, the retention of ischial tuberosities in *Oreopithecus* would favor a phylogenetic position outside the crown hominid clade (Hammond et al., 2020) but would be compatible with a stem hominoid, hylobatid, or even stem hominid status.

The phylogenetic utility of the *Oreopithecus* postcranial features is further hindered by the fact that, unlike dryopithecines, nyanzapithecids are not very well known from a postcranial viewpoint. The postcranially best known nyanzapithecid (including, among other elements, the radius, ulna, and femur) is *Turkanapithecus* (Leakey et al., 1988), which resembles proconsulids but displays some minor differences, perhaps indicating enhanced climbing abilities (Rose, 1993, 1997; Harrison, 2010). The scarcer postcranials of *Rangwapithecus* (Preuschoft, 1973; Harrison, 1982; Langdon, 1986; Nengo & Rae, 1992; Gebo et al., 2009; Patel et al., 2017), some of them only tentatively assigned to this taxon, are similar to those of proconsulids and generally indicative of arboreal quadrupedalism (Harrison, 2010). The elbow complex of *Turkanapithecus*, in particular, suggests the possession of climbing abilities similar to those of proconsulids (i.e., intermediate between those of stem catarrhines and those of *Oreopithecus* and crown hominoids) but evinces the lack of clear suspensory adaptations (Gebo et al., 2009). Two humeral heads of *Nyanzapithecus* (or *Mabokopithecus*) are also similar to those of proconsulids (Gebo et al., 1988; McCrossin, 1992; Arias-Martorell et al., 2015). All in all, available evidence, even if not abundant, indicates that Early and Middle Miocene nyanzapithecids lacked many of the derived postcranial features shared between *Oreopithecus* and extant

hominoids. The phylogenetic implications of this fact, however, are subject to interpretation (Hill et al., 2013). Of course, under the nyanzapithecoid hypothesis some degree of independent evolution of crown hominoid-like features in *Oreopithecus* seems inescapable, irrespective of the phylogenetic relationships of nyanzapithecoids. On the other hand, this would be consistent with the contention that such features independently evolved between hylobatids and hominoids — their absence in nyanzapithecoids thus not necessarily indicating a stem hominoid status for this group and its putative descendant, *Oreopithecus*.

The cranium

Evaluating the cranial morphology of *Oreopithecus* is challenging, owing to the crushed nature of all the available specimens, including the most complete ones. Hürzeler (1960) made a first attempt at a cranial reconstruction based on the 1958 skeleton, which was subsequently emended by Szalay & Berzi (1973). Under the supervision of E. Delson, while at the American Museum of Natural History in New York the cranium of the skeleton was prepared in 1983-1984 by O. Simonis (Delson, 1986), but only a short description was provided in abstract form (Delson & Szalay, 1985). More recently, additional drawn reconstructions were provided by Harrison & Rook (1997) and Moyà-Solà & Köhler (1997), being published the same year that Clarke's (1997, 2010) provided a physical reconstruction based on the actual fossil (Figs 7 and 8d). The latter reconstruction does not seem particularly reliable regarding the neurocranium (which had not been previously prepared due to its poor preservation; Delson & Szalay, 1985) but reasonably amends some aspects of all previous reconstructions. In particular, Clarke's (1997, 2010) reconstruction differs from those of Harrison & Rook (1997) and Moyà-Solà & Köhler (1997) in the possession of a less orthognathous facial profile and a more airorhynchous orientation of the neurocranium relative to the splanchnocranium. Based on these and other relevant papers (Harrison, 1987a, 1991), the cranium of *Oreopithecus* is characterized by a small

neurocranium with prominent nuchal and sagittal crests (in both sexes), anteriorly located orbits with a thickened supraorbital region, marked temporal lines that constitute a distinct trigone, a broad interorbital region, flaring and upwardly curved zygomatic arches, low and anteriorly situated zygomatic roots, a high and narrow nasal aperture, nasals inferiorly flanked by wing-like projections of the nasal processes of the maxilla, and a moderately deep subnasal clivus. The most important difference of Clarke's (1997, 2010) restored cranium relative to previous reconstructions (Hürzeler, 1960; Harrison & Rook, 1997; Moyà-Solà & Köhler, 1997) is the possession of a longer face than previously inferred.

Harrison (1987a) considered that the cranial morphology of *Oreopithecus* approaches the ancestral catarrhine morphotype, more closely resembling the extinct pliopithecoids as well as the extant colobine monkeys and hylobatids (Fig. 8b-c) but differing in some derived traits — such as the anteriorly placed zygomatic root as well as the robust and upwardly curved zygomatic (interpreted, together with other features, as adaptations for powerful mastication). Some African nyanzapithecoids are represented by relatively complete cranial material that can be compared with that of *Oreopithecus*. This material includes a partial cranium of the medium-sized *Turkanapithecus kalakolensis* Leakey & Leakey, 1986 (see also Leakey et al., 1988; Harrison, 2010) from Kalodirri, Kenya (17.5 Ma; Van Couvering & Delson, 2020) and a nearly complete infantile cranium of *Nyanzapithecus alesi* Nengo et al., 2017 from Napudet, Kenya (13.3 Ma), which at adulthood would have been similar in size to the former taxon (about the size of a siamang). The cranium of *Turkanapithecus* (Fig. 8e) is characterized by a short and low face with a distinct and domed snout, a low anterior root of the zygomatic (close to the alveolar level), and the lower orbital rim at about the same level as the upper edge of the nasal aperture; the nasal aperture is broad and ovoid, while the nasals are broad and superiorly and inferiorly expanded; the orbits are subcircular and separated by a broad interorbital region, with the lacrimal fossa located slightly anteriorly to the

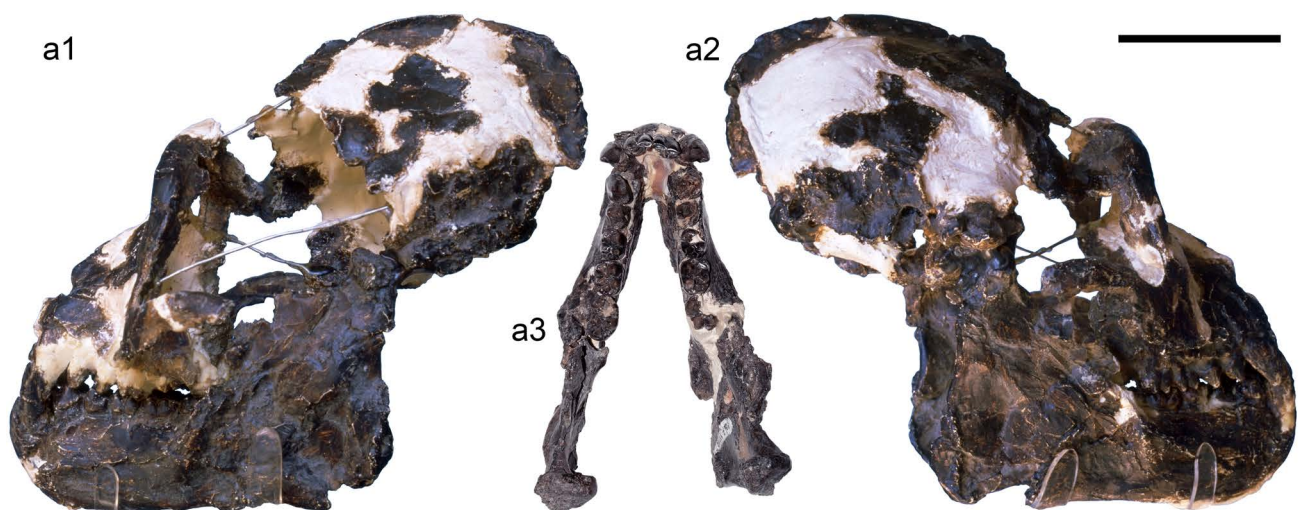


Fig. 7 - (color online) Cranium of *Oreopithecus bambolii* Gervais, 1872 (partial skeleton IGF 11778) as reconstructed by Clarke (1997), on display at the Museo di Storia Naturale dell'Università degli Studi di Firenze. a1) Left lateral view. a2) Right lateral view. a3) Mandible in occlusal view. Photographs kindly provided by E. Cioppi (a1-2) and S. Bartolini-Lucenti (a3). Scale bar equals 5 cm.

