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New Idea

Current evidence indicates a Eurasian origin for the Last Common Ancestor of African apes and humans, and supports a new hypothesis suggesting that the Zanclean Megaflood (5.3 Ma) may have played a role in the ultimate divergence of *Pan* and *Homo*

Frances A.M. Mansfield and Mario Vaneechoutte

Frances A.M. Mansfield (fceska68@gmail.com), Kato Lachonia, Volos, 37300, Greece

Mario Vaneechoutte (Mario.Vaneechoutte@ugent.be), Faculty of Medicine and Health Sciences, Ghent University, Belgium

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Abstract

While the established paradigm of human evolution asserts that the lineages leading to the extant great apes and *Homo* arose in Africa, the large number of fossil discoveries from Europe in recent decades support arguments for a European origin of the Hominidae (all great apes) and, plausibly, also a European common ancestor of the Homininae (African great apes, *Australopithecus* species, and the genus *Homo*). Meanwhile, a lack of consensus remains regarding the phylogenetic placement of australopithecine fossil species in Africa, with substantial evidence indicating that some of them may align more closely to extant African great apes than to *Homo*. Based on a novel interpretation of existing fossil, genetic, paleogeographic and paleoclimatic evidence, this paper aims to put forward a new hypothesis regarding the separate divergences of *Gorilla*, *Pan*, and *Homo*. We support existing arguments that the last common ancestor of African great apes and *Homo* may have lived in Europe in the late Miocene, and we put forward a new hypothesis as to where, when, and why the separate lineages may have started to diverge. Extreme conditions during the Vallesian Crisis (11.6–8.0 Ma) and the Messinian Salinity Crisis (6.0–5.3 Ma) may have forced separate branches of European hominids to migrate out of the Mediterranean region. We argue that the lineages leading to *Gorilla* and *Pan* independently migrated into Africa, while the lineage leading to *Homo* went in another direction. Thereafter, the Zanclean Megaflood (5.3 Ma)—which caused the Mediterranean to refill very quickly—may have cut off the migration route between Eurasia and Africa at the Sinai Peninsula, isolating a small population (the putative *Homo* lineage) on the Arabian Peninsula/ Red Sea coast during a period of hyperaridity. The other group (*Pan* lineage) crossed into Africa, where it subsequently diversified into various species of *Australopithecus*.

Keywords: human evolution; last common ancestor; *Gorilla/Pan/Homo* divergence; Messinian Salinity Crisis; Zanclean flood; Red Sea

The Established Paradigm of *Gorilla* / *Pan* / *Homo* divergences

The foundational paradigms of human evolution, formulated in the 19th century prior to the discoveries of any supporting fossil evidence (Darwin 1871, Lamarck 1809), were based on a number of assumptions which still underlie the majority of current paradigms. For instance, Darwin (1871) speculated that it was “probable” that our ape ancestors arose in Africa, and this was based on the knowledge that our closest living relatives, gorillas and chimpanzees, today live only in Africa. However, the fossil ape, *Dryopithecus fontani*, had been discovered in France only a few years earlier, causing Darwin to add that apes might equally have arisen anywhere in the Old World. It was also assumed that the last common ancestor of apes and humans must have been a knuckle-walking quadruped, based on the knowledge that extent African apes tend to walk on their knuckles. Then came the assumptions that humans departed from the other great apes by adopting bipedal locomotion in order to either/or free the hands, fashion tools, carry children or food, reduce vulnerability to solar radiation, hunt game and/or walk/run across open savanna grasslands when the forests retreated in Africa (*i.e.*, the savanna theory).

Nevertheless, there has been a gradual accumulation of contradictory evidence in recent decades leading to the decline of the savanna theory and the growing realization that hominoid orthogrady (upright posture and/or locomotion) and arboreal facultative bipedalism long predate the divergence of *Pan*/*Homo*. Accumulating evidence strongly suggests that the *Homo/Pan/Gorilla* last common ancestor may have already been capable of some type of bipedal locomotion, both on the ground and in the trees, and that knuckle-walking arose more recently and independently in chimpanzees/bonobos and gorillas. Furthermore, the lack of hominid fossils from Africa during the mid-Miocene (between ca. 13–10 Ma), stands in stark and telling contrast to the discovery of many fossil species with great ape morphology from Eurasia—primarily Europe—from the same period. Nevertheless, the essence of the original narrative of human evolution remains and forms the basis of most current research into human origins.

Flaws in the Standard Paradigm

Despite major advances in many fields surrounding the quest for human origins, and an increasing number of anthropoid fossil discoveries in recent decades, there remain a great many unanswered questions regarding the evolution of the genus *Homo*, and there is still no conclusive evidence to inform us when or where *Pan* and *Homo* diverged, who was the last common ancestor (LCA), or how it moved or behaved. Although an increasing number of academics and palaeoanthropologists support that the Homininae, and subsequently, *Pan* and *Homo*, may have diverged in Europe or Asia, the majority view of human ancestors emerging in Africa from an earlier *Australopithecus* species prevails, even though to date no conclusive evidence for a line of descent between any particular African "hominin" species and *Homo* has been established.

It has been argued that the evidence for an African origin of the Homininae (the branch including the extant African apes and humans) is in many respects flawed or at least inconclusive (Andrews 1992, 2020, Begun 1992, 2001, 2005, 2009, Begun et al. 2012, Böhme et al. 2020, de Bonis and Koufos 2004, Fuss et al. 2018, Stewart and Disotell 1998, Wood and Harrison 2011). At the same time, there is general agreement that no confirmed pre-Pleistocene fossils of chimpanzee or gorilla ancestors have ever been found in Africa (Almecija et al. 2021, Andrews 1992, 2020, Begun 2005, Hill and Ward 1998, McBrearty and Jablonski 2005). Statistically, it would be highly improbable that all the hominid fossils dating from the late Miocene to the early Pleistocene in Africa are hominins, *i.e.*, belonging to the human lineage after diverging from *Pan*, and yet, the majority are almost invariably classified as such, sometimes with the exclusion of *Paranthropus* species that are generally seen to be paraphyletic. This conclusion is reached mainly due to the presence of some shared features between australopithecines and *Homo* that are presumed to be derived from a common ancestor; for example, characters indicative of bipedalism, as well as an inaccurate assumption that African apes are primitive and thus less changed than humans since the *Pan/Homo* last common ancestor (PH-LCA) (Almecija et al. 2013, Diogo 2018, Senut 2016, White 2015, Wood and Harrison 2011).

The suggestion that australopithecines may be viewed as closer to the African apes than to the human lineage is not new (Kleindienst et al 1975, Oxnard 1975, Verhaegen 1990, 1994). It has moreover been pointed out that evidence of bipedalism is likely erroneously associated with being on a direct lineage to humans (Andrews 2020, Crompton et al. 2008, Filler 2007, Thorpe et al. 2014, Wood and Harrison 2011), as an upright posture and the origins of bipedalism may in fact stem from the early Miocene, for example, in orthograde apes such as *Morotopithecus bishopi*, already ~21 Ma (Young and MacLatchy 2004). This is supported by strong indications that orthograde bipedalism developed as an arboreal adaptation (vertical climbing) in crown hominids (Almecija et al. 2021, Crompton et al. 2008, Filler 2007, Senut 2003, Thorpe et al. 2014 (and responses), Ward 2019, White 2015). The fact that all extant great apes can and do walk, wade, and run bipedally, and that the *Hylobatidae* (the lesser apes, *i.e.* East Asian gibbons and siamangs) are the most terrestrially bipedal of all (Rosen et al. 2022), only serves to further support the view that orthograde arboreal bipedalism arose in the early Miocene in a common ancestor of all apes (hominoids). Furthermore, the traditional view that bipedalism evolved on the African savanna is now no longer supported by many paleoanthropologists (Bender et al. 2012, deMenocal 2004, Crompton et al. 2010, Pickford et al. 2017, Tobias 1995, White et al. 2009, 2015, WoldeGabriel et al. 2009), but see Davies et al. 2020).

Further evidence suggests that many of the features generally considered primitive in the African apes, such as shorter and stiffer lower backs, tall and narrow ilia, knuckle-walking features of the wrist, sexual dimorphism, larger canines, and abducted halluces, are probably derived rather than primitive as is generally assumed

(Almecija et al. 2021, Andrews 2020, Morton 1926, Schultz 1925, Ward et al. 2019, White 2015, Wood and Harrison 2011). This would imply that the common ancestor of chimpanzees and humans may have been unlike extant apes in a number of its characters (Duda and Zrzavý 2013) or unlike any living species (Almecija et al. 2021, White et al. 2015). There is now strong evidence that several traits seen in extant African apes, such as knuckle-walking and abducted halluces, long-presumed to be primitive conditions representative of the *Gorilla/Pan/Homo* last common ancestor (GPH-LCA), to the contrary, developed independently and in parallel in *Pan* and *Gorilla* lineages (Almecija et al. 2021, Crompton et al. 2008, Dainton and Macho 1997, Kivell and Schmitt 2009, Morimoto et al. 2012, Morton 1926, Rosen et al. 2022, Simpson et al. 2018, Thorpe et al. 2014 (and responses)), and these, therefore, should no longer be definitively considered as primitive conditions.

Furthermore, if a taxon displays features for both bipedalism and arboreal climbing, it is generally assumed that the species is somehow transitional between a more arboreal primitive form and a more derived terrestrial form. If, however, we were to accept growing lines of evidence that a crown hominid may have already been capable of various modes of terrestrial bipedalism prior to the divergence of extant apes and humans, any descendant species displaying a mosaic of features may just as likely have been evolving more arboreal and extant ape-like characters over time.

Upon reviewing the descriptions of presumed hominin fossils from Africa from the late Miocene to the early Pleistocene (from *Sahelanthropus tchadensis*, ~7.0 Ma, through *H. habilis*, ~2.31–1.65 Ma) one finds, contrary to expectation, that many of the earlier species tend to display a number of presumed derived features, while later species often display more presumed primitive features. For example, small male canines are generally considered a derived condition in humans, as all extant male great apes have large canines, which are assumed to be primitive retentions. However, *Ardipithecus ramidus* (4.4 Ma) had small canines, comparable to modern humans, while the later species, *Australopithecus africanus* (ca. 3.3–2.1 Ma) had much larger ones (Suwa et al. 2021).

Furthermore, Senut et al. (2001) describe a more "human-like" femur for *Orrorin tugenensis*, ca. 6.0 Ma than for later australopithecines, while Crompton et al. (2008, following Aiello & Dean 1990, Ward et al. 2001) point out that the earliest known *Australopithecus* species, *Australopithecus anamensis* (4.2 Ma) possessed a modification of the talar trochlea that permitted the leg to pass directly forwards during mid-stance, whereas later australopithecines did not possess this more 'human-like' condition. In addition, some late austral-pithecines, such as *Australopithecus sediba* (1.98 Ma), display more arboreal post-cranial characters than earlier australopithecines, such as *A. afarensis* (Harcourt-Smith and Aiello 2004, Harper et al. 2021, Rein et al. 2017).