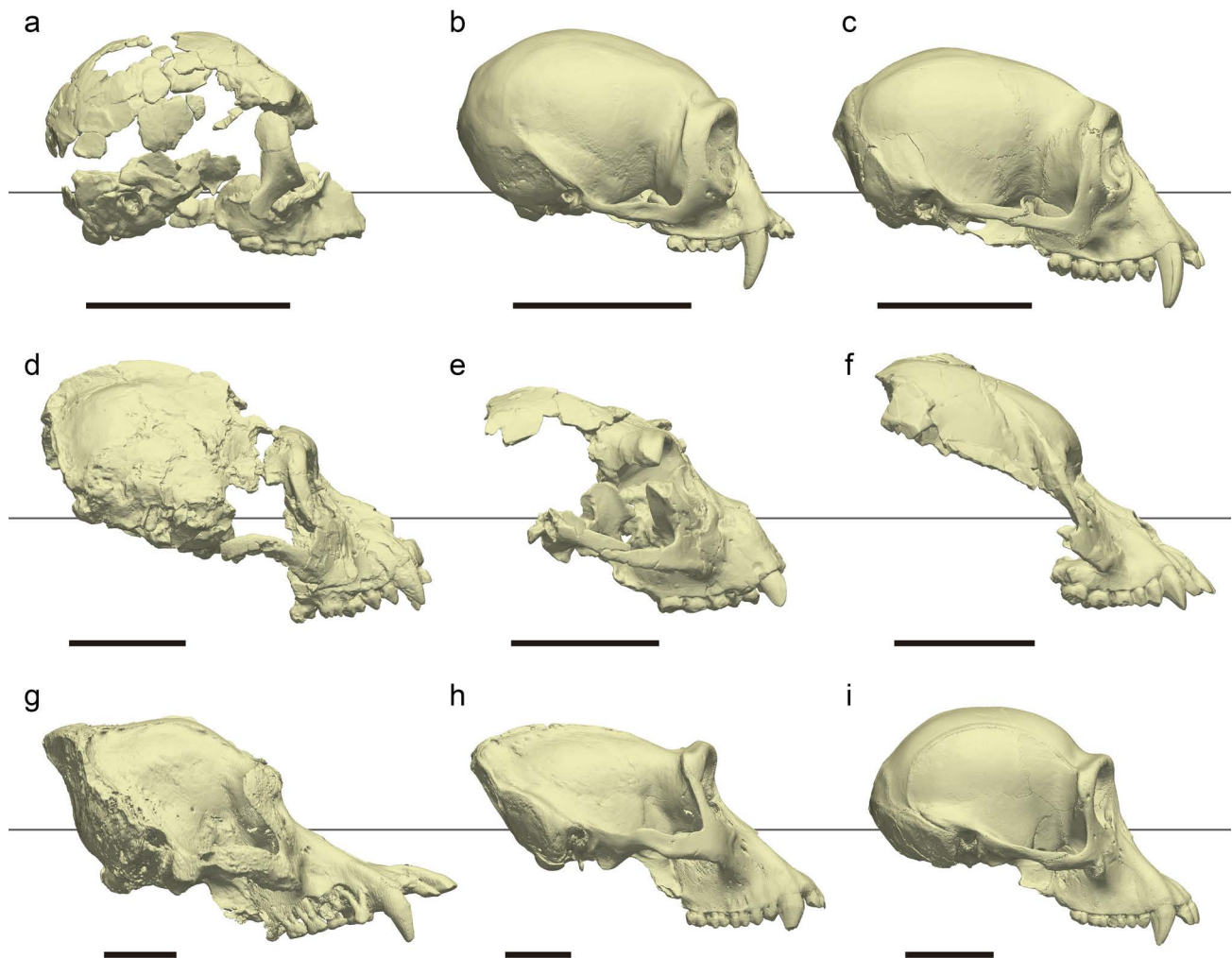


Fig. 8 - (color online) Cranium of *Oreopithecus* according to Clarke's (1997) reconstruction compared with a selection of extant and extinct catarrhine crania in right lateral view. a) *Pliobates cataloniae* Alba et al., 2015 (IPS58443, holotype). b) *Hylobates lar* (Linnaeus, 1771) (MCZ 41416). c) *Symphalangus syndactylus* (Raffles, 1821) (AMNH 102724). d) *Oreopithecus bambolii* Gervais, 1872 (IGF 11778). e) *Turkanapithecus kalakolensis* Leakey & Leakey, 1986 (KNM-WK 16950, holotype). f) *Ekembo heseloni* (Walker et al., 1993) (KNM-RU 7290, holotype). g) *Pongo abelii* Lesson, 1827 (PRICT No. 796). h) *Gorilla gorilla* (Savage in Savage & Wyman, 1847) (AMNH-A 99.9686). i) *Pan troglodytes* (Blumenbach, 1775) (AMNH-M 51204). Crania are oriented with the Frankfurt plane horizontal (only tentatively in *Turkanapithecus* and *Ekembo*, owing to non-preserved portion). Scale bars equal 5 cm. Illustrations correspond to renders of 3D models: (a) courtesy of the Institut Català de Paleontologia Miquel Crusafont, according to the reconstruction by Alba et al. (2015); (b) downloaded from MorphoSource (<https://doi.org/10.17602/M2/M2965>); (c) downloaded from MorphoSource (<http://n2t.net/ark:/87602/m4/M26157>); (d) kindly provided by S. Bartolini-Lucenti, from the original housed in the Museo di Storia Naturale dell'Università degli Studi di Firenze; (e) downloaded from African Fossils (<https://africanfossils.org/hominids/knmwk-16950>); (f) scanned by one of the authors from a cast of the original housed in the National Museums of Kenya; (g) downloaded from the Digital Morphology Museum of the Primate Research Center, Kyoto University (<http://dmm.pri.kyoto-u.ac.jp/dmm/WebGallery/dicom/dicomProperty.html?id=810>); (h) downloaded from MorphoSource (<http://n2t.net/ark:/87602/m4/M22292>); (i) downloaded from MorphoSource (<http://n2t.net/ark:/87602/m4/M21952>).

orbital rim and protruding inferolateral orbital rims; the supraorbital area is somewhat thickened and displays a slightly depressed glabellar region and a shallow supraorbital notch; the zygomatic arches are deep and flaring, slightly inclined upwardly; the temporal lines are marked and probably converged into a sagittal crest, while the nuchal crest is strongly developed. As far as it can be ascertained, *Nyanzapithecus* displays a similar cranial morphology, characterized by a relatively short face and a wide interorbital area, coupled with some differences, such as the lacrimal fossa aligned with the medial orbital margin, the lesser developed supraorbital region, or the different orientation of the zygomatic,

which might nevertheless be simply due to its infantile developmental stage. It is also noteworthy that *N. alesi* displays a fully ossified external acoustic meatus (Nengo et al., 2017), more fully comparable to that of extant apes than that of *Ekembo* (Alba et al., 2015). A fragmentary specimen of *Nyanzapithecus pickfordi* Harrison, 1986b indicates that the premaxilla is short and robust, with a large and anteriorly placed, paired incisive foramen (Harrison, 1986b).

Overall, in terms of cranial morphology (Fig. 8d), *Oreopithecus* displays many resemblances to nyanzapithecids, hylobatids, and even pliopithecoids, their short and low face differing from the pattern displayed

by extant great apes (Fig. 8g-i) and, to a lesser extent, putative stem hominids such as *Pierolapithecus*. In particular, hominids possess a taller face with a higher anterior root of the zygomatic, higher orbits relative to the nasal aperture, and higher lower facial but lesser midfacial prognathism, with the frontal process of the maxillae, the inferior portion of the nasals, and the orbits being more or less aligned (Moyà-Solà et al., 2004; Pugh et al., 2023). Nengo et al. (2017) interpreted the cranial similarities between nyanzapithecids (including *Oreopithecus*) and hylobatids to have been independently evolved, given that such cranial morphology is present to some extent in putative stem catarrhines such as pliopithecoids and also in colobine monkeys. But this very same argument has been used by other authors to argue that this represents the ancestral hominoid condition from which the unequivocally derived morphology of great apes evolved (e.g., Alba et al., 2015), in further agreement with Harrison's (1987a) opinion that the cranial morphology of *Oreopithecus* largely reflects that of the ancestral catarrhine morphotype. Even assuming that such a facial morphology has evolved several times in catarrhine evolution, this does not preclude a close phylogenetic relationship between *Oreopithecus* and nyanzapithecids. In fact, similarities in the rather hylobatid-like configuration of the nasals (interpreted as an autapomorphic feature of *Oreopithecus* by Harrison & Rook, 1997) has been interpreted by other authors as a synapomorphy uniting *Turkanapithecus* and *Oreopithecus* (Jansma, 2011). All in all, the cranial configuration of *Oreopithecus* is supportive of a closer phylogenetic link with nyanzapithecids than dryopithecines, and compatible with either a stem hominoid status (as supported by some cladistic analyses; Nengo et al., 2017; Gilbert et al., 2020a) or even a stem hylobatid status (as recovered by others; Pugh, 2022).

The interpretation above is at odds with the contention by other authors that *Oreopithecus* displays some crown hominid synapomorphies (Andrews et al., 1996; Harrison & Rook, 1997; Moyà-Solà & Köhler, 1997), such as the configuration of the p3 (with a short mesial honing facet and frequently with a well-developed metaconid), the moderately deep subnasal clivus (intermediate between that of hylobatids and extant great apes), the African ape-like configuration of the incisive canals (with the foramina opening more posteriorly than in *Nyanzapithecus*), the obliterated subarcuate fossa, and the dryopithecine-like supraorbital configuration. However, some of these features are not very well known among nyanzapithecids. Although the subarcuate fossa morphology of nyanzapithecids has not been previously described, the endocast reconstruction of *N. alesi* (see Nengo et al., 2017, fig. 1h) shows a moderately pronounced and bulging cerebellar paraflocculus — the structure housed in the fossa when present — that appears flat and blunt in lateral view. This suggests partial filling with matrix of a deep subarcuate fossa similar to that of *Ekembo* (Kunimatsu et al., 2019) but deeper than that of *Oreopithecus* (Harrison & Rook, 1997; Rook et al., 2004) and dryopithecines (Moyà-Solà & Köhler, 1993, 1995, 1997; Kordos & Begun, 1997, 2001). An obliterated subarcuate fossa is also present in *Nacholapithecus* (Kunimatsu et al., 2019), which is customarily (e.g.,

Pugh, 2022) but not exclusively (Kunimatsu et al., 2019) interpreted as a stem hominoid instead of a hominid. A well-developed subarcuate fossa is also variably absent in hylobatids and has been lost in some large cercopithecoids and other primates, probably being related to size and other factors (Straus, 1960; Gannon et al., 1988; Spoor & Leakey, 1996), suggesting that this structure could have independently been lost several times during catarrhine evolution. Hence, it seems more likely that an obliterated subarcuate fossa and other hominid-like features of *Oreopithecus* evolved independently than assuming a reversal of its overall facial configuration. In summary, the cranial similarities between *Oreopithecus*, hylobatids, and/or nyanzapithecids must not necessarily indicate a close relationship (being alternatively plesiomorphic or homoplastic). However, the cranial morphology of *Oreopithecus* does not particularly support a stem hominid status, and much less its hypothesized origin from European dryopithecine ancestors.

The cranial capacity of *Oreopithecus* also deserves some mention here, as it has been variously interpreted in the literature, depending on the phylogenetic hypothesis favored by each author. Based on an incorrect appreciation of the poorly preserved neurocranium, Straus & Schön (1960) tentatively concluded that the cranial capacity of *Oreopithecus* falls within the great ape degree of variation in both absolute and relative brain size. However, a much lower estimate was provided by Szalay & Berzi (1973), and multiple later authors have shown that *Oreopithecus* displays in fact a low degree of encephalization (i.e., brain size relative to body mass) as compared with extant great apes (Jungers, 1987; Harrison, 1989; Martin, 2000; Begun & Kordos, 2004; Alba, 2010). As remarked by Alba (2010), great apes are more encephalized than both Old World monkeys, hylobatids, and proconsulids such as *Ekembo*. Therefore, the low encephalization degree of *Oreopithecus* is compatible with a stem hominoid status but might be alternatively interpreted as a secondary reduction if interpreted as a stem hominid (Begun & Kordos, 2004). The latter authors related the low degree of encephalization of *Oreopithecus* with its purportedly specialized folivorous diet (Harrison, 1987a; Ungar, 1996; Harrison & Rook, 1997; Kay & Ungar, 1997; Carnieri & Mallegni, 2003), contrasting with the mainly frugivorous diet of extant great apes. However, other studies have supported a more mixed and/or abrasive diet for *Oreopithecus* (Moyà-Solà & Köhler, 1997; Galbany et al., 2005; Williams, 2013; DeMiguel et al., 2014; Nelson & Rook, 2016). In fact, irrespective of diet, brain size reduction in *Oreopithecus* would also make sense in relation to evolution under insularity conditions in a predator-free environment (Moyà-Solà & Köhler, 1997; Alba et al., 2001b; Köhler & Moyà-Solà, 2003; Alba, 2010). However, as noted above, no brain size reduction need be hypothesized if *Oreopithecus* is not a great ape to begin with. Therefore, encephalization per se is likely of little use for deciding among the various competing phylogenetic hypotheses put forward for *Oreopithecus*.

The study of inner cranial structures embedding strong phylogenetic signal, such as the semicircular canals of the inner ear (Urciuoli et al., 2020), provide additional evidence to help evaluate previously proposed hypotheses. The bony labyrinth of *Oreopithecus* was

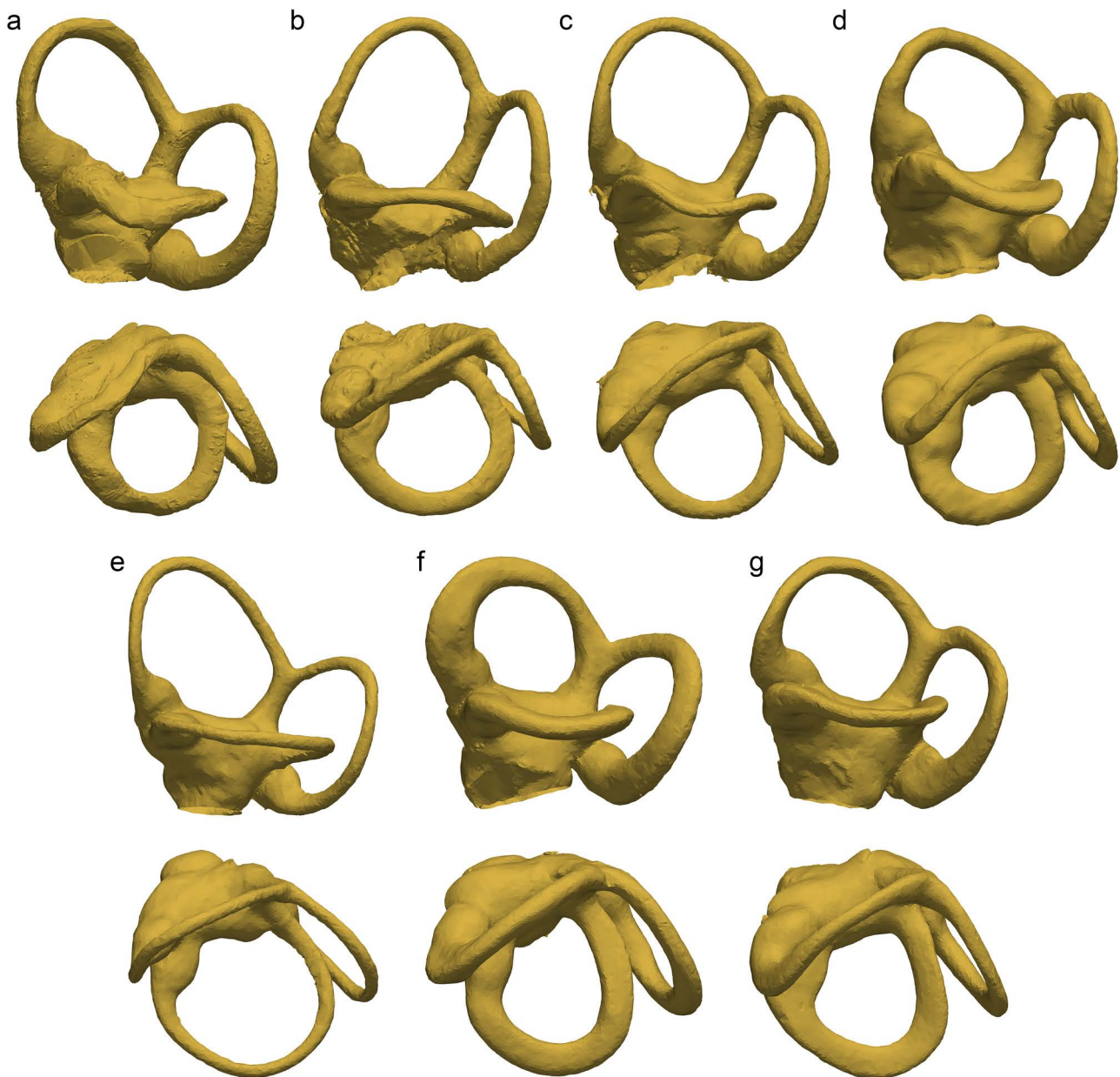


Fig. 9 - (color online) The bony labyrinth semicircular canal morphology of *Oreopithecus* as compared with that of selected extant and extinct anthropoids in lateral (top) and superior (bottom) views. a) *Oreopithecus bambolii* Gervais, 1872 (Bac 183). b) *Aegyptopithecus zeuxis* Simons, 1965 (DPC 12081). c) *Epipliopithecus vindobonensis* (Zapfe & Hürzeler, 1957) (NMBOE 303). d) *Hispanopithecus laietanus* Villalta Comella & Crusafont Pairó, 1944 (IPS18000, mirrored). e) *Symphalangus syndactylus* (Raffles, 1821) (AMNH-M 106583). f) *Pongo pygmaeus* (Linnaeus, 1760) (SENCK 6782). g) *Pan troglodytes* (Blumenbach, 1775) (CEEC 50001799). Not to scale. Images shown are renders of 3D models available from MorphoSource or segmented from microCT scans obtained from different sources: (a) downloaded from MorphoSource (<https://doi.org/10.17602/M2/M166428>; Urciuoli et al., 2020, incorrectly labeled as Bac 208); (b) downloaded from MorphoSource (<http://n2t.net/ark:/87602/m4/M36825>); (c) downloaded from MorphoSource (<https://doi.org/10.17602/M2/M113935>; Urciuoli et al., 2021a); (d) downloaded from MorphoSource (<https://doi.org/10.17602/M2/M126217>; Urciuoli et al., 2021b); (e) scanned by one of the authors; (f) accessed through the Senckenberg digital repository; (g) downloaded from European Synchrotron Radiation Facility (ESRF) heritage database for palaeontology, evolutionary biology and archaeology (<http://paleo.esrf.eu/picture.php?/2504/category/1977>; Nengo et al., 2017).

originally described by Rook et al. (2004), who based on linear measurements concluded that its semicircular canals most closely resemble those of extant great apes. Subsequently, Ryan et al. (2012) inferred, based on the possession of small canal radii relative to body size — indicative of decreased locomotor agility (Spoor et al., 2007) — that *Oreopithecus* displayed a deliberate arboreal locomotion, similar to European dryopithecines but slower

than that of proconsulids. More recently, in a series of papers comparing the semicircular canal morphology of *Oreopithecus* (Fig. 9a) and other extinct catarrhines (Fig. 9b-d) with a wide sample of extant anthropoids by means of 3D geometric morphometric techniques, Urciuoli et al. (2020, 2021a, b, 2022) were able to refine previous inferences based on this anatomical area. Urciuoli et al. (2020), in particular, showed that *Oreopithecus* displays

hominid-like volumetric proportions of the semicircular canals — which might be related to its large body size and a slow orthograde positional behaviors — but an overall shape that is more plesiomorphic than that of crown hominoids and which differs in multiple respects from that of extant hylobatids (Fig. 9e). A subsequent study focused on dryopithecines (Urciuoli et al., 2021b) indicated that the latter (Fig. 9d) are less derived than extant great ape genera (Fig. 9e-f) — with chimpanzees more closely approaching the inferred ancestral condition for hominids — but more so than *Oreopithecus*. The latter taxon, in contrast, appears more derived toward the crown hominoid condition than the pliopithecoid *Epipliopithecus* (Fig. 9c; Morimoto et al., 2020; Urciuoli et al., 2021a). The preliminary study of an additional individual of *Oreopithecus* highlights further the similarities with pliopithecoids (*Epipliopithecus*), proconsulids (*Ekeambo*), and hylobatids but also indicates several differences as compared to the latter (Urciuoli et al., 2022) — although the lack of data from stem hylobatids makes it difficult to reliably reconstruct the ancestral morphotype from which crown hominoids evolved. Overall, these studies on the semicircular canals evince no particular similarities with dryopithecines or crown hominoids and are more consistent with a stem hominoid status for *Oreopithecus*, thus indirectly supporting the nyanzapithecoid hypothesis. More detailed comparisons with the semicircular canals of *N. alesi*, which have not been described in detail and could not be included in the aforementioned analyses, would be required to further test this hypothesis — although Nengo et al. (2017) noted similarities in this regard among *Nyanzapithecus* and *Oreopithecus*, and differences in relative size as compared with hylobatids.

The dentition

The peculiar dental morphology of *Oreopithecus* was for many decades the main source of disagreements about its phylogenetic relationships. However, once the cladistic paradigm became widespread in paleoanthropology, the debate shifted toward giving more importance to the postcranial remains and the *Oreopithecus* dentition was dismissed as a reliable source of phylogenetic evidence because of being highly autapomorphic. While it is currently considered that the *Oreopithecus* dental morphology is somewhat convergent with that of cercopithecoids due to functional reasons (e.g., Harrison, 1987a; Harrison & Rook, 1997), similarities with nyanzapithecids are again under close scrutiny in the light of recent cladistic analyses (Nengo et al., 2017; Gilbert et al., 2020a; Pugh, 2022). Providing a detailed account of all the relevant dental features of *Oreopithecus* is here precluded by space constraints, so readers are mostly referred to previous contributions that provided detailed descriptions and illustrations (Hürzeler, 1949, 1951, 1958, 1968; Heberer, 1952; Butler & Mills, 1959; Szalay & Delson, 1979; Butler, 1986; Harrison, 1986b, 1987a; Alba et al., 2001a; Zanolli et al., 2010, 2016; Rossie & Cote, 2022). We will nevertheless delve somewhat further into the upper and lower molar occlusal morphology of *Oreopithecus*, as it is most relevant for discussing various phylogenetic relationships proposed for this taxon over the years.