Meanwhile, detailed analyses of *Australopithecus* fossils reveal that, other than features related to bipedalism, they tend to display many characters more similar to great apes than to humans. For instance, *A. afarensis* had a number of features that align closely to modern gorillas (Johanson 1981, Rak et al. 2007, Tallman 2016, Verhaegen 1996), while *A. africanus* often appears to align closely with chimpanzees (Tobias 1998). Ferguson (Ferguson 1989) had already pointed out that the cranial capacity of KNM-WT 17000 at 410 cc (*P. aethiopicus*, male specimen, ca. 2.5 Ma) was smaller and more ape-like than those belonging to earlier australopithecines.

It is our view that all australopithecines, extant apes and humans diverged from a European long-backed, orthograde Miocene ancestor that was already capable of different degrees of bipedalism in the trees and on the ground, or while wading in shallow water, and that this trend continued, in parallel, in various species of *Australopithecus* in Africa throughout the Pliocene, some of which eventually reduced their lumbar vertebrae and independently adopted a semi-erect, knuckle-walking posture as they moved closer to the morphologies of gorillas and chimpanzees (Kleindienst et al. 1975, Verhaegen 1990, 1994). We suggest that the notion that common ancestors of apes and humans were "ape-like = primitive" has misled the discussion on human evolution for more than a century, and perhaps a review of which features should be classified as "primitive" and which as "derived" is long overdue.

Finally, most students of paleoanthropology agree that the earliest *Homo erectus/H. ergaster* fossil specimens bear marked dissimilarities with any presumed *Australopithecus* ancestor, which makes it difficult to establish any direct transition or relationship between the two groups (Aiello and Wells 2002, Asfaw et al. 2002, Dennell and Roebroeks 2006, Du and Alemseged 2019, Hawks et al. 2000, Pilbeam and Simons 1965, Wood and Collard 1999, but see Kimbel and Villmoare 2016). Moreover, *H. erectus* predates some late australopithecines by 800,000 years (*i.e., A. sediba*) and although this does not preclude a direct relationship, probability models render it highly unlikely that the latter could have been direct human ancestors (Du and Alemseged 2019, Herries et al. 2020).

The numerous reasons why the majority of the presumed hominin fossils found in Africa prior to 2.5 Ma may be closer to extant African apes than to humans are beyond the scope of this review, but have been addressed by the authors in a recent paper (Vaneechoutte et al. 2024). We contend that the existing African bias—*i.e.*, the perception that any hominid fossil found in Africa that displays characters indicative of bipedal morphology must definitively be regarded as a putative human ancestor, and the rejection of any evidence of the same indications when these same characters appear outside of Africa—is detrimental to the endeavor of science to answer remaining questions about ape and human evolution.

Origin of the Homininae

Ever since Darwin suggested (*The Descent of Man, 1871*) that Europe—or anywhere in the Old World—could equally be considered as the birthplace for the Homininae, the question of where our early ancestors evolved continued to be debated between proponents for Africa and proponents for Asia for almost half a century. The discovery in South Africa in 1924 of the Taung Child (a juvenile cranial fossil of *A. africanus*) (Dart 1925), refocused attention on Africa, and Africa was further endorsed with the discovery of Lucy (*A. afarensis*) by Donald Johanson in the 1970s (Johanson et al. 1978). With the subsequent discovery of a great many, apparently bipedal, hominid fossils in Africa, the matter seems to have been settled. Nevertheless, in light of discoveries in recent decades of fossil species from Europe displaying morphologies similar to extant great apes, an increasing number of paleoanthropologists have since proposed that Europe may have been the birthplace of the Homininae. In fact, many of the features seen in australopithecines in Africa that are often cited as an indication of a species belonging to the human lineage—such as an anteriorly situated foramen magnum, short but broad ilia, relatively small canines, vertically implanted incisors, enlarged molars, loss of premolar shearing function, reduced prognathism—are also found in many of the fossil apes from Europe (Alba and Moyà-Solà 2009, Andrews 1992, 2020, Begun 1992, 2009, 2010, Begun et al. 2012, Böhme et al. 2017, 2019, de Bonis et al. 1990, de Bonis and Koufos 1994, 2004, Fuss et al. 2017, Lutz et al. 2017, Moyà-Solà et al. 2004, 2009, Sevim-Erol et al. 2023, Spassov et al. 2012, Stewart and Disotell 1998, Wood and Harrison 2011).

Indeed, the large number and huge diversity of Miocene ape/hominid species from Europe fill the gap in the fossil record that exists in Africa between ~13–10 Ma, reinforcing the suggestion that it was Europe—not Africa—where Miocene apes were proliferating and diversifying (Begun 2006). Stewart and Disotell (1998) considered a number of dispersal scenarios of African apes into Europe in the early Miocene (~20 Ma) and concluded that a European origin of the African great ape and human clade, with a later Miocene migration (<10 Ma) back into Africa, was the most parsimonious explanation. They suggest that "*this gap in the African hominoid fossil record may represent historical reality*" (Stewart and Disotell 1997: R587).

Many of the European Miocene fossils display great ape characters, and several were clearly orthograde and/or capable of facultative bipedalism; for example, *Danuvius guggenmosi* (11.6 Ma) (Böhme et al. 2019), *Rudapithecus hungaricus* (ca. 10 Ma) (Ward et al. 2019), *Ouranopithecus macedoniensis* (9.6-8.7 Ma) (de Bonis and Koufos 2014) and *Oreopithecus bambolii*, (ca. 9-7 Ma) (Crompton 2008; Köhler 1997; Moyà-Solà et al. 2009). The discovery from Greece in 1944 (von Koenigswald 1972) and from Bulgaria in 2012 (Spassov et al. 2012) of the late Miocene hominid *Graecopithecus freybergi* (7.2 Ma) with hominin affinities (Böhme et al. 2017; Fuss 2017), as well as the notable lack of any contemporaneous crown hominid fossils from Africa, reinforces arguments for a European origin of the African great apes. More recently, the reclassification of a fossil previously attributed to the genus *Ouranopithecus*, now as *Anadoluvius turkae* (8.7 Ma) from Anatolia in modern day Türkiye, displaying morphological affinities with modern-day gorillas, suggests that there was "*a radiation of early members of the gorilla clade*" around this time, and corroborates the evidence that hominines may have originated in Eurasia during the late Miocene (Sevim-Erol et al. 2023: 7). As some of their discoverers have pointed out, many of these species would have been regarded as potential human ancestors had they been found in Africa.

Furthermore, the discovery in 2002 (although controversially not published until 2017) of several sets of bipedal, hominin-like footprints in Trachilos, Crete (Gierlinski et al. 2017), and dated to 6.05 Ma (Kirscher et al. 2021), reinforces the view that bipedal hominids existed on and around the coasts of the Southern European, Tethys/Mediterranean Sea right up to the onset of the Messinian Salinity Crisis (MSC) (5.9–5.3 Ma).

The Possible Origin of the Homininae in Miocene Europe

Detailed analyses of the paleohabitats occupied by Miocene apes provide clues about why orthograde climbing in early-mid Miocene hominids may have led to facultative (postural) arboreal bipedalism, followed by habitual (occasional) terrestrial bipedalism by the late Miocene/early Pliocene. The oldest Eurasian hominoid fossil (ENG. 4/1) is estimated to date from ~17.0 Ma from Engelswies in southern Germany (Heizmann and Begun 2001, Böhme et al. 2011) and was found in "*a lakeshore environment near dense subtropical rain forest vegetation, where paratropical temperatures (mean annual temperature around 20°C) and humid conditions (mean annual precipitation >1.100mm) prevailed*." (Böhme et al. 2011: 332). Indeed, Europe experienced extremely warm conditions with high levels of precipitation during the middle Miocene, creating a "washhouse" climate (Böhme et al. 2008). After the Langhian (Badenian) flooding (~14.5 Ma) and prior to the onset of the Vallesian (11.6–8.0 Ma), vast areas of

Europe were characterized by "*widespread open marine settings*" (Sant et al. 2019: 2226) as much of central Europe was flooded by the central Paratethys Sea and the proto-Mediterranean Sea, creating a large number of isolated islands and inland seas, especially around today's Hungary, Slovakia, Romania, Austria and Poland. All pre-Vallesian, mid-Miocene ape fossil deposits were found in close association with sub-tropical humid forests and a mosaic wetland environment, which would have been typical for Europe at that time. For example, *Pierolapithecus* (13–12.5 Ma), *Anoiapithecus* (11.9 Ma) and *Hispanopithecus* (11.1–9.5 Ma) fossils hail from the Vallès-Penedès Basin, Catalonia, which at the time was a large lake, surrounded by temperate evergreen forest and swampy woodlands, and their fossils were found alongside those of otters and beavers (Andrews 2020, Kordos and Begun 2002). *Danuvius guggenmosi* (11.6 Ma) fossils were found in the Northern Alpine Foreland Basin of Hammerschmiede (Germany) in 20 m thick floodplain deposits along with fish, mollusks and other animals (Fuss et al. 2015). *Rudapithecus* (ca. 10 Ma) fossils were found in a shallow valley near Rudabánya in Hungary, which was at different times an ancient lake or a swamp forest (Andrews 2020, Deane et al. 2013, Kordos and Begun 2002).

Such environments, combined with fossil evidence of orthograde locomotion in these European species, support arguments for an "aquarboreal" lifestyle, whereby apes climbed vertically up and down trees and waded bipedally to reach nutrient rich resources, such as aquatic herbaceous vegetation, in bodies of water, much like extant lowland gorillas, bonobos, and even orangutans still do (Doran and McNeilage 1998, Verhaegen et al. 2002, 2011). Changes in dentition and enamel thickness during the mid-Miocene indicate that European apes were consuming less soft foods such as fruit and were instead adapting to a diet consisting of tougher foods, such as papyrus and aquatic sedges (Alba et al. 2010, de Bonis and Melentis 1977, de Bonis and Koufos, 2014).