The molars of *Oreopithecus* (Fig. 10) are elongate and high-crowned, displaying a marked occlusal relief with

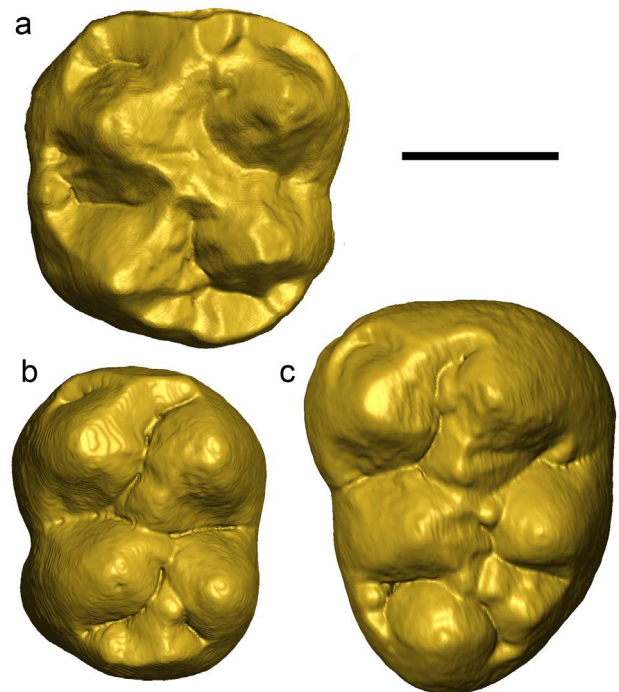


Fig. 10 - (color online) Dental morphology of *Oreopithecus bambolii* Gervais, 1872 as illustrated by renders of 3D models in occlusal view of upper (a) and lower (b-c) molars. a) Right M2 (SMF/PA/F10056, mirrored) from Baccinello VI (Grosseto), housed in the Senckenberg Research Institute of Frankfurt a.M. b) Right m2 (FS1996#Fi99, mirrored) from Fiume Santo, housed in the Dipartimento di Scienze della Terra (Paleo[Fab]Lab) dell'Università degli Studi di Firenze. c) Left m3 (FS1996#Fi97) from Fiume Santo, housed in the Dipartimento di Scienze della Terra (Paleo[Fab]Lab) dell'Università degli Studi di Firenze. Note the prehypocrista joining the crista obliqua in the M2 and mesoconid and associated crests in the m2 and m3. Scale bar equals 5 mm.

prominent cusps and deep notches, and the development of accessory cusps and crests, particularly in the lower molars (Figs 10b-c and 11a-h). The upper molars (Fig. 10a) display four well-developed and voluminous cusps, the lingual ones being slightly more distally located than the buccal ones. The long and oblique preprotocrista gives rise to a protoconule (=paraconule) that is located close to the mesial marginal ridge. The protoconule lingually encloses a very restricted (almost pit-like) mesial fovea, located slightly toward the buccal moiety of the crown. A single oblique and short crest originates from the paracone, bifurcating into a mesially directed preparacrista and a transversely aligned hypoparacrista that joins the protoconule, thereby completely enclosing the mesial fovea. The postparacrista and premetacrista are tenuously developed and do not join each other, the bases of their respective cusps being separated by a deep groove. The trigon basin is distally delimited by a well-developed crista obliqua constituted by the continuous hypometacrista + postprotocrista, sometimes with a distinct metaconule at their junction, which does not appear well expressed by a distinct dentine horn at the level of the enamel-dentine junction (Olejniczak et al., 2004). In some unworn specimens, it can be appreciated that the hypometacrista does not originate from the metacone apex but rather from the distal end of the premetacrista. The hypocone is linked

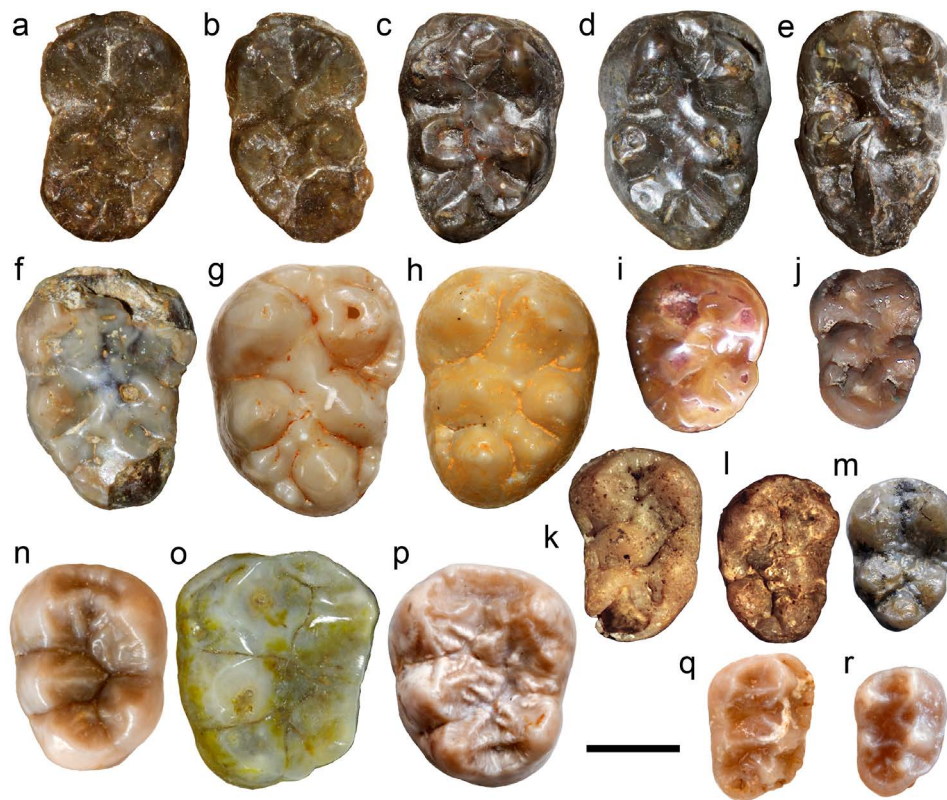


Fig. 11 - (color online) Lower third molars of *Oreopithecus bambolii* Gervais, 1872 (a-h) as compared with a sample of nyanzapithecids (i-m), dryopithecine hominids (n-p), and pliopithecoids (q-r), in occlusal view. a-b) Left (a) and right (b) m3 antimeres (IGF 4335, holotype) from Montebamboli. c-d) Left (c) and right (d) m3 antimeres (IGF 4331) from Casteani. e) Right m3 (IGF 4351) from Casteani. f) Right m3 (IGF 4883V) from Baccinello V2 (Trasubbie outcrop). g) Right m3 (FS1996#Fi 63) from Fiume Santo. h) Left m3 (FS1996#Fi 97) from Fiume Santo. i) Left m3 of *Turkanapithecus kalakolensis* Leakey & Leakey, 1986 (KNM-WT 76300) from Kalodirr. j) Left m3 of *Rangwapithecus gordonii* (Andrews, 1974) (KNM-KT 31234) from Lower Kapurtay. k) Left m3 of *Mabokopithecus clarki* Von Koenigswald, 1969 (KNM-MB 76, holotype) from Maboko. l) Right m3 of *M. clarki* (KNM-MB 9742) from Maboko. m) Left m3 of *Nyanzapithecus pickfordi* Harrison, 1986b (KNM-MB 11661, paratype). n) Left m3 of *Dryopithecini* indet. ("*Sivapithecus*" *occidentalis* Villalta Comella & Cruafont Pairó, 1944 sp. inq; IPS1826+IPS1827, holotype) from Can Vila. o) Left m3 of *Dryopithecus fontani* Lartet, 1856 (Harlé 44) from Saint Gaudens. p) Left m3 of *Hispanopithecus laietanus* Villalta Comella & Crusafont Pairó, 1944 (IPS1822) from Can Llobateres 1. q) Right m3 of *Pliopithecus canmatensis* Alba et al., 2010b (IPS41956, paratype) from ACM/C5-A8. r) Right m3 of *Barberapithecus huerzeleri* Alba & Moyà-Solà, 2012 (IPS1724o, holotype), from Castell de Barberà. Photographs kindly provided by S. Bartolini-Lucenti (a-h), reproduced from Rossie & Cote (2022, fig. 8a, f, h) with permission from John Wiley & Sons (i-j, m), kindly provided by Y. Kunimatsu (k-l), reproduced from Alba et al. (2020, fig. 2d, k) (n-o, in the case of *Dryopithecus* from a picture kindly provided by the Muséum d'Histoire Naturelle de Bordeaux), and reproduced from Alba et al. (2020, fig. 8K) (p). Scale bar equals 5 mm.

to the crista obliqua by a short prehypocrista directed toward the metaconule. There is a continuous lingual cingulum that does not extend beyond the hypocone and is particularly well developed along the mesiolingual corner of the crown, whereas the buccal cingulum is less developed and discontinuous.

In terms of upper molar proportions and overall morphology (cusp inflation and mesiodistal crown elongation), *Oreopithecus* resembles both *Nyanzapithecus* and *Samburupithecus* (Harrison, 1986b; Nengo et al., 2017; Pugh, 2022). Although similarities vary depending on the species, these taxa appear somewhat more derived in upper molar morphology than *Rangwapithecus*, which displays more abundant enamel wrinkling, less distinct crests, and less elongate molars (particularly the M3). Harrison (1986b, 1987a) supported a phylogenetic link between *Nyanzapithecus* and *Oreopithecus* mostly on the basis of upper cheek tooth similarities with *N. pickfordi*, including the elongated upper molars with a hypocone-metaconule crest (Harrison, 1986b, fig. 4b). Further

similarities include the restructuring of the mesial end of the crown (resulting in a pit-like mesial fovea), except that both the preparacrista and the hypoparacrista separately originate from the paracone apex. The latter pattern is also displayed by *Nyanzapithecus harrisoni* Kunimatsu, 1997, which nevertheless possesses a somewhat more plesiomorphic occlusal pattern in which the prehypocrista is directed toward the protocone and there is no connection between the hypocone and the crista obliqua (Kunimatsu, 1997, fig. 4). In contrast, similarly to *Rangwapithecus*, *N. alesi* lacks a distinct mesial fovea (with the preprotocrista and preparacrista being more transversely oriented toward each other) and displays abundant enamel wrinkling — including multiple small crests that originate from the hypocone, although none of them clearly connects this cusp with the crista obliqua (Nengo et al., 2017, fig. 2f, m). *Samburupithecus* (Ishida & Pickford, 1997, fig. 2; Begun, 2015, pl. 4), in turn, also differs from *Oreopithecus* and *N. pickfordi* in the lack of a hypoparacrista and a distinct mesial fovea (with the preprotocrista and preparacrista

being confluent with the protoconule), but it most closely resembles both taxa in the presence of a crest linking the hypocone with the crista obliqua (Pugh, 2020, fig. 2.13, 2022), which is more evident in the M3, even if shorter than in *Oreopithecus* and without forming a distinct cuspule at their junction.