Based on the shape of the ilium in *A. afarensis*, biomechanical models have shown that wading in water would have been a far more energy efficient form of bipedalism than terrestrial bipedalism (Kuliukas et al. 2009). Moreover, captive bonobos exhibit bipedalism 90% of the time when in water compared to only 2% of the time on the ground (Kuliukas 2002). An ape or early hominid, already orthograde for vertical climbing, would sustain an upright posture in order to forage in deeper water while leaving the forelimbs free for harvesting, but also because it simply would not be advantageous to both revert to a quadrupedal position and keep the head above the surface. All extant great apes (orangutans, gorillas, chimpanzees, and bonobos) are known to occasionally wade through water bipedally in order to harvest aquatic vegetation. Due to their relatively shorter hindlimbs, they revert to semi-erect locomotion (knuckle-walking) on the ground and travel over open spaces quadrupedally, whereas *Homo* evolved much longer lower limbs, which would make quadrupedal locomotion slow, energetically expensive, inconvenient and impractical. There are no clear models to support a transition from orthogrady in the trees to obligate bipedalism in an open terrestrial environment. Wading, however, may provide a more parsimonious model to explain the transition to sustained terrestrial bipedalism than do models based on postural feeding (Hunt 1996), solar radiation/thermoregulatory considerations (Wheeler 1985), locomotor efficiency (Rodman and McHenry 1980) or persistence hunting (Liebenberg 2006) hypotheses.

Returning to the significance of the paleoclimate at the peak of the Vallesian (~9.7 Ma), temperatures in Europe dropped and seasonality increased, leading to a general drying out of the continent with more xerophilous woodland, a loss of tropical fruit trees, and an increase in open grasslands. By the late Miocene (~9.0–6.0 Ma), with the gradual drying of the Paratethys Sea, shallow wetland habitats expanded and became more seasonal, gradually becoming less forested, cooler and drier (Agusti 2007, Eronen and Rössner 2007). During this time, many mammals including apes went extinct in Europe (Agusti 1990), but those that survived appear to have been hard-object feeders in more open, yet specialized niches. For example, *Ouranopithecus macedoniensis*, a large terrestrial ape the size of a female gorilla, lived in frequently flooded riverine grasslands and fed on roots, tubers and graminoids including sedges and rushes (Merceron et al., 2017).

One lineage that may have originated in Europe but migrated to Africa earlier than the *Pan/Homo* lineages is that which is ancestral to extant gorillas. Genetic analysis suggests that the *Gorilla* lineage diverged from the ancestors of *Pan/Homo* during or shortly after the mid Miocene Vallesian Crisis, ± 8–6 Ma (Chen 2001, Glazko and Nei 2003, Horai et al. 1995, Stauffer et al. 2001). De Bonis and Koufos (1994, 2004, 2014, Koufos and de Bonis 2006) noted marked similarities between *O. macedoniensis* from Greece and the East African *A. afarensis*, and they suggested: "*May be, in the future, some discoveries will demonstrate the presence in Africa of* Ouranopithecus *itself or of a very similar genus but, until this, the Greek genus is the most appropriate to be the sister group of the Mio-Pliocene hominins*" (de Bonis and Koufos 2004: 259). This was only shortly before the discovery of *Nakalipithecus nakayamai* (9.9–9.8 Ma) from Kenya, which was described as resembling *O. macedoniensis* as well as being similar in dental size to orangutans and female gorillas (Kunimatsu 2007). The most recent analysis reveals that *A. turkae* shares a suite of derived characters with *O. macedoniensis* and *G. freybergi* with which it forms a clade (Serim-Erol 2023).

Each of these taxa has been noted to share features with extant gorillas (Ioannidou et al. 2019, Rak et al. 2007, Serim-Erol 2023). Therefore, we suggest that it cannot be excluded that *A. turkae* from Anatolia represents an early branch of the *Gorilla* lineage that diverged from *O. macedoniensis* (or a shared common ancestor) in Europe and whose descendants migrated to Africa, giving rise to various genera which have also been noted to share derived features with extant gorillas, such as, *S. tchadenensis* (ca. 7.0 Ma) (Meyer et al. 2023, Wolpoff et al. 2007), *A. ramidus* (4.4 Ma) (Prang 2019, Suwa et al. 2009) and *A. afarensis* (3.9–2.9 Ma) (de Bonis and Koufos 1994).

During and after the Vallesian and throughout the MSC, as conditions changed dramatically in Europe, many species disappeared, but there was also a mass exodus of fauna from the region (Agusti 1999, 2007, Böhme et al. 2021, Leakey et al. 1996, Nargolwalla 2009). Many animals that later became endemic to Africa, such as ancestors of today's giraffes, hippos, bovines, rhinos, horses, zebras, felids, *etc*., probably migrated away from the Mediterranean region by following the receding forests southward in search of a more constant subtropical environment. There is no reason to suppose that hominids were not amongst them, especially as after 7.0 Ma, an increasing diversity of bipedal hominids starts to appear in Africa.

On the other hand, only a handful of ape species are known to have survived in Europe in the late Miocene, after which time no fossil apes are found there. The last known is *Oreopithecus bambolii*, a species which inhabited a swampy island in the Sardinia/Tuscany region until ca. 7.0–6.0 Ma, when the island would have reconnected to the mainland and become accessible to large terrestrial predators (Harrison and Harrison 1989, Köhler and Moyà-Solà 1997).

Graecopithecus freybergi lived on the Greek mainland and in Bulgaria approximately 7.2 Ma (Böhme et al. 2017, Fuss et al. 2017, Spassov et al. 2012). A mandible assigned to *G. freybergi* was found at Pyrgos, Vassilis, close to the Kifissos river in the Athens basin, which at the time would have consisted of a mosaic environment of savanna grassland, springs, marshes, swamps, rivers and pockets of woodland (Pikermian biome) (Böhme et al. 2017, Böhme et al. 2020). According to Böhme, *G. freybergi's* diet would have been closer to modern humans than to modern great apes, often including wetland plants such as cattails, and she suggests that bipedalism arose on the European savanna as opposed to the African savanna. In our opinion, however, the transition from arboreal orthogrady to habitual terrestrial bipedalism more likely occurred as a result of frequent wading and foraging in open and seasonally flooded environments, which were typical of Europe during the late Vallesian. As conditions became drier, it is possible that foraging along waterways may have eventually led some hominids to the coasts, where they would have found a diversity of food sources to be exploited on the beaches, in tide pools or in shallow waters. They may have lost many of their more arboreal features as they became more proficient bipeds. There is one crucial piece of evidence which indicates that at least one species of bipedal hominids might have done just this.

The Trachilos ichnofossils indicate the presence of bipedal hominids in Crete 6.05 Ma

The controversial human-like tracks from Trachilos on the island of Crete from 6.05 Ma in the late Miocene (Gierlinski et al. 2017) as well as the observed hominin affinities in the dental morphology of *G. freybergi* (Fuss et al. 2017, 2018), together indicate that a bipedal hominid, possibly a hominine, survived in Europe right up to the onset of the MSC, ~6.0 Ma. Yet the potential significance of these discoveries has not been given the same level of attention as any discovery from Africa, perhaps because—as noted by several paleoanthropologists (Begun 2018 as cited in Chung 2018, Böhme et al. 2020, Fuss et al. 2018, Gierlinski et al. 2017)—they do not correlate with the current generally accepted paradigm of human evolution, which states that great apes and humans diverged from a common ancestor in Africa.

Although no hominid fossils have been found on the island, the Trachilos footprints suggest that a viable population of bipedal hominids managed to occupy a niche there from the early-mid Miocene at least until the onset of the MSC (ca. 10.0–6.0 Ma). This is because Crete started to disconnect from the Greek mainland approximately 10.8–9.6 Ma due to the formation of the Mid-Aegean trench (Poulakakis et al. 2005, van Hinsburgen and Meulenkamp 2006). Fauna from the late Miocene in Crete consisted of large, non-endemic mammals such as saber-toothed carnivores, hyaenids, proboscideans, three-toed hipparion horses, suids, and various other species that had migrated there some time prior to the island's full separation, and the footprints left behind at Trachilos indicate that a species of hominid must have been among them.

While much attention has been given to the bipedal tracks from Laetoli, 3.7 Ma (Leakey 1981), presumed to have been made by *A. afarensis*, the much older Trachilos footprints tend to be dismissed as insignificant, and yet they appear more human-like with an adducted hallux, an entaxonic digital array (the inner digits being strongly developed), a strong ball impression, clear propulsion off the transverse axis, and a narrow heel (Gierlinski et al. 2017, Kirscher 2021). From comparing the derived features in ape and human feet, McNutt (2018) hypothesized that the PH-LCA would likely have had a narrow heel and a number of other features that are evident in the ichnofossils from Trachilos. In contrast, while the *Australopithecus* ichnofossils from Africa present a combination of characters that suggest both bipedal and arboreal tendencies (Venkadesan 2020), the Trachilos prints lack any suggestion of arboreality but reveal clear signals for habitual plantigrade bipedalism (Gierlinski et al. 2017).

Although the Trachilos discovery has been proclaimed as "*exciting and tantalizing*" (Crompton 2017: 692), doubt has been raised about the date of the tracks and their validity in the context of human evolution (Meldrum and Sarmiento 2018). Recently, Zachariasse and Lourens (2022) suggested that the tracks may possibly date to the late Pliocene, ~3.0 Ma, but their results were inconclusive: "*the Trachilos sediments belong either to the Pliocene or to the Upper Tortonian-Messinian*" (p.8). Their main reason for proposing a much later date is that they cannot account for how any hominins might have reached Crete six million years ago, failing to consider that they may have been there since the island's separation from the Greek mainland. Other research has consolidated the accuracy of the dating and rebutted Meldrum's arguments that they appear more similar to tracks made by other apes such as gorillas (Kirsher et al. 2021, Vanarsdale, pers. comm.), whereas it could be argued that the Laetoli tracks appear more similar to mountain gorilla (*G. g. beringei*) tracks (*e.g.,* Schultz 1925) when viewed side by side (Figure 1).

It is not known which species may have left its tracks at Trachilos in Western Crete but there are a few possible contenders. A number of genera of hominids are known to have survived in Europe in the late Miocene but one candidate genus is perhaps *Ouranopithecus*, which had a wide range over Greece and the Balkans (de Bonis and Melentis 1977; de Bonis et al. 1990; Koufos and de Bonis 2006) approximately 10–9 Ma, or around the time that Crete was beginning to separate from the Greek mainland. *O. macedoniensis* was a large—presumed terrestrial—ape that may have been capable of bipedal locomotion as it displayed certain post-cranial similarities to "*the bipedal primate* Homo" (de Bonis and Koufos 2014). If members of this species had ranged as far as Crete, then connected to the Peloponnesian Peninsula, its descendants may have still been there four million years later. Another contender is *G. freybergi* (7.2 Ma), and although postcranial remains have not yet been described, it is nonetheless considered a very closely related sister taxon to *O. macedonensis* and its dental morphology has prompted a number of paleoanthropologists to consider it as a candidate for the PH-LCA or the oldest known hominin (Fuss et al. 2017, 2018). However, unless much older fossils are found, *G. freybergi* is probably too young to have become stranded on Crete ~10.0–9.0 Ma.

Figure 1. Footprints. Top row, left to right: Laetoli 3.7 Ma (Leakey 1981)—presumed to have been made by *A. afarensis;* Mountain gorilla (*G. berengei*). Bottom row, left to right: Trachilos 6.0 Ma (Gierlinski et al. 2017); *Homo sapiens.*

The Trachilos tracks date to just prior to the onset of the Messinian Salinity Crisis (MSC), which began approximately 5.9 Ma when the African tectonic plate pushed up against the European plate, lifting the crust at the straits of Gibraltar, thereby shutting off the inflow of water from the Atlantic Ocean and causing the Mediterranean Sea to largely evaporate, perhaps within a thousand years (Krijgsman et al. 1999). After 5.9 Ma and during the MSC, Crete would have reconnected with the mainland as land bridges formed and the evaporating sea would have caused coastal conditions became increasingly inhospitable. The MSC ended 5.33 Ma when the Atlantic crust at Gibraltar subsided, water started flowing in again and the Mediterranean basin quickly refilled, maybe even in less than two years (Blanc 2002, Garcia-Castellanos et al. 2009, Garcia-Castellanos 2020, Poulakakis et al. 2005). Therefore, the 6.05-million-year-old Trachilos footprints were apparently made when Crete was still an island, but not long before the sea began to evaporate. It is therefore possible that descendants of the Trachilos trackmakers were able to migrate to the mainland and perhaps eventually, their descendants might have migrated away from the drying Mediterranean basin altogether, following the coasts with other fauna that migrated to Africa.

Initial Divergence of *Gorilla*, *Pan*, *Homo*

Analyses of human, chimpanzee and gorilla genomes show that divergence between these lineages was much more complicated than previously supposed (Mailund 2012, Patterson et al. 2006, Popadin et al. 2022, Rogers and Gibbs 2014). Patterson et al. (2006) suggest that "*the hominin and chimpanzee lineages initially separated but then exchanged genes before finally separating less than 6.3 Myr ago*" (p.1106). Incomplete lineage sorting (ILS) in human and great ape genomes shows that for approximately 15% of the genome, chimpanzee DNA sequences share a more recent common ancestor with *Gorilla* than with humans, while another 15% suggests that gorillas and humans are more closely related (Rogers and Gibbs, 2014). Cechova et al. (2020) analyzed the male specific regions (MSY) of all great apes and found that the Y chromosomes of humans and gorillas were more similar than those of humans and chimpanzees, despite the latter sharing a more recent common ancestor. Furthermore, the presence of a pseudogene on chromosome 5 (ps5) of gorillas, chimpanzees, and humans points to a distant interspecies hybridization that occurred approximately 6.0 Ma, independently between the three diverging lineages (Popadin et al. 2022). This pseudogene is speculated to have come from a hominine species (now extinct) that would have already diverged from a shared common ancestor. Whatever advantage this pseudogene transferred to its descendants at the time, it "*…was independently fixed in the gorilla and the human/chimp nascent populations, which by that time were probably substantially separated*" (p. 9).

Strong selection across chromosome X occurred during the *Pan/Homo* divergence and Patterson et al. (2006) suggest that this is consistent with a scenario in which, after initially diverging, later introgression would have created infertile males and fertile females. If the fertile females then mated back into the ancestral population, X chromosomes derived entirely from the ancestral population would thereby be transmitted to the nascent population, which would consist of both fertile males and females. They argue that this would allow "*nascent species to derive traits from several ancestral populations, combining them to adapt to new environments*" (Patterson et al. 2006: 1106).

This complicated history of distant divergence and subsequent interbreeding between *Gorilla*, *Pan* and *Homo* before the final separation of *Pan/Homo*, could hypothetically be explained by an initial allopatric separation of a group of Miocene hominids from an ancestral group for a period of 3–4 million years, after which they subsequently reunited with the descendants of the ancestral group ca. 6.0 Ma. These dates correspond with the period during which Crete would have been an island, between ~10.0–6.0 Ma. For example, an ancestral ape species may have initially diverged into separate lineages when one small group of individuals, now extinct, became isolated on Crete around the time it became an island, ca. 10.0 Ma, (*e.g.,* ancestors of the Trachilos hominids). After 5.9 Ma when sea-levels fell during the MSC, descendants of the Trachilos population might have migrated back to mainland Europe, where they interbred with descendants of the ancestral population—possibly the last common ancestor of chimps and humans (PH-LCA)—after the *Gorilla* lineage had already separated. Around the same time, they also interbred with this separate ancestral *Gorilla* population, creating a new hybrid species with a genome closer to *Gorilla*/*Homo* (GH) than to *Pan.* Thus, they transferred ps5 independently to the human, chimpanzee and gorilla lineages. This may also help to explain why 15% of our genome is more similar to gorillas than chimpanzees, and possible later introgression between *Pan* and *Gorilla* ancestors in Africa might account for 15% of the genome which suggests chimpanzees share a more recent common ancestor with gorillas than with humans (Figure 2).

This hypothetical scenario is offered merely as a suggestion intended to show how genetic evidence might be reconciled with fossil evidence and with geographic/geological evidence from the southern Mediterranean in the late Miocene, in order to explain some of the apparent anomalies in the genomes of *Gorilla*, *Pan* and *Homo*. Although such a hypothesis would be difficult to prove in the absence of any genetic material, in light of more recent fossil discoveries from Europe, we propose it is equally as valid a hypothesis as any which postulates a connection between African australopithecines and *Homo* in the absence of any genetic data.

Ultimate Divergence of *Pan / Homo*

As previously mentioned, many species migrated away from the Mediterranean and into Africa during the MSC, although there was almost no faunal migration in the opposite direction until the mid-Piacenzian (~3.0 Ma). It was this unidirectional migration that caused much of Africa's extant fauna to diversify and become endemic in Africa over the last five million years (Böhme 2021, de Bonis and Koufos 1994). It is highly probable that hominids also migrated away from the Mediterranean Sea during the MSC, possibly following the Anatolian rim of the Mediterranean basin south and along the northern coast of the Arabian and Sinai

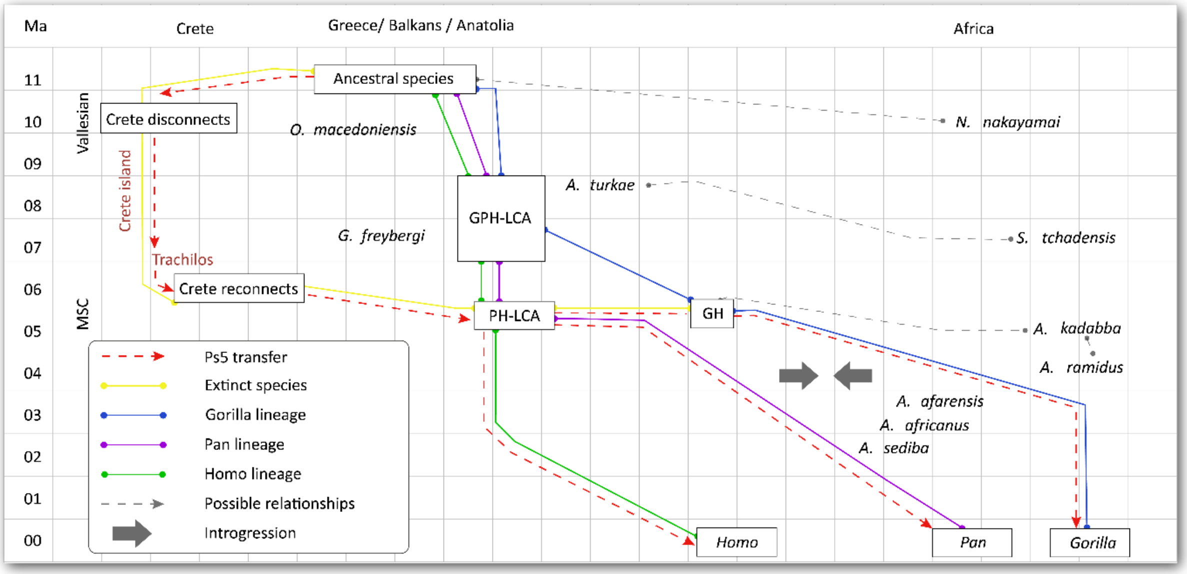

Figure 2. Hypothetical scenario: if individuals from a population ancestral to GPH (now extinct) became isolated on Crete ca. 10.0 Ma, their descendants may have subsequently interbred with 2 separate populations when Crete reconnected to the mainland ca. 6.0 Ma; one ancestral to *Pan/Homo* (PH-LCA), the other ancestral to *Gorilla* (GH), thereby transferring a pseudogene on chromosome 5 (ps5) independently to *Pan/Homo* descendants and to *Gorilla* descendants.

peninsulas. It is indeed possible that there were multiple migrations of different hominid species from Europe to Africa between 10.0–6.0 Ma, giving rise to various orthograde, evidently bipedal genera in Africa such as *Sahelanthropus*, *Orrorin*, *Ardipithecus* and *Australopithecus*.

The dating of the Trachilos footprints at 6.05 Ma is significant because, according to the majority of phylogenetic analyses, *Pan* and *Homo* ultimately diverged between 6.2–4.4 Ma (Chen and Li 2001, Horai et al. 1995, Kumer et al. 2005, Patterson et al. 2006, Stauffer et al. 2001, Yang, 2002). In order to understand what might have caused the ultimate divergence of *Pan* and *Homo*, it is necessary to consider paleoenvironmental, climatic and geological conditions in and around the Mediterranean region. The most significant event that occurred around the presumed date of divergence in that region is the Zanclean Mega-flood, 5.33 Ma, which marks the beginning of the Pliocene. In what is comparable to mere moments in geological time, the straits of Gibraltar opened up, and water from the Atlantic Ocean came rushing in, causing as much as 90% of the Mediterranean basin to refill, possibly in less than two years (Garcia-Castellanos et al. 2009, Garcia-Castellanos et al. 2020).

So great was the impact of the Zanclean flood, 5.33 Ma, that the waters of the Mediterranean might have mingled with those of the Red Sea, submerging the land bridge between the Arabian and African plates, thereby cutting off the migratory route into Africa and potentially flooding the Ethiopian Afar Danakil depression of the Middle Awash region (Hutchinson and Engels 1970). Examination of macrofauna from Egyptian coastal waters of Marsa Alam and Ras Banas in the northern Red Sea reveal 35 species, including corals, bivalves, gastropods and echinoids, with both Indo-Pacific and Mediterranean affinities (Kassab and Ahmed 1994), suggesting a “*mixed-geographic realm…via the Red Sea, during a Late Miocene-Pliocene time*” (Kora and Abdel-Fattah 2000: 221).