The lower molars of *Oreopithecus*, which are structurally more complex than the upper ones in terms of occlusal morphology, also display similarities with nyanzapithecids, coupled with some differences (additional and more developed crests and cups in *Oreopithecus*) that make it difficult to determine whether similarities between these taxa are homologous or homoplastic. The lower molars of *Oreopithecus* (Figs 10b-c and 11a-h) are elongate and waisted (constricted) at about mid-crown length, and display four voluminous and prominent, transversely aligned main cusps, together with a well-developed secondary cuspule (termed mesoconid or centroconid) at the center of the talonid basin, as well as a distally located hypoconulid. The latter is small and centrally located in m1-m2, and larger and distobuccally situated in the m3, where it is frequently accompanied by a distolingual tuberculum sextum. In the m1 and some m2, there is a mesiolingually located cuspule (usually termed paraconid) at the end of the premetacristid. The mesial cusps are linked by a transverse and not very well-developed (and frequently interrupted) crest, whereas additional transverse crests can be found between the hypoconid and the entoconid. Three distinct and obliquely oriented crests of the talonid merge at the mesoconid, respectively originating from the protoconid, the metaconid, and the hypoconid. The homology of these crests, together with those linking the protoconid with the metaconid, have been subject to different interpretations regarding their homology with those of other catarrhines (see below). There is no lingual cingulid and the buccal one is restricted to the mesiobuccal aspect of the protoconid.

The possession of a paraconid in some lower molars (frequently in m1, sometimes in m2), together with other features (bicuspid p3, presence of mesoconid in the lower molars) led several authors to support a link between *Apidium* and *Oreopithecus* (Gregory, 1920; Simons, 1960). However, Szalay & Delson (1979) convincingly argued that, based on their position and associated crest pattern, the mesoconids of these taxa are unlikely to be homologous (see also Harrison, 1987a). The same probably applies to the purported paraconid, which might have been independently acquired (rather than primitively retained) in *Oreopithecus*. This is further supported by the possession in the latter taxon of multiple catarrhine dental synapomorphies that are not displayed by *Apidium* (e.g., lack of second premolars and sectorial p3; Harrison, 1987a). With regard to the mesial crests of the mesoconid, the interpretation of their evolutionary origin hinges to some extent on the homology of the transverse crests linking the protoconid and the metaconid (Fig. 9). There are two main different interpretations of all these crests: 1) the hypoprotocristid and hypometacristid, which separate the mesial fovea from the talonid basin, are transversely aligned and do not correspond to the oblique crests converging toward the mesoconid (Szalay & Delson, 1979; Rossie & Cote, 2022); or 2) the hypoprotocristid and hypometacristid are obliquely oriented and merge at

the mesoconid, with the mesial fovea being divided by secondary crests usually absent from most catarrhines (Harrison & Rook, 1997; Zanolli et al., 2016). Under both interpretations of the mesial crests of the mesoconid, it has often been considered that the oblique crest originating from the hypoconid corresponds to the cristid obliqua, which would extend until the metaconid and bear the mesoconid at about its midlength (Heberer, 1952; Szalay & Delson, 1979; Harrison, 1987a; Zanolli et al., 2010), or at least to its distal portion (prehypocristid), which would terminate at the mesoconid (Harrison & Rook, 1997; Hill et al., 2013). However, this is far from clear, as equating the crest connecting the hypoconid with the mesoconid with the cristid obliqua is at odds with the fact that the latter is constituted by the prehypocristid + postprotocristid (e.g., Harrison & Gu, 1999), with the latter originating from the protoconid. Homologizing the hypoconid-mesoconid crest exclusively with the prehypocristid is more reasonable in spatial terms, in which case the crest linking the metaconid with the mesoconid might be interpreted as the hypometacristid (as in the second interpretation above; Harrison & Rook, 1997), as an extension of the prehypocristid, or as a newly developed crest (termed mesometacristid by Rossie & Cote, 2022); the metaconid-mesoconid crest cannot correspond to the postmetacristid, as this crest is present and mesiodistally aligned toward the entoconid in *Oreopithecus*. As noted above, similar uncertainties apply to the oblique crest linking the protoconid and the mesoconid, being interpretable as either the hypoprotocristid (as in the second interpretation above; Harrison & Rook, 1997), an obliquely oriented postprotocristid (a mesiodistally aligned crest originating from the protoconid is not clearly present in *Oreopithecus*), or as a neomorphic crest (the mesoprotocristid of Rossie & Cote, 2022). There is also the possibility that the crest connecting the hypoconid with the mesoconid is similarly neomorphic instead of homologous with the prehypocristid. In summary, it seems clear that *Oreopithecus* displays a neomorphic cusp and neomorphic crests, but determining what crests are neomorphic and which ones are homologous with those of other catarrhines is complicated by the fact that the latter might have changed their orientation or even been lost during the evolution of the lineage that led to *Oreopithecus*.

The likelihood of the multiple possible homologies discussed above for the crests merging at the mesoconid in *Oreopithecus* (Fig. 12a) should be discussed not only in relation to dryopithecines (Figs 11n-p and 12b) but also dentally more plesiomorphic taxa. Although dental similarities between the lower molars of *Oreopithecus* and nyanzapithecids have long been noted (Leakey, 1968; Simons, 1969; Von Koenigswald, 1969; Harrison, 1986b, 1987a; Hill et al., 2013), the possible homology between the mesial crests of the mesoconid in *Oreopithecus* and those more incipiently developed in Early and Middle Miocene African nyanzapithecids (*Turkanapithecus*, *Rangwapithecus*, and *N. pickfordi*; Fig. 11i-m) was not directly addressed until recently (Rossie & Cote, 2022). As explained above, these authors termed these crests mesoprotocristid and mesometacristid (collectively referred to as mesocristids) and supported their homology with those of *Oreopithecus*, albeit they did not discount

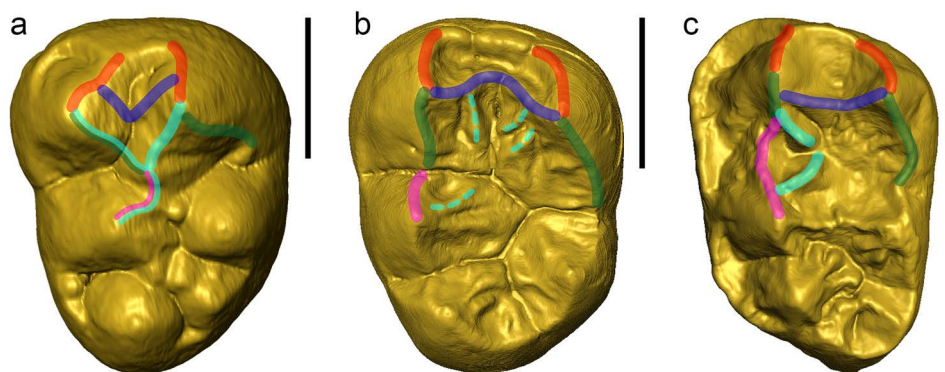


Fig. 12 - (color online) Possible homologies of the trigonid and mesoconid cristids of *Oreopithecus* compared with those of dryopithecines and pliopithecoids. a) Left m3 of *Oreopithecus bambolii* Gervais, 1872 (FS1996#Fi 97) from Fiume Santo. b) Left m3 of *Dryopithecini* indet. (“*Sivapithecus*” *occidentalis* species inquirenda; IPS1826+1827, holotype) from Can Vila. c) Right m3 of *Pliopithecus canmatensis* Alba et al., 2010b (IPS41956, paratype; mirrored) from ACM/C5-A8. Illustrations correspond to renders of 3D models: (a) authors’ unpublished data, original housed in the Museo di Storia Naturale dell’Università degli Studi di Firenze; (b) downloaded from MorphoSource (<https://doi.org/10.17602/M2/M166380>), original housed in the Institut Català de Paleontologia Miquel Crusafont; (c) authors unpublished data, original housed in the Institut Català de Paleontologia Miquel Crusafont. Color legend: red, preprotocristid and premetacristis; indigo, hypoprotocristid and hypometacristid; green, postprotocristid and postmetacristid; magenta, prehypocristid; cyan, accessory cristids (mesocristids, enamel folds, or arms of the pliopithecine triangle, respectively). It is assumed that the hypoprotocristid and hypometacristid in *Oreopithecus* are more or less transversely aligned as in other catarrhines, at least an additional cristid (mesometacristid) must have been acquired. Furthermore, it is uncertain whether the mesoprotocristid and the hypoconid-mesoconid cristid are homologous to the postprotocristid and prehypocristid, respectively, or whether the latter cristids have been lost. Scale bars equal 5 mm.

the possibility that they had independently evolved. We concur with Rossie & Cote (2022) that an extension of the prehypocristid up to the metaconid is more difficult to support than its interpretation as a neomorphic crest (mesometacristid), but the main problems of their interpretation concern instead the homology of the buccal crests (purportedly, mesoprotocristid and prehypocristid) if it is assumed that *Oreopithecus* evolved from nyanzapithecids. In the latter, the mesocristids are generally less developed and more indistinct than in *Oreopithecus*, and do not give rise to a mesoconid at their junction — with the exception of the m3 holotype of *Mabokopithecus* (Fig. 11k), which further displays more distinct mesoprotocristid and mesometacristid than other nyanzapithecids (Von Koenigswald, 1969; Harrison, 1986b, 2010; Rossie & Cote, 2022) as well as the m3 of the unnamed large nyanzapithecoid species from Fort Ternan, which according to Harrison (2010) also possesses a small mesoconid. Harrison’s (2010) asserted that, in the latter taxon, the mesoconid is located at the merging between the prehypocristid and the postprotocristid, which agrees with his earlier interpretations of *Oreopithecus* (Harrison, 1987a) but is at odds with his later interpretation that the mesiobuccal crest of the mesoconid would correspond to the hypoprotocristid (Harrison & Rook, 1997).