During the Pliocene, global temperatures were several degrees warmer than today, and sea levels were up to 35 meters higher than current sea-levels (De la Vega et al. 2020, Dwyer and Chandler 2009), creating new opportunities as well as formidable challenges for any species forced to adapt to coastal zones. The late Miocene/early Pliocene biogenic bloom (7.0 Ma–3.5 Ma) was at its peak around 5.3 Ma, and this would have encouraged biodiversity and provided particularly rich sources of seafood in coastal areas (Dickens and Owen 1994).

Nevertheless, flooded coastal areas during the Pliocene would not have been restricted to the Red Sea. Alternative aquatic biomes such as rivers, lakes, mangroves and swamp forests were likely exploited by a variety of hominid species. For example, *A. kadabba* (WoldeGabriel et al. 2001), *A. ramidus* (Gani and Gani 2011), and *A. afarensis* (Johanson and Edey 1981) are now recognized as having inhabited a mosaic of woody or forested wetlands in the Middle Awash region of Ethiopia's Afar rift valley, rather than open savanna. We propose that fossil evidence of numerous bipedal hominids in Africa after 7.0 Ma, reflects an "aquarboreal" shallow-wading and foraging lifestyle that persisted after these species diverged from an already orthograde, possibly habitually bipedal common ancestor during the Messinian. Some of these species would have later adapted to the drier forest environments that developed during the Pleistocene, and eventually adopted a semi-erect knuckle-walking form of locomotion, as the ancestors of today's gorillas, chimpanzees, and bonobos.

Proto-*Homo* in Isolation

Despite having almost identical DNA, comparison of human and chimpanzee genomes reveals that where the two genomes differ, they differ significantly. For example, Hughes et al. (2010) found the male specific regions of the Y chromosome (MSY) in chimpanzees and humans to be "*remarkably divergent*", suggesting that the two lineages diverged considerably and rapidly after separating: "*Indeed, at six million years of separation, the difference in MSY gene content in chimpanzee and human is more comparable to the difference in autosomal gene content in chicken and human, at 310 million years of separation*" (p.5). Cechova et al. (2020) found that *Pan* "*experienced accelerated substitution rates"*, in agreement with Chen and Li (2001) who demonstrate that the human lineage has evolved significantly more slowly than the chimpanzee and gorilla lineages. This confirms previous genomic data revealing that chimpanzees have up to three times more DNA sequence variation in their genome than humans (Kaessman et al. 2001). Such radical differences in genome sequence and MSY indicate that the *Pan* and *Homo* lineages finally and definitively separated from each other within the past six million years (or more recently than 5.4 Ma, according to Patterson et al. 2006) with no possibility of introgression, and that *Pan* diverged further from the LCA than *Homo*, possibly as a result of a higher ratio of males to females and/or greater sperm competition in the *Pan* lineage (Cechova et al. 2020) than in the putative *Homo* lineage.

Genetic data also support the idea that *Homo* evolved from a small, isolated population, perhaps only a few thousand individuals, that would have been isolated for a long enough period of time (the long-necked bottle) for equilibrium to be reached in the majority of neutral gene systems (Chen and Li 2001, Harpending et al. 1998, Hawks et al. 2000). Approximately two million years ago, the *Homo* lineage began to appear in Africa, but it was significantly different from any australopithecine species that came before. Until then, there is a dearth of evidence regarding the identity and location of the original members of our genus. "*All the currently available genetic, paleontological, and archaeological data are consistent with a bottleneck in our lineage more or less at about 2 MYA*." (Hawks et al. 2000: 17). Accordingly, Harpending et al. (1998: 1967) conclude that the direct ancestors of *Homo* must have occupied "*an area the size of Swaziland or Rhode Island*" for at least one or two million years before the appearance of our genus.

Intriguingly, *Pan troglodytes* endogenous retroviral genes (PtERV-1) are present in all African primates but absent from the human genome and all non-African primates. The presence of PtERV-1 in African apes is believed to have been the result of "*a retroviral infection that bombarded the genomes of chimpanzees and gorillas independently and concurrently, 3-4 million years ago*" (Yohn et al. 2005: 0577). This strongly indicates that our ancestors were most probably not even in Africa during the Pliocene (Benveniste and Todaro 1976, Polavarapu et al. 2006), but this is rarely commented upon, and attempts to explain how *Homo* ancestors may have managed to evade viruses that affected all other extant African apes have proved inconclusive (Kaiser et al. 2007, Perez-Caballero et al. 2008). The most parsimonious explanation is that our ancestors were not in Africa during the middle Pliocene and may instead have evolved in "*an ecological niche that physically separated them from the source of the infectious PtERV1 virus*" (Kaiser et al. 2007 b).

All things considered, we suggest that whatever caused the *Pan* and *Homo* lineages to ultimately diverge 5–6 million years ago most likely resulted in the putative *Homo* lineage remaining isolated from all other Hominini for a long period (possibly the entire Pliocene) in a relatively small region, and this would explain the absence of PtERV1 genetic elements in our genome, and many of the aberrant features unique to our genus. Then, approximately ~1.8–1.6 Ma, there is the first indisputable evidence of our genus *Homo*, radically different from small-brained, short-legged australopithecines or habilines in Africa. Fossils of *H. erectus* (*s.l.*) appear more or less synchronously in locations as far apart as eastern China and southern Africa. The *Pan* lineage, on the other hand, did not become isolated and thus was able to further expand and diverge within the African continent as various lineages of the more robust bipedal hominids, such as South African *A. africanus*, *A. sediba* and *Paranthropus robustus*, all of which possess numerous characters that align with extant chimpanzees/ bonobos.

Out(side) of Africa

We propose that the species representing the LCA of humans and chimpanzees formed part of a continuous migration of fauna from southern Eurasia to northern Africa during the Messinian, between 5.9–5.3 Ma, via Anatolia and across the northern Sinai region of the Arabian Peninsula. Ultimately, a small group of individuals, ancestral to *Homo*, may have been cut off and separated from other hominids, ancestral to *Pan*, when, at 5.33 Ma, the Zanclean flood refilled the Mediterranean and submerged the land bridge between the African and Arabian plates, at which point the connection between the two continents was lost. This date would be consistent with the majority of genetic analyses for the timing of the *Pan*/*Homo* divergence. The lineage that made it to the African continent—eventually leading to the *Pan* lineage—may have migrated south along the African Red Sea and/or Nile River valley and continued southward at Afar, following the many substantial waterways and lakes along the East African Rift Valley and Coastal Forest. This may explain why existing fossil evidence fails to demonstrate a clear progression from primitive/ape-like features towards more derived/human-like features, and why there is no obvious progression from quadrupedalism towards bipedalism in the australopithecines (Harcourt-Smith and Aiello 2004, Harper et al. 2021). Hawks et al. (2000: 4) could see no obvious connection between australopithecines or habilines and the "*new species*", *i.e.*, *Homo*. They noted: *"... the fact that no gradual series of changes in earlier australopithecine populations clearly leads to the new species, and no australopithecine species is obviously transitional. This may seem to be an unexpected statement, because for 3 decades habiline species have been interpreted as being just such transitional taxa, linking* Australopithecus *through the habilines to later* Homo *species*." Instead, they believe that *Homo* evolved from a small group that had become isolated from the parent group, causing a "*genetic revolution*" in our human ancestors.

We suggest that, unlike the ancestors of australopithecines and extant African apes, the proto-human group remained isolated on the Arabian Peninsula. Between 5.6 and 3.3 Ma, the Arabian Peninsula went through a stage of hyperaridity (Böhme 2021), so any species trapped there would have been isolated between the Red Sea and a lifeless desert—an impenetrable barrier. The Arabian coast of the Red Sea, approximately 2000 km in length, would have offered both challenges and opportunities to a small population of littoral foraging hominins during the Pliocene. Global mean surface temperatures were several degrees warmer than today, and the Arabian Peninsula would have been extremely warm and lacking in tree cover for shade (Vaks et al. 2013). Putative hominins, probably already facultatively or habitually bipedal, having descended from aquarboreal apes, may have spent much of their time foraging for aquatic food sources on the coasts and eventually in the water, where they could also have kept cool. It has been suggested that the suite of modifications acquired by *Homo* could in no way have been acquired in a desert, savanna or forested environment, but most probably in a littoral environment (Hardy 1960, Morgan 1972, Vaneechoutte et al. 2011, Verhaegen 2013).

During the Pliocene when sea levels were up to 24–35 m higher, shallow-water coastal shelves would have covered a large area (Dickens and Owen 1994, Mitchell et al. 2020). The Red Sea area contains a great diversity of coral reefs and atolls, and an abundance of edible flora and fauna, terrestrial and littoral/aquatic (Bailey et al. 2007), including sea grasses, seaweed, mollusks (*e.g.*, bivalves, cephalopods), crustaceans (*e.g.*, crabs, shrimps, lobsters), fish, turtles, birds, eggs—all of which, unlike muscle meat, humans can eat raw and with minimal processing. Just as macaques often forage for crabs and shellfish on the beaches and in tide pools, smashing them open with rocks (Gumert and Malaivijitnond 2012), so too could our earliest putative *Homo* ancestors have done, with this eventually leading to more sophisticated tool creation and use in their descendants (*H. erectus*).

As regards food, the evidence is clear that an aquatic diet, rich in omega 3, long-chain polyunsaturated fatty acids (LC-PUFA) such as docosahexaenoic acid (DHA), arachidonic acid (AA), eicosapentaenoic acid (EPA), and other essential brain nutrients such as iodine, selenium and taurine, play an important role in healthy fetal development (Odent 2017), increased longevity (Shibata 2001, Yamori 2009), and overall good health (Venugopal 2017). The same aquatic nutrients may have been pivotal to encephalization in *Homo* (Broadhurst et al. 2011, Crawford et al. 1999, IMIM 2021, Tobias 2011). Salt consumption (Messerli et al. 2021) and the activity of swimming itself (Chase 2008) have also been shown to be greatly beneficial to human health and longevity.

Unfortunately, there is no fossil evidence to support this scenario. Sea levels have fluctuated so many times since the early Pliocene that whatever evidence there may once have been would have long been washed away, although a case could be made that evidence might still be found in locations relative to when sea-levels were at their highest, up to 35 m above current levels, perhaps in caves that would have been close to the Pliocene high-water mark. As Bailey et al. (2007) point out, however, nobody has been looking for fossils in this area because everyone's attention has been focused on Africa.

Nevertheless, in terms of comparative biological anatomy, we find that a significant number of our unique human modifications, such as loss of pelage, an increase in subcutaneous fat, encephalization, eccrine gland proliferation, multi-pyramidal lobulated kidneys, loss of olfactory ability, voluntary breath control, an improved diving response, larger, more streamlined bodies, concealed ovulation, fat newborns with *vernix caseosa* and well-developed swimming motion reflexes relative to their inability to walk for the first year(s), menopause, and a number of other features, are also found—in some cases exclusively—in aquatic, semi-aquatic, ex-aquatic and littorally adapted species (Hardy 1960, Morgan 1972, Vaneechoutte et al. 2011, Verhaegen 2013). Finally, the Red Sea has no crocodiles, an argument against aquatic evolutionary hypotheses that crops up from time to time (Giles 2010)—an argument that moreover overlooks the rather more significant risks a vulnerable hominin would potentially have faced from the large variety of terrestrial predators that already existed at that time on the African savanna.

Pleistocene Dispersal of Early *Homo*

The Arabian Peninsula is located between southern Africa and eastern China, and this more central location might help to resolve the enduring question of whether *Homo* originated in Africa or Asia (Wood 2011). If the original members of our genus *Homo* had been cut off from the rest of the world in the Red Sea coastal zone during the Pliocene, the drop in sea-levels in the early Pleistocene, ~2.6 Ma, would have opened up coastal or fluvial migration routes in several directions all at once; places where evidence of early *Homo* appears: west into Africa (Nariokotome, Koobi Fora), north into Georgia (Dmanisi), east into Indonesia (Java) and China (Yuanmou).

A skullcap attributed to a juvenile *Homo erectus* from southern Africa, 2.04 Ma (Herries et al. 2020) currently stands as possibly the first of its species. However, older tools, dated to 2.14 Ma, and considered to be related to hominin activity (small flint blades perhaps used to open shellfish) appear in central China/Loess plateau at the site of a paleogeographic river valley (Zhu et al. 2018). A bovid bone with cutmarks, possibly even older than 2.5 Ma (Dennell 1998, Malassé 2016), is known from the Siwaliks Hills (river channels, estuary) along with many more stone tools from the Pabbi Hills, Pakistan 1.9 Ma (Dennell 2004). The earliest full cranial *H. erectus* fossils are known from five individual specimens from Dmanisi, Georgia, at the site of a confluence of two rivers, dated to between 1.85–1.77 Ma (Ferring et al. 2011, Gabunia et al. 2000, Lordkipanidze et al. 2005, Vekua et al. 2002, Vekua and Lordkipanidze 2010) and from southwest China dated to 1.7 Ma (Zhu et al. 2008). The more parsimonious conclusion is that *Homo* originated somewhere more central between southern Africa and eastern China, and closer still to the Indo-Gangetic floodplains of northern India and Pakistan, whereafter members of our nascent genus radiated in multiple directions at different times, corresponding to falls in global sea-levels, *i.e.*, after 2.6 Ma.

Conclusions

Clearly, an overturning of the established paradigm whereby human ancestors arose in Africa from australopithecine ancestors, would have a profound impact on current research, debate and direction. We have not yet reached that point, but we suggest that there is certainly now sufficient evidence to support further research into alternative paradigms.

To summarize, there is an abundance of hominoid fossils with great ape morphology from mid-Miocene Europe (from *Pieralopithecus*, 12.5 Ma, through *Rudapithecus*, 10.0 Ma), a time when the climate was warm, sub-tropical and humid and covered with lush evergreen forest surrounded by lakes, rivers, swamps and marshes. It is possible that orthograde apes may have foraged in or near bodies of water, leading to the evolution of more bipedal modes of locomotion. During the same period no hominoid fossils are known from Africa. This suggests that the *Hominidae* likely evolved during that period in Europe rather than Africa, although this is an ongoing debate for which there is no consensus.

Mid-late Miocene European genera such as *Ouranopithecus* (9.8 Ma), *Anadoluvius* (8.7 Ma) and *Graecopithecus* (7.2 Ma) arguably display characters that could align with the Homininae (African apes, australopithecines and humans). Changes to the environment during the Vallesian suggest that these species may have been traveling more widely across open spaces, perhaps bipedally, and changes in dentition indicate their diet switched from softer to harder foods, possibly aquatic papyrus and sedges. During this period, the lineage leading to *Gorilla* diverged from a common ancestor and may have migrated to Africa.

Furthermore, ichnofossils from Trachilos, Crete (6.0 Ma) indicate that bipedal hominids existed on the island shortly before the onset of the Messinian Salinity Crisis (5.9 Ma), after which time, Crete would have reconnected to the Greek mainland. During the MSC, there was a huge unidirectional migration of European fauna toward Africa, and the LCA of *Pan/Homo* may have been among them. All other European apes appear to have gone extinct.

Intriguingly, the timing of the Zanclean flood (5.33 Ma), which may have severed the only existing land bridge between Europe and Africa (Suez), coincides with the majority of estimates for the divergence date of *Pan/Homo*. This extreme geological event, which marks the beginning of the Pliocene, may explain how an already bipedal last common ancestor (LCA), migrating along the Anatolian coasts southward in search of better conditions during arid Messinian conditions, might have diverged into two distinct lineages 5.3 million years ago. It may plausibly also explain why Africa became colonized by a variety of bipedal hominids after 5.0 Ma, some of which appear increasingly apelike over time, and why *Homo* lacks the PtERV1 retroviral genes that affected all African apes.

Furthermore, the Zanclean Flood/Red Sea hypothesis proposes a link between the last known fossil evidence of hominids in Europe (Trachilos, Crete, 6.0 Ma) and the earliest known evidence of *Homo* from Africa and Asia ca. 2.0 Ma. The Red Sea coast of the Arabian Peninsula with its warm shallow waters and rich marine biodiversity is plausible as a location where proto-hominins might have been isolated for much of the Pliocene (5.3–2.6 Ma). Trapped between the sea and an inhospitable arid desert, they may have become more dependent on nutrient-rich littoral and shallow water resources, gradually adapting to a lifestyle that involved more swimming and shallow diving. Existential challenges would have significantly reduced the population during this time, forcing the survivors through a long bottleneck, which is supported by genetic evidence. This would also explain why today there exist such stark morphological differences between *Pan* and *Homo*, despite their genomes being so similar.

Moreover, the Arabian Peninsula presents a location from where a new genus, *Homo*, could migrate coastally in multiple directions (Africa to the west, Dmanisi, Georgia to the north, Pakistan, China and Indonesia to the east) only once sea levels fell again in the early Pleistocene, thereby giving rise to multiple variations of *Homo erectus/ergaster*. Furthermore, the Red Sea's equidistant location from many of the fossil sites where Pleistocene *Homo* fossils or various attributed stone tools appear almost simultaneously from ~2.0 Ma onwards, would help to answer some of the lingering questions that remain about whether *Homo* evolved in Africa or in Asia and how members of this genus appear to have migrated so far in a relatively short time.

The 'aquatic ape hypothesis' (Hardy 1960, Morgan 1972, Vaneechoutte et al. 2011, Verhaegen 2013), although still controversial, suggests that many of the unique features that exist in *Homo* but not in *Pan* nor in any other primate or terrestrial animal, can best be explained by a semi-aquatic or littoral-foraging phase of adaptation, most probably in a confined coastal area. This hypothesis has long been criticized and is still largely ignored, mainly on the grounds that there exists no fossil evidence for such a scenario. Despite this, an accumulation of evidence from comparative biology clearly points to a long series of anatomical and physiological modifications that can be more parsimoniously explained if we assume that our ancestors occupied a coastal niche for a significant period of time (5.3–2.6 Ma) after their divergence from the *Pan* lineage and prior to the emergence of *Homo* (~2.0 Ma). This hypothesis is supported by genetic evidence suggesting a small ancestral population passed through a long period of isolation in a constrained area, and by the absence of endo-retroviral genes from our genome, which indicates that our ancestors would likely not have been in Africa during the Pliocene.

History has shown us that dismissing alternative hypotheses in order to maintain prevailing paradigms can lead us in the wrong direction, wasting both time and resources. We believe there is sufficient evidence to encourage further research towards a new hypothesis that places the divergence of *Pan/Homo* outside of Africa. We propose that paleoanthropologists should consider investigating specific locations on the Arabian coast of the Red Sea that would have been at, or close to, sea level during the Pliocene (*i.e.*, up to 35 m above current sea-levels) in search of fossils, associated tools, or evidence of early hominin activity. More evidence regarding the impact of the Zanclean Megaflood on the Red Sea and African coastal areas is also required. Renewed objective scrutiny of presumed "hominin" fossil species from Africa is further recommended to bring balance to the question of why australopithecine and habiline species are almost invariably considered to be closer to the human lineage than to extant great ape lineages, which themselves appear to have no fossil ancestors in Africa. Consideration of anatomical features in the *Homo* lineage that are best explained by a period of littoral or semi-aquatic adaptation is long overdue. At the very least, it is time to allow alternative hypotheses some exposure in order to invite further discussion and research.

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Referees

Stephen Munro – National Museum of Australia
stephen.munro@nma.gov.au

Algis Vincent Kuliukas – University of Western Australia
algis.kuliukas@uwa.edu.au

References

Agustí, J., 2007. The Biotic Environments of the Late Miocene Hominids. Pages 979-1010 *in* Henke, W. and I. Tattersall, editors. Handbook of Paleoanthropology. Springer, Berlin, Heidelberg. CrossRef

Agusti J., and S. Moya-Sola. 1990. Mammal extinctions in the Vallesian (Upper Miocene). Pages 425–432 *In* Kauffman E.G.,and Walliser O.H., editors. Extinction Events in Earth History. Springer, Berlin, Heidelberg. CrossRef

Agusti, J., Rook, L., and P. Andrews, editors, 1999. Hominoid Evolution and Climatic Change in Europe, Volume 1: The paleoecology of the Pikermian Biome and the savanna myth. Cambridge University Press, New York. CrossRef

Aiello, L.C., and J.C.K. Wells. 2002. Energetics and the evolution of the genus *Homo*. Annual Review of Anthropology 31: 323–338. CrossRef

Alba, D., and S. Moya-Sola. 2009. The origin of the great-ape-and-human clade (Primates: Hominidae) reconsidered in the light of recent hominoid findings from the Middle Miocene of the Vallès-Penedès Basin (Catalonia, Spain). Paleolusitana 1: 75–83.