To determine the homology of the buccal crests, it is necessary to focus on earlier nyanzapithecids such as *Rangwapithecus* (Fig. 11j), where the three crests of the mesoconid are present and confluent to one another, even if no distinct mesoconid is present (Hill et al., 2013; Rossie & Cote, 2022). Interestingly, a short prehypocristid directed toward the protoconid is present in some lower molars of *Rangwapithecus* (Hill et al., 2013), and this is even more clear-cut in those of the purported oldest nyanzapithecoid, *Rukwapithecus* (even if not explicitly noted by Stevens et al., 2013). According to this, the crest linking the hypoconid with the mesoconid in more

derived nyanzapithecids cannot correspond to a portion of the cristid obliquid (prehypocristid), and the same interpretation would apply to *Oreopithecus* if it originated from this group. In turn, the oblique crest running from the protoconid toward the talonid basin in *Rangwapithecus* was interpreted by Hill et al. (2013) as the postprotocristid, but it might alternatively be interpreted as a different crest, with the postprotocristid being extremely short and directed toward the prehypocristid, as in *Rukwapithecus*. To account for this duplicity of crests, Hill et al. (2013) put forward an alternative interpretation, by noting that the oblique buccal crests of the protoconid and hypoconid in nyanzapithecids (and by extension of *Oreopithecus*) could be homologous to the mesial and distal arms of the pliopithecine triangle of pliopithecoids (Hill et al., 2013) rather than a twisted cristid obliqua (prehypocristid and postprotocristid). Although Szalay & Delson (1979) noted that the m3 of *Oreopithecus* does not particularly resemble that of pliopithecoids, we concur with Hill et al. (2013) that the configuration of the buccal oblique crests of the talonid in *Rangwapithecus* and *Oreopithecus* (Fig. 12a) closely resembles that of the pliopithecine triangle (Figs 11q-r and 12c) — characteristic of most members of this Eurasian clade of putative stem catarrhines (e.g., Hürzeler, 1954b; Harrison & Gu, 1999; Begun, 2002) — except that they generally display a distinct cristid obliqua linking the hypoconid with the protoconid (or the hypoprotocristid), which is reduced in *Rangwapithecus* and absent in more derived nyanzapithecids as well as *Oreopithecus*.

Such similarities with pliopithecoids might have been independently acquired, given that pliopithecoids are generally considered stem catarrhines (e.g., Urciuoli et al., 2021a and references therein). However, strictly from the viewpoint of dental topology, the main problem of the pliopithecoid hypothesis is that, as noted by Hill et al. (2013), a mesometacristid like that of nyanzapithecids and *Oreopithecus* is not usually present in pliopithecoids,

with the possible exception of a corresponding faint cristid present in the m2 of *Pliopithecus antiquus* (Blainville, 1839) from La Grive (Hürzeler, 1954b, fig. 31; Alba et al., 2010b, fig. 11a). However, similar difficulties are faced by the more orthodox hypothesis that the mesometacristid is an extension of the prehypocristid, as in early nyanzapithecids such as *Turkanapithecus* (Fig. 11i) the former crest originates from the metaconid and does not merge with the purported prehypocristid. Although Hill et al. (2013) considered the pliopithecoid and the nyanzapithecoid hypotheses as alternatives to the possible dental homologies of *Oreopithecus*, indeed they are not mutually exclusive. Nyanzapithecids and pliopithecoids could be more closely related than customarily assumed (implying that the latter are members of the hominoid total group instead of stem catarrhines) or nyanzapithecids might have retained a more plesiomorphic occlusal pattern that became further derived in other hominoid lineages. However, the latter hypothesis is not supported by the fact that older nyanzapithecids display a more plesiomorphic molar morphology than later ones (*Nyanzapithecus* and *Samburupithecus*), thus favoring the view that similarities such as the pliopithecine triangle and the additional cristids displayed by nyanzapithecids in the lower molars were independently acquired.

Similarly to the semicircular canals of the inner ear, the enamel-dentine junction shape embeds strong phylogenetic signal and is thus suitable for evaluating systematic affinities (Zanolli et al., 2022a). Remarkably in the light of the hypothesis put forward by Hill et al. (2013), a recent analysis of enamel-dentine junction shape based on 3D geometric morphometrics confirmed that *Oreopithecus* does indeed possess dental similarities with pliopithecoids (Zanolli et al., 2022b). This preliminary analysis included dryopithecines, nyanzapithecids, and pliopithecoids and found closer morphometric affinities with the latter than to any of the two other groups (Zanolli et al., 2022b). The results for nyanzapithecids are too preliminary, as they were based on two lower molars respectively attributed to *N. pickfordi* and *N. harrisoni*. Given the seemingly greater similarities in occlusal morphology with the lower molars of *Rangwapithecus*, the unnamed large species from Fort Ternan, and especially the m3 holotype of *Mabokopithecus*, more exhaustive analyses would be required before ruling out the nyanzapithecoid hypothesis based on enamel-dentine junction shape. Unfortunately, the difficulties to scan this material, coupled with the lack of lower molars for *Samburupithecus* and taxonomic uncertainties surrounding the unpublished nyanzapithecoid sample from Maboko — with some authors favoring the synonymy between *Nyanzapithecus* and *Mabokopithecus* (Harrison, 2010) and others considering them distinct (Benefit et al., 1998) — will likely hinder performing the required comparisons in the near future. However, at the very least the preliminary results of Zanolli et al. (2022b) support that *Oreopithecus* shows no particular dental affinities with dryopithecines. There is also evidence from tooth paleohistology that *Oreopithecus* displayed faster enamel formation rates than extant great apes and dryopithecines (Zanolli et al., 2016). However, whether this reflects an underlying difference in crown formation times (and, hence, life history) — resembling the accelerated dental development documented for the

pliopithecoid *Anapithecus* (Le Cabec et al., 2017) — or simply a result of the thicker enamel and higher cusps of *Oreopithecus* is uncertain (Zanolli et al., 2016). In either case, the endostructural dental similarities found between *Oreopithecus* and pliopithecoids by Zanolli et al. (2022b) are intriguing and particularly notable given that the mesial and distal arms of the pliopithecine triangle are barely reflected at the enamel-dentine junction, whereas in contrasts all the structures of the outer enamel surface in *Oreopithecus* (including the crests of the mesoconid) are well reflected endostructurally (Zanolli et al., 2016). The evolutionary meaning of such similarities remains uncertain, being interpretable as either homoplastic or symplesiomorphic rather than synapomorphic.

DISCUSSION: *OREOPITHECUS* WITHIN THE FRAMEWORK OF MIOCENE APE PHYLOGENY

Despite recent advances in Miocene ape phylogenetics (e.g., Nengo et al., 2017; Pugh, 2022), as well as refinements in the study of the dental, cranial, and postcranial anatomy of *Oreopithecus* (e.g., Zanolli et al., 2016; Hammond et al., 2020; Urciuoli et al., 2020), the debate about its phylogenetic relationships is far from being conclusively settled. Some of the hypotheses supported in previous decades, particularly that *Oreopithecus* is a cercopithecoid (Delson, 1979; Szalay & Delson, 1979; Rosenberger & Delson, 1985) or a crown hominoid derived from dryopithecines (i.e., a great ape; Harrison & Rook, 1997; Moyà-Solà & Köhler, 1997; Köhler & Moyà-Solà, 2003) appear now weakly supported based on dental and cranial morphology, while the postcranial evidence is of ambiguous interpretation (Hammond et al., 2020). In contrast, the hypothesis that *Oreopithecus* is phylogenetically linked with Miocene apes from Africa (Leakey, 1968; Von Koenigswald, 1969; Harrison, 1986b, 1987a; Benefit & McCrossin, 2001) has gained much ground during the last decade (Rossie & Cote, 2022), particularly after some cladistic analyses have recovered *Oreopithecus* as a member of the nyanzapithecoid clade (Nengo et al., 2017; Gilbert et al., 2020a) or as the sister taxon of *Samburupithecus* (Pugh, 2022), whose nyanzapithecoid affinities had previously been noticed (Harrison, 2010).

Somewhat surprisingly, the implications of *Oreopithecus* being a late nyanzapithecoid — or, more correctly, of *Nyanzapithecus* and allied taxa being oreopithecids, as dictated by the rules of zoological nomenclature — have not been thoroughly explored. Rather the contrary, it has been merely assumed that this would imply a stem hominoid status for *Oreopithecus* and that the cranial similarities with hylobatids are homoplastic (Nengo et al., 2017). But we argue that alternative hypotheses deserve consideration, even if not supported by currently available most parsimonious cladograms including nyanzapithecids. This rationale is based, among others, on the dental similarities between *Oreopithecus* and pliopithecoids (Hill et al., 2013; Zanolli et al., 2022b), and the contention that Miocene ape phylogenetics might be misguided by a problem of long-branch attraction between hominids, hylobatids, and maybe *Oreopithecus* (Urciuoli & Alba, 2023). As such, it

is currently uncertain whether we are close to resolving the phylogenetic position of *Oreopithecus* or whether this taxon is but the tip of the iceberg with regard to uncertainties regarding Miocene ape phylogeny.

Dental similarities between Oreopithecus, nyanzapithecids, and pliopithecoids

The possibility that the peculiar dental morphology of *Oreopithecus* — characterized, among others, by elongate molars with high cusps and well-developed accessory crests and cusps well distinct at the enamel-dentine junction level — is autapomorphically derived from an ancestral condition similar to that of nyanzapithecids remains a very suggestive hypothesis but requires further testing (Rossie & Cote, 2022). This is supported by similarities in both the upper molars (protohypocrista directed toward the metaconule located at the crista obliqua; Harrison, 1986b, 1987a) and the lower molars (the presence of three confluent oblique crests in the talonid; e.g., Rossie & Cote, 2022). Nevertheless, until further fossil evidence shows a more clear-cut evolutionary series from the nyanzapithecoid mesocristids into the mesial crests of the *Oreopithecus* mesoconid, the homology of these structures will remain debatable — particularly in the light that the mesiolingual crest of the hypoconid cannot be homologized with the prehypocristid, at least in nyanzapithecids (Hill et al., 2013). The alternative interpretation that the buccal crests of the mesoconid might be homologous with the mesial and distal arms of the pliopithecine triangle (Hill et al., 2013) has received some support from a recent analysis of enamel-dentine shape morphology indicating closer affinities with pliopithecoids (Zanolli et al., 2022b). This inevitably leads us to discuss below the heterodox hypothesis that pliopithecoids might be stem hominoids.