Alba, D.M., Fortuny, J., and S. Moyà-Solà. 2010. Enamel thickness in the Middle Miocene great apes Anoiapithecus, Pierolapithecus and Dryopithecus. Proceedings of the Royal Society B: Biological Sciences 277: 2237–2245. CrossRef

Almécija, S., Tallman, M., Alba, D., Pina, M., Moyà-Solà, S., and W.L. Jungers. 2013. The femur of *Orrorin tugenensis* exhibits morphometric affinities with both Miocene apes and later hominins. Nature Communications 4: 2888. CrossRef

Almécija, S., Hammond, A.S., Thompson, N.E., Pugh, K.D., Moyà-Solà, S., and D.M. Alba. 2021. Fossil apes and human evolution. Science 372: eabb4363. CrossRef

Andrews P., 1992. Evolution and environment in the Hominoidea. Nature 17:641–646. CrossRef

Andrews, P., 2020. Last common ancestor of apes and humans: Morphology and environment. Folia Primatologica 91:122–148. CrossRef

Asfaw, B., Gilbert, W.H., Beyene, Y., Hart, W. K., Renne, P. R. Woldegabriel, G., et al. 2002. Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia. Nature 416:317–320. CrossRef

Bailey, G., Flemming, N., King, G., Lambeck, K., Momber, G., Moran, L. et al. 2007. Coastlines, submerged landscapes, and human evolution: The Red Sea Basin and the Farasan Islands. Journal of Island and Coastal Archaeology. 2:127–160. CrossRef

Begun D.R., 1992. Miocene fossil hominids and the chimp-human clade. Science 257(5078):1929–1933. CrossRef

Begun D.R. 2001. African and Eurasian Miocene hominoids and the origins of the Hominidae. Pages 231–253 *in* de Bonis L., Koufos G., and P. Andrews, editors. Hominoid Evolution and Environmental Change in Europe, Volume 2. Cambridge University Press, Cambridge. CrossRef

Begun, D.R., 2005. *Sivapithecus* is east and *Dryopithecus* is west, and never the twain shall meet. Anthropological Science 113: 53–64. CrossRef

Begun, D.R. and J. Gurche. 2006. Planet of the Apes. Scientific American https://www.scientificamerican.com/article/planet-of-the-apes-2006-06/. CrossRef

Begun, D.R., 2009. Dryopithecins, Darwin, de Bonis, and the European origin of the African apes and human clade. Geodiversitas 31(4): 789–816. CrossRef

Begun, D.R., 2010. Miocene Hominids and the origins of the African apes and humans. Annual Review of Anthropology 39: 68–84. CrossRef

Begun, D.R., Nargolwalla, M.C., and L. Kordos. 2012. European Miocene hominids and the origin of the African ape and human clade. Evolutionary Anthropology: Issues, News, and Reviews 21(1): 10–23. CrossRef

Bender, R., Tobias, P.V., and N. Bender. 2012. The Savannah Hypotheses: Origin, reception and impact on paleoanthropology. History and Philosophy of the Life Sciences 34: 147–184.

Benveniste, R., and G. Todaro. 1976. Evolution of type C viral genes: evidence for an Asian origin of Man. Nature 261:101–108. CrossRef

Blanc, P-L. 2002. The opening of the Plio-Quaternary Gibraltar Strait: Assessing the size of a cataclysm. Geodinamica Acta 15: 303–317. CrossRef

Böhme, M., Ilg, A., and M. Winklhofer. 2008. Late Miocene "washhouse" climate in Europe. Earth and Planetary Science Letters 275: 393–401. CrossRef

Böhme, M., Hayfaa, A.A., Prieto, J., Bachtadse, V., and G. Schweigert. 2011. Bio-magnetostratigraphy and environment of the oldest Eurasian hominoid from the Early Miocene of Engelswies (Germany). Journal of Human Evolution 61: 332–339. CrossRef

Böhme, M., Spassov, N., Ebner, M., Geraads, D., Hristova, L., Kirscher, U. et al. 2017. Messinian age and savannah environment of the possible hominin Graecopithecus from Europe. PLOS ONE 12(5): e0177347. CrossRef

Böhme, M., Spassov, N., Fuss, J., Tröscher, A., Deane, A. S., Prieto, J. et al. 2019. A new Miocene ape and locomotion in the ancestor of great apes and humans. Nature 575: 489–493. CrossRef

Böhme, M., Braun, R. and F. Breier. 2020. Ancient bones–Unearthing the astonishing new story of how we became human. Greystone Books, Berkeley.

Böhme, M., Spassov, N., Majidifard, M.R., Gärtner, A., Kirscher, U., Marks, et al. 2021. Neogene hyperaridity in Arabia drove the directions of mammalian dispersal between Africa and Eurasia. Communications Earth and Environment 2: 85. CrossRef

Broadhurst, C.L., Crawford, M., and S. Munro. 2011. Littoral Man and Waterside Woman: The Crucial Role of Marine and Lacustrine Foods and Environmental Resources in the Origin, Migration and Dominance of Homo sapiens. Pages 16-35 *in* Vaneechoutte, M., editor. Was Man More Aquatic in the Past Fifty Years after Alister Hardy–Waterside Hypotheses of Human Evolution. Bentham Science.

Cechova, M., Vegesna, R., Tomaszkiewicz, M., Harris, R.S., Chen, D., Rangavittal, S., et al. 2020. Dynamic evolution of great ape Y chromosomes. Proceedings of the National Academy of Sciences 117(42): 26273–26280. CrossRef

Chase, N., Sui, X., and S. Blair. 2008. Swimming and all-cause mortality risk compared with running, walking, and sedentary habits in men. International Journal of Aquatic Research and Education 2(3): 213–223. CrossRef

Chen, F-C., and W-H. Li. 2001. Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees. American Journal of Human Genetics 68: 444–456. CrossRef

Chung, E. 2018. One Hell of an Impression. CBC News, February 23, 2018. https://newsinteractives.cbc.ca/longform/human-footprints-greece/

Crawford, M.A., Bloom, M., Broadhurst, C. L., Schmidt, W. F., Cunnane, S. C., Galli, et al. 1999. Evidence for the unique function of docosahexaenoic acid during the evolution of the modern hominid brain. Lipids 34: S39–47. CrossRef

Crompton, R.H., Vereecke, E.E., and S.K. Thorpe. 2008. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. Journal of Anatomy 212(4): 501–543 . CrossRef

Crompton, R., Sellers, W., and S. Thorpe. 2010. Arboreality, terrestriality and bipedalism. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365: 3301–3314. CrossRef

Crompton, R.H. 2017. Making the case for possible hominin footprints from the Late Miocene (c. 5.7 Ma) of Crete? Proceedings of the Geologists' Association 128: 692–693. CrossRef

Dainton, M., and G. Macho. 1999. Did knuckle walking evolve twice? Journal of Human Evolution 36: 171–94. CrossRef

Dart, R.A. 1925. *Australopithecus africanus*: The man-ape of South Africa. Nature 115(2884): 195–199. CrossRef

Darwin, C., Kebler, L., and J. Meredith. 1871. The Descent of Man And Selection in Relation to Sex. J. Murray, London. CrossRef

Davies, T.J., Daru, B.H., Bezeng, B.S. Charles-Dominque, T., Hempson, G.P., Kabongo, R.M. et al. 2020. Savanna tree evolutionary ages inform the reconstruction of the paleoenvironment of our hominin ancestors. Scientific Reports 10: 12430. CrossRef

Deane, A.S., Nargolwalla, M.C., Kordos, L., and D.R. Begun. 2013. New evidence for diet and niche partitioning in *Rudapithecus* and *Anapithecus* from Rudabánya, Hungary. Journal of Human Evolution 65(6): 704–714. CrossRef

de Bonis, L., Bouvrain, G., Geraads, D., and G. Koufos. 1990. New hominid skull material from the late Miocene of Macedonia in Northern Greece. Nature 345: 712–714. CrossRef

de Bonis, L., and G. Koufos. 1994. Our ancestors' ancestor: *Ouranopithecus* is a Greek link in human ancestry. Evolutionary Anthropology: Issues, News, and Reviews 3: 75–83. CrossRef

de Bonis, L., and G. Koufos. 2004. *Ouranopithecus* et la date de séparation des hominoïdes modernes. Comptes Rendus Palevol 3: 257–264. CrossRef

de Bonis, L., and G. Koufos. 2014. First discovery of postcranial bones of *Ouranopithecus macedoniensis* (Primates, Hominoidea) from the late Miocene of Macedonia (Greece). Journal of Human Evolution 74: 21–36. CrossRef

de Bonis, L., and J. Melentis. 1977. Les primates hominoides du Vallésien de Macédoine (Grèce). Étude de la machoire inférieure. Geobios 10 (6): 849–855. CrossRef

de la Vega, E., Chalk, T.B., Wilson, P.A., Bysani, R.P., and G.L. Foster. 2020. Atmospheric CO_2 during the Mid-Piacenzian Warm Period and the M2 glaciation. Scientific Reports 10: 11002. CrossRef

deMenocal, P.B. 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. Earth and Planetary Science Letters 220 (1-2): 3–24. CrossRef

Dennell, R.W. 1998. Grasslands, Tool-Making and the Hominid Colonization of Southern Asia: A Reconsideration. Pages 280–303 *in* Petraglia, M.D. and R. Korisettar, editors. Early Human Behaviour in Global Context. Routledge, London.

Dennell, R., 2004. Hominid dispersals and Asian biogeography during the lower and early middle Pleistocene, c. 2.0-0.5 Mya. Asian Perspectives 43: 205–226. CrossRef

Dennell, R., and W. Roebroeks. 2006. An Asian perspective on early human dispersal from Africa. Nature 438: 1099–104. CrossRef

Dickens, G.R., and R.M. Owen. 1994. Late Miocene-early Pliocene manganese redirection in the central Indian Ocean: Expansion of the Intermediate Water oxygen minimum zone. Paleoceanography 9(1): 169–181. CrossRef

Diogo, R. 2018. First detailed anatomical study of Bonobos reveals intra-specific variations and exposes just-so stories of human evolution, bipedalism, and tool use. Frontiers in Ecology and Evolution 6: 53. CrossRef

Doran, M.D., and A. McNeilage. 1998. Gorilla ecology and behavior. Evolutionary Anthropology 6: 120–130. CrossRef

Dowsett, H.J., Robinson, M.M., Stoll, D.K., Foley, K.M., Johnson, A.L.A., Williams, M., et al. 2013. The PRISM (Pliocene palaeoclimate) reconstruction: Time for a paradigm shift. Philosophical Transactions of the Royal Society A 371: 20120524. CrossRef

Du, A., and Z. Alemseged. 2019. Temporal evidence shows *Australopithecus sediba* is unlikely to be the ancestor of *Homo*. Science Advances 5(5). CrossRef

Duda, P., and J. Zrzavý. 2013. Evolution of life history and behavior in Hominidae: Towards phylogenetic reconstruction of the chimpanzee-human last common ancestor. Journal of Human Evolution 65(4): 424–446. CrossRef

Dwyer, G.S., and M.A. Chandler. 2009. Mid-Pliocene sea level and continental ice volume based on coupled benthic Mg/Ca palaeotemperatures and oxygen isotopes. Philosophical Transactions of the Royal Society A. 367: 157–168. CrossRef

Eronen, J.T., and G.E. Rössner. 2007. Wetland paradise lost: Miocene community dynamics in large herbivorous mammals from the German Molasse Basin. Evolutionary Ecology Research 9: 471–494

Ferguson, W.W. 1989. A new species of the genus *Australopithecus* (Primates-Hominidae) from the Plio/Pleistocene deposits West of Lake Turkana in Kenya. Primates 30: 223–232. CrossRef

Ferring, R., Oms, O., Agustí, J., Berna, F., Nioradze, M., Shelia, T., et al. 2011. Earliest human occupations at Dmanisi (Georgian Caucasus) dated to 1.85–1.78 Ma. Proceedings of the National Academy of Science 108(26):10432–10436. CrossRef

Filler, A.G. 2007. Homeotic evolution in the Mammalia: Diversification of Therian axial seriation and the morphogenetic basis of human origins. PLoS ONE 2(10): e1019. CrossRef

Fuss, J., Prieto, J., and M. Böhme. 2015. Revision of the boselaphin bovid *Miotragocerus monacensis* Stromer, 1928 (Mammalia, Bovidae) at the Middle to Late Miocene transition in Central Europe. Neues Jahrbuch für Geologie und Paläontologie–Abhandlungen 276(3): 229–265. CrossRef

Fuss, J., Spassov, N., Begun, D.R., and M. Böhme. 2017. Potential hominin affinities of *Graecopithecus* from the Late Miocene of Europe. PLoS ONE 12(5): e0177127. CrossRef

Fuss, J., Spassov, N., Böhme, M., and D.R. Begun. 2018. Response to Benoit and Thackeray (2017): A cladistic analysis of *Graecopithecus*. South African Journal of Science. 114(5-6): a0267. CrossRef

Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher, C. C. 3rd, Ferring, R., Justus, A., et al. 2000. Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: taxonomy, geological setting, and age. Science 288(5468): 1019–1025. CrossRef

Gani, M., and N. Gani. 2011. River-margin habitat of *Ardipithecus ramidus* at Aramis, Ethiopia 4.4 million years ago. Nature Communications 2: 602. CrossRef

Garcia-Castellanos, D., Estrada, F., Jiménez-Munt, I., and C. Gorini. 2009. Catastrophic flood of the Mediterranean after the Messinian salinity crisis. Nature 462: 778–781. CrossRef

Garcia-Castellanos, D., Micallef, A., Estrada, F., Camerlenghi, A., Ercilla, G., Periáñez, R., et al. 2020. The Zanclean megaflood of the Mediterranean–Searching for independent evidence. Earth-Science Reviews 201: 103061. CrossRef

Gargani, J., Moretti, I., and J. Letouzey. 2008. Evaporite accumulation during the Messinian Salinity Crisis: The Suez Rift case. Geophysical Research Letters 35: L02401. CrossRef

Gierliński, G.D., Niedźwiedzki, G., Lockley, M.G., Athanassiou, A., Fassoulas, C., Dubicka, Z., et al. 2017. Possible hominin footprints from the late Miocene (c. 5.7 Ma) of Crete? Proceedings of the Geologists' Association 128(5-6): 697–710. CrossRef

Giles, J. 2010. Naked love: The evolution of human hairlessness. Biological Theory 5(4): 326–336. CrossRef

Glazko, G.V., and M. Nei. 2003. Estimation of divergence times for major lineages of primate species. Molecular Biology and Evolution 20(3): 424–434. CrossRef

Gumert, M.D., and S. Malaivijitnond. 2012. Marine prey processed with stone tools by Burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. American Journal of Physical Anthropology 149(3): 447–457. CrossRef

Harcourt-Smith, W.E., and L.C. Aiello. 2004. Fossils, feet and the evolution of human bipedal locomotion. Journal of Anatomy 204: 317–431. CrossRef

Hardy, A. 1960. Was man more aquatic in the past? New Scientist 7: 642–645.

Harper, C.M., Ruff, C.B., and A.D. Sylvester. 2021. Calcaneal shape variation in humans, nonhuman primates, and early hominins. Journal of Human Evolution 159: 103050. CrossRef

Harpending, H.C., Batzer, M.A, Gurven, M., Jorde, L.B., Rogers, A.R., and S.T. Sherry. 1998. Genetic traces of ancient demography. Proceedings of the National Academy of Science USA 95(4): 1961–1967. CrossRef

Harrison, T.S, and T. Harrison. 1989. Palynology of the late Miocene *Oreopithecus*-bearing lignite from Baccinello, Italy. Palaeogeography, Palaeoclimatology, Palaeoecology 76(1-2): 45–65. CrossRef

Hawks, J., Hunley, K., Lee, S.H., and M. Wolpoff. 2000. Population bottlenecks and Pleistocene human evolution. Molecular Biology and Evolution 17(1): 2–22. CrossRef

Heizmann, E.P.J., and D.R. Begun. 2001. The oldest Eurasian hominoid. Journal of Human Evolution 41(5): 463–481. CrossRef

Herries, A., Martin, J.M., Leece, A.B., Adams, J.W., Boschian, G., Joannes-Boyau, R., et al. 2020. Contemporaneity of *Australopithecus*, *Paranthropus*, and early *Homo erectus* in South Africa. Science 368(6486): eaaw7293.CrossRef

Hill, A., and S. Ward. 1998. Origin of the Hominidae: The record of Africa large hominoid evolution between 14 My and 4 My. American Journal of Biological Anthropology 31: 49–83. CrossRef

Horai, S., Hayasaka, K., Kondo, R., Tsugane, K., and N. Takahata. 1995. Recent African origin of modern humans revealed by complete sequences of hominoid mitochondrial DNAs. Proceedings of the National Academy of Science USA 92(2): 532–536. CrossRef

Hughes, J.F., Skaletsky, H., Pyntikova, T., Graves, T.A., van Daalen, S.K., Minx, P.J., et al. 2010. Chimpanzee and human Y chromosomes are remarkably divergent in structure and gene content. Nature 463(7280): 536–539. CrossRef

Hunt, K.D.D. 1996. The postural feeding hypothesis: An ecological model for the evolution of bipedalism. South African Journal of Science 92(2): 77–90.

Hutchinson, R.W., and G.G. Engels. 1970. A discussion on the structure and evolution of the Red Sea and the nature of the Red Sea, Gulf of Aden and Ethiopia Rift Junction; Tectonic significance of regional geology and evaporite lithofacies in Northeastern Ethiopia. Philosophical Transactions of the Royal Society of London, Series A, Mathematical and Physical Sciences 267(1181): 313–329. CrossRef

IMIM (Hospital del Mar Medical Research Institute). 2021. Higher levels of omega-3 acids in the blood increases life expectancy by almost five years: A 1% increase in this substance in the blood is associated with a change in mortality risk similar to that of quitting smoking. ScienceDaily.sciencedaily.com/releases/2021/07/210722113004

Ioannidou, M., Koufos, G., de Bonis, L., and K. Harvati. 2019. A new three-dimensional geometric morphometrics analysis of the *Ouranopithecus Macedoniensis* cranium (Late Miocene, Central Macedonia, Greece). American Journal of Physical Anthropology170(2): 295–307. CrossRef

Johanson, D.C., White, T.D., and Coppens. 1978. A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of Eastern Africa. Kritlandia, The Cleveland Museum of Natural History.

Johanson, D.C., and M. Edey. 1981. Lucy: The beginnings of humankind. Simon & Schuster, New York.

Kaessmann, H., Wiebe, V., Weiss, G., and S. Pääbo. 2001. Great ape DNA sequences reveal a reduced diversity and an expansion in humans. Nature Genetics 27: 155–156 . CrossRef

Kaiser, S.M., Malik, H.S., and M. Emerman. 2007. Restriction of an extinct retrovirus by the human Trim5α antiviral protein. Science 316(5832): 1756–1758. CrossRef

Kaiser S.M., Malik, H.S., and M. Emerman. 2007b. Supporting online material from: Restriction of an Extinct Retrovirus by the Human Trim5α Antiviral Protein. Science 316(5832): 1756–1758. CrossRef

Kassab, A.S., and S.G. Ahmed. 1994. Miocene-Pleistocene macrofossils from the coastal plain between Marsa Alam and Ras Banas, Red Sea, Egypt. Bulletin Faculty of Science, Assiut University 23: 451–485.

Kimbel, W.H., and B. Villmoare. 2016. From *Australopithecus* to *Homo*: The transition that wasn't. Philosophical Transactions of the Royal Society B 371: 20150248. CrossRef

Kirscher, U., El Atfy, H., Gärtner, A., Dallanave, E., Munz, P., Niedźwiedzki, G., et al. 2021. Age constraints for the Trachilos footprints from Crete. Scientific Reports 11: 19427. CrossRef

Kivell, T., and D. Schmitt. 2009. Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. Proceedings of the National Academy of Sciences of the United States of America 106: 14241–14246. CrossRef

Kleindienst, M.R., Burton, F.D., and A. Kortlandt. 1975. On new perspectives on ape and human evolution. Current Anthropology 16(4): 644–651. CrossRef

Köhler, M., and S. Moyà-Solà. 1997. Ape-like or hominid-like? The positional behavior of *Oreopithecus bambolii* reconsidered. Proceedings of the National Academy of Sciences 94(21): 11747–11750. CrossRef

Kora, M., and Z. Abdel-Fattah. 2000. Pliocene and Plio-Pleistocene macrofauna from the Red Sea coastal plain (Egypt): Biostratigraphy and biogeography. Geologica et Palaeontologica 34: 219–235.

Kordos, L., and D.R. Begun. 2002. Rudabánya: A late miocene subtropical swamp deposit with evidence of the origin of the African apes and humans. Evolutionary Anthropology 11: 45–57. CrossRef

Koufos, G., and L. de Bonis. 2006. New material of *Ouranopithecus macedoniensis* from late Miocene of Macedonia (Greece) and study of its dental attrition. Geobios 39: 223–243. CrossRef

Krijgsman, W., Hilgen, F., Raffi, I., Sierro, F.J., and D.S. Wilson. 1999. Chronology, causes and progression of the Messinian salinity crisis. Nature 400: 652–655. CrossRef

Kuliukas A. 2002. Wading for food the driving force of the evolution of bipedalism? Nutrition and Health 16(4): 267–289. CrossRef

Kuliukas, A.V., Milne, N., and P. Fournier. 2009. The