Both Hill et al. (2013) and Zanolli et al. (2022b) conceived a possible phylogenetic link between *Oreopithecus* and either nyanzapithecoid or pliopithecoids as alternative hypotheses, as the former are customarily considered stem hominoids and the latter stem catarrhines. However, both hypotheses are not necessarily mutually exclusive if pliopithecoids are stem hominoids more closely related to nyanzapithecids. Under this (very speculative) hypothesis, the possession of variously developed supplementary crests in the talonid might be a plesiomorphic feature of this hominoid subclade, having been independently stressed in *Oreopithecus* and pliopithecoids. This hypothesis appears misguided in the light of current knowledge about catarrhine evolution because pliopithecoids are considered a clade of stem catarrhines (i.e., preceding instead of postdating the cercopithecoid-hominoid split; e.g., Harrison, 1987b, 2013; Andrews et al., 1996; Begun, 2002, 2017) — as further supported by most cladistic analysis (Rossie & MacLatchy, 2006; Stevens et al., 2013; Nengo et al., 2017; Rossie & Hill, 2018; Gilbert et al., 2020a; Ji et al., 2022). Only the most parsimonious cladogram of Alba et al. (2015) and one of the two most parsimonious trees obtained by Zalmout et al. (2010) have thus far supported a stem hominoid status for pliopithecoids and, incidentally, also the African dendropithecids — the latter result being more frequently supported by some cladistic analyses (Rac, 2004; Rossie & Hill, 2018; Ji et al., 2022) — which would entail some degree of independent evolution of

multiple features among crown catarrhines (e.g., the fully ossified tubular ectotympanic).

In the light of the current state of the art, it would be easy to just conclude that dental similarities between *Oreopithecus* and pliopithecoids are simply convergences. After all, a phylogenetic link between pliopithecoids and *Oreopithecus* would have far-reaching implications for catarrhine evolution as a whole, and would imply that paleoanthropologists have been misguided by the application of the cladistic paradigm during the last four decades. But, on the other hand, paleoanthropologists have often gone astray with regard to *Oreopithecus*. Given Urciuoli & Alba's (2023) contention that the main branching patterns of hominoid evolution are still uncertain (see next subsection for further details) the pliopithecoid hypothesis deserves further consideration in the future. Supposedly, cladistic analyses can only discern between homology and homoplasy a posteriori, based on most parsimonious cladograms. However, if two structures (such as the mesoprotocristid of nyanzapithecids and the mesial arm of the pliopithecine triangle) are coded differently in a cladistic matrix, it is being assumed a priori that these structures cannot be homologous. This exemplifies how preconceived notions about catarrhine evolution may potentially bias in an unconscious fashion the results of cladistic analyses at the character coding stage. Furthermore, although pliopithecoids are considered to have an African origin, they are first recorded in the Early Miocene of China ~19-18 Ma (Harrison & Gu, 1999; Harrison et al., 2020). Their purported stem catarrhine status implies a ghost lineage much longer than 10 Myr (Begun, 2017), which would automatically disappear if they were considered members of the stem hominoid lineage (Alba et al., 2015).

As explained in the following paragraphs, the arguments against a hominoid status for pliopithecoids are basically the same that have been used since the advent of cladistics to discount a phylogenetic link between them and hylobatids. Until the 1970s, pliopithecoids, dendropithecids, and other small-bodied catarrhines from East Africa such as *Limnopithecus* were customarily considered likely ancestors of hylobatids (see reviews in Simons & Fleagle, 1973 and Fleagle, 1984). In the early 1980s, Thenius (1981a, b) even proposed that hylobatids diverged early from other catarrhines and that their resemblances with “pongids” (i.e., great apes) were the result of parallel evolution. Consequently, this author classified hylobatids in a superfamily of their own (Hylobatoidea), distinct from both cercopithecoids and hominoids. Of course, we now know, based on molecular data (e.g., Perelman et al., 2011; Springer et al., 2012), that hylobatids and hominids constitute a clade. However, this does not imply that many of the derived features shared by the extant members of these groups could not have largely evolved in parallel, as suggested by Thenius (1981a, b), which would be compatible with pliopithecoids being stem hylobatids instead of stem catarrhines as favored during the last decades.

The possibility that pliopithecoids are ancestral to hylobatids and that the latter might have largely evolved in parallel with hominids were readily dismissed during the 1980s and 1990s due to the spread of the cladistic paradigm among paleoanthropologists, which led some

authors to emphasize the synapomorphic nature of postcranial similarities between lesser and great apes (e.g., Harrison, 1987b; Pilbeam, 1996, 1997; Harrison & Rook, 1997). Under such an assumption, it was concluded that *Oreopithecus* is a crown hominoid (Harrison, 1987a; Sarmiento, 1987) and it was argued that similarities between hylobatids and pliopithecoids are not phylogenetically informative because of being symplesiomorphic rather than synapomorphic. Indeed, a hominoid status for pliopithecoids would require the independent evolution of many features not only between hylobatids and hominids, but even between cercopithecoids and hominoids, both postcranial (e.g., carpometacarpal joint of the hinge type and loss of the entepicondylar foramen in the distal humerus) and cranial (e.g., an elongated external auditory meatus). And yet, this is precisely what the small-bodied catarrhine *Pliobates* suggests, as it combines a hylobatid-like cranial morphology with derived postcranial features more hominoid-like than those of dendropithecids or the pliopithecoid *Epipliopithecus*, coupled with some plesiomorphic postcranial and craniodental characters, such as an incompletely ossified tubular ectotympanic (Alba et al., 2015). The postcranial features of *Pliobates* that are derived toward crown hominoids explain why this taxon was recovered as a stem hominoid by Alba et al. (2015) but must be considered homoplastic by those supporting its stem catarrhine (pliopithecoid) status (Nengo et al., 2017; Gilbert et al., 2020a). While this is plausible, the same argument might apply to the postcranial similarities shared by *Oreopithecus* and/or hylobatids with extant hominids. If this was the case, as supported by Pugh's (2022) separate analyses of craniodental and postcranial features, the late divergence between hylobatids and hominids supported by most parsimonious cladograms, as well as the stem hominid status of *Oreopithecus* recovered by some analyses would be an artifact caused by the same problem of long-branch attraction (Urciuoli & Alba, 2023) — see below for further details.

Oreopithecus, hylobatids, and the big picture of hominoid evolution

The enduring difficulties to place *Oreopithecus* (and hylobatids) into a coherent systematic scheme should be taken as a serious warning that Miocene ape phylogeny may be far less accurately resolved than customarily assumed (Urciuoli & Alba, 2023), even when pliopithecoids are left out of the equation. This is nicely illustrated by the diverging results obtained by different authors regarding the phylogenetic position of nyanzapithecids — recovered by Rossie & Hill (2018) as closely related to some dendropithecids but as more basal hominoids than proconsulids and afropithecids, or else recovered as more derived than proconsulids by Nengo et al. (2017). The cladistic results of all these authors only coincide in placing proconsulids, afropithecids, and nyanzapithecids within the hominoid stem lineage. Yet a close relationship between hylobatids and hominids, exclusive of most Early and Middle Miocene African apes, is at odds with molecular estimates that situate the crown hominoid divergence in the Early Miocene. A late divergence between hylobatids and hominids is also

difficult to reconcile with evidence currently available from the fossil record for the oldest known hominoids from the Oligocene, which apparently already belong to two distinct lineages, nyanzapithecids and proconsulids (Stevens et al., 2013; Hammond et al., 2019). If this is correct, and nyanzapithecids and proconsulids are both stem hominoid clades as indicated by most parsimonious cladograms, where did crown hominoids come from?

Although extant hominoids might suggest at first sight that the postcranial similarities between hylobatids and hominids are synapomorphic, the fossil record of hominids suggests otherwise. This is most clearly suggested by the contradictory evidence provided by the extinct pongine *Sivapithecus*, which despite its orang-like facial morphology (Pilbeam, 1982) displays postcranial features much more plesiomorphic than expected (Pilbeam et al., 1990; Madar et al., 2002; Morgan et al., 2015). Following Larson's (1998) seminal paper supporting the case of an independent evolution of postcranial similarities in the trunk and forelimb between hylobatids and hominids — thus echoing the earlier views by Thenius (1981a, b) explained above — subsequent fossil discoveries have reinforced such view. This is the case of the dryopithecine *Pierolapithecus*, best interpreted as a stem hominid (Alba et al., 2015; Pugh, 2022) and which, despite multiple evidence indicating the possession of an orthograde body plan, lacks the suspensory-specific adaptations of extant great apes (Moyà-Solà et al., 2004; Almécija et al., 2009; Alba, 2012).

More conclusively determining to what extent hylobatids and hominids evolved in parallel is hindered by the uncertain origin of hylobatids, which as explained above are not unambiguously recorded until the latest Miocene (Harrison, 2016; Ji et al., 2022). In other words, we do not have the slightest idea of what stem hylobatids from the Early and Middle Miocene looked like. However, either they are completely unknown and the group actually has a long ghost lineage of more than 10 Myr — as implied for example by Nengo et al.'s (2017) most parsimonious cladogram — or they evolved from one of the families (incorrectly) recovered as stem hominoids by the most parsimonious cladograms performed during the last decade. Gilbert et al. (2020b) hypothesized that hylobatids originated from proconsulid or dendropithecoid ancestors. This would imply that either of these clades would belong to the hominoid crown group, or else that they are not natural groups as currently defined, with some of its members being stem hylobatids instead. Given the modifications that either hypothesis would entail in terms of dental and postcranial changes along the evolution of the hylobatid stem lineage, an alternative origin of hylobatids from nyanzapithecids and/or pliopithecoids should probably not be entirely discounted. Ji et al. (2022) recently recovered the dendropithecoid *Micropithecus* as a stem hylobatid, but dismissed this possibility by invoking dental convergence, and further rejected the hylobatid status of the Middle Miocene *Kapi* of India mostly based on the presence of a poorly-developed crest considered homologous with the mesial arm of the pliopithecine triangle. Given the presence of similar (even if not necessarily homologous) crests in nyanzapithecids and *Oreopithecus*, it may be questioned whether this evidence is enough to discount the previously proposed

stem hylobatid status of *Kapi* (Gilbert et al., 2020a), or even whether these two hypotheses are mutually exclusive (see previous section).

The origin of *Oreopithecus* has proven as elusive as that of crown hylobatids. Given the stem hylobatid status favored by Pugh's (2022) cladistic analysis for *Oreopithecus* and *Samburupithecus* — even if dismissed by this author by alluding to postcranial convergence and the assumption that their cranial similarities are plesiomorphic — these two enduring problems in hominoid phylogenetics might not be unrelated after all. Besides the contradictory cladistic results obtained by different authors for Miocene apes (see above), there are additional indications that the main branching topology of the hominoid total group is not accurately resolved. Most relevant in this regard are the strikingly divergent results recovered by Pugh (2022) based on craniodental and postcranial features separately. The former recovered *Oreopithecus* and *Samburupithecus* as a sister clade of stem hylobatids, but the resulting clade branches off from a much more basal position than customarily favored for hylobatids and *Oreopithecus* by cladistic analyses including postcranial features. The latter, in contrast, recovered *Oreopithecus* as stem hominid more derived than hylobatids and many other Miocene apes customarily considered great apes. Pugh (2022) attributed the “jumping abilities” of hylobatids and *Oreopithecus* across these cladograms to the possession of homoplastic postcranial similarities with hominids (Larson, 1998; Alba, 2012; Pugh, 2022). On the same basis, Urciuoli & Alba (2023) went one step further by hypothesizing that hominoid phylogeny might be affected by a problem of long-branch attraction. According to the latter hypothesis, the independent acquisition of similar postcranial adaptations in hylobatids, hominids, and likely *Oreopithecus* would have saturated the true phylogenetic signal to a large extent, resulting in a restricted crown hominoid clade that artifactually excludes the most basal stem hylobatids and hominids. This problem would be further aggravated by the decimated biodiversity of extant hominoids (at least, compared to their Miocene relatives) and the large amount of missing data for most fossil apes (due to their usual fragmentary preservation).

The long-branch attraction hypothesis proposed by Urciuoli & Alba (2023) would imply that hylobatids diverged from a much more basal position than generally assumed. In particular, this would mean that some taxa customarily considered stem hominoids might indeed be crown members of this clade (either stem hylobatids or hominids) and even that some taxa generally considered stem catarrhines (such as dendropithecoids or perhaps even pliopithecoids) might indeed be hominoids after all, as supported to some extent by a few analyses (Zalmout et al., 2010; Alba et al., 2015; Rossie & Hill, 2018; Ji et al., 2022). The stem hylobatid status recovered by Pugh (2022) for *Oreopithecus* and *Samburupithecus* is also supported by the craniodental analysis alone and thus cannot merely result from presumably homoplastic postcranial similarities. This makes us wonder what result would be obtained if a craniodental cladistic analysis further including pliopithecoids and a wider representation of nyanzapithecids was performed by further employing a character definition that does not rule

out a priori the potential homology between the talonid supplementary crests of pliopithecoids, nyanzapithecids, and *Oreopithecus*. At the very least, the closer dental similarities found by Zanolli et al. (2022b) between *Oreopithecus* and pliopithecoids are intriguing and deserve further research because, if correct, they would imply that we need to rethink anew all that we accept about Miocene ape phylogeny. If, as argued in Urciuoli & Alba (2023), something is rotten in Miocene ape phylogenetics, maybe the problem is not that *Oreopithecus* does not fit well with Miocene ape phylogeny but rather that the latter is more inaccurate than we dare to admit.

SUMMARY AND CONCLUSIONS

Although extraordinary progress has been made in modern hominoid genomics and phylogenetics, as well as in living and extinct ape comparative and functional morphology — including *Oreopithecus* — much remains to be done regarding Miocene ape phylogeny in general and the systematic position of *Oreopithecus* in particular. The craniodental evidence does not support a phylogenetic link with dryopithecines or, more generally, a great ape status for *Oreopithecus*, which had been supported in the past based on postcranial similarities with crown hominoids and a few cranial resemblances to hominids. In turn, there is an increasing recognition that the purported postcranial synapomorphies between hylobatids and hominids could have largely evolved in parallel between these groups and other lineages, thus not being at odds with a stem hominoid status for this taxon that is supported by some based on dental similarities with nyanzapithecids. The cranial morphology of *Oreopithecus* does indeed generally resemble that of African nyanzapithecids, as well as hylobatids and pliopithecoids, but it is uncertain whether this reflects the plesiomorphic condition of hominoids or was independently acquired by these groups, which are customarily considered not to be closely related. The inner ear morphology neither particularly favors a close phylogenetic relationship with modern hylobatids nor is conclusive regarding its nyanzapithecoid affinities — so that evidence from Miocene stem hylobatids, currently missing, and a more detailed inspection of nyanzapithecids would be required to further test their relationship. In turn, dental evidence more clearly supports the hypothesis that *Oreopithecus* is a late descendant of nyanzapithecids, which could have dispersed from Africa into the Tusco-Sardinian Paleobioprovince during the Late Miocene. Yet a preliminary analysis of enamel-dental junction shape evinces closer morphometric affinities with pliopithecoids, which is at odds with their generally accepted status as stem catarrhines unless interpreted as symplesiomorphic. Given major uncertainties surrounding the main patterns of hominoid evolution — from the uncertain origin of hylobatids to the arguably controversial branching topology among main extinct hominoid groups — such similarities with pliopithecoids deserve further consideration in the future.

So, here we are, more than 150 years after the original description of *Oreopithecus*, with some reasonably convincing answers but more questions than ever before, not only regarding this taxon but the phylogeny of

Miocene apes as a whole. This is probably to be expected as knowledge advances and — frustrating as it may be — is probably for the good, because only by making the right questions to the fossil record can we ever hope to eventually get the correct responses. However, the amount and importance of unanswered questions makes us wonder whether we are at the verge of a major paradigm shift in fossil hominoid systematics. Are the supplementary talonid crests of *Oreopithecus*, nyanzapithecids, and pliopithecoids homologous or homoplastic? Are we sure that pliopithecoids are stem catarrhines instead of hominoids and that they had nothing to do with the origin of hylobatids? What about dendropithecids? Even if the dental similarities between *Oreopithecus* and nyanzapithecids imply a close phylogenetic relationship, does this mean that they must be considered stem hominoids? Or, in other words, are most parsimonious cladograms of Miocene apes affected by a long-branch attraction problem, so that hylobatids occupy a more basal position than customarily assumed relative to Early and Middle Miocene hominoid taxa? And, if so, what Oligocene and Early Miocene apes are truly stem hominoids and which ones are more closely related to either hylobatids or hominoids?

Although *Oreopithecus* fits relatively well within the current narrative of hominoid evolutionary history based on most parsimonious cladograms as a derived stem hominoid of African origin related to nyanzapithecids, such a narrative has many weaknesses — from the uncertain origins and long ghost lineages that must be hypothesized for pliopithecoids and hylobatids, to the contradictory phylogenetic signal provided by craniodental and postcranial data for both *Oreopithecus* and hylobatids. Therefore, it would be premature to conclude that *Oreopithecus* can be ultimately interpreted as a stem hominoid, given indications that Miocene ape phylogeny might be affected by a long-branch attraction problem and that, as a result, the systematic status and branching order of proconsulids, nyanzapithecids, and afropithecids remains uncertain (Urciuoli & Alba, 2023). Maybe the time has come to stop considering that *Oreopithecus* is an oddball Miocene ape or an enigma that must be solved within the current framework of Miocene ape phylogeny. At the very least, *Oreopithecus* is not alone in not fitting well current schemes of catarrhine evolution, as the same applies to hylobatids and pliopithecoids, at least when chronostratigraphic and paleobiogeographic evidence is taken into account.

The true phylogeny of a particular group is, by definition, unknowable and morphology-based phylogenetic inference is affected by many problems, from pervasive homoplasy to abundant missing data. Therefore, deciphering to what extent the current most parsimonious cladograms including Miocene apes and other catarrhines are accurate will surely constitute a huge challenge for the next decades. Yet there is hope to progressively resolve some of the aforementioned unsettled questions thanks to advances in several fronts, as discussed by Almécija et al. (2021) and Urciuoli & Alba (2023), which would likely help more reliably decipher the phylogenetic relationships of *Oreopithecus*. Decreasing the proportion of missing data and increasing taxon sampling by means of future discoveries of Miocene

apes remains would surely help determine the polarity of change of multiple features as well as to better identify homoplasy. Paleoproteomics also offers the prospect to more securely resolve the systematic affinities of extinct hominoid lineages, particularly those that survived into the Plio-Pleistocene (e.g., *Gigantopithecus*; Welker et al., 2019), even if it is currently uncertain whether ongoing efforts to retrieve phylogenetically informative amino acid data from Late Miocene taxa such as *Oreopithecus* (Cieszynska et al., 2021; Cieszynska, 2022) will ultimately succeed. From the viewpoint of phylogenetic inference methods, multiple improvements — the scoring of new characters from areas embedding high phylogenetic signal (such as the enamel-dentine junction; Zanolli et al., 2022a, b), the implementation of implicit character weighting in parsimony analyses (Goloboff, 1997), a better integration of 3D geometric morphometric data with phylogenetic inference methods (currently restricted to landmark-based analyses; Goloboff & Catalano, 2016) — might eventually result in more robust cladograms for Miocene apes.

Above all, to evaluate to what extent Miocene ape phylogenetics may be affected by a long-branch attraction problem (Urciuoli & Alba, 2023), it would be desirable to compare the results of parsimony analyses (which disregard temporal data) with those of total-evidence analyses combining molecular with fossil (both morphologic and chronostratigraphic) data using tip-dating Bayesian methods (see review in Pozzi & Penna, 2022). Although it has been shown that temporal data play an important role in faithfully reconstructing phylogeny (e.g., Mongiardino Koch et al., 2021) and tip-dating analyses have been performed in some primate groups (Beck et al., 2023), they have yet to be widely applied to Miocene apes (but see Pugh, 2020). In the meantime, we should not forget that the state-of-the-art Miocene ape phylogeny is based on most parsimonious cladograms, which do not take the age of fossils and molecular divergence times into account and might be misguided by potentially homoplastic postcranial similarities between hylobatids and hominoids. Although it has been increasingly accepted during the past couple of decades that such similarities are probably homoplastic to a large extent, the consequences of this fact are seldom considered. When they are taken into account, the whole edifice of Miocene ape evolution trembles like a house of cards that is about to crumble. So, instead of shoehorning *Oreopithecus* into the current paradigm of hominoid phylogeny, we should perhaps be ready to explore alternative (even if unorthodox) possibilities and start rethinking of this taxon as part of the solution rather than the problem — i.e., one of the keys for disentangling the still largely unresolved puzzle of Miocene ape phylogeny.

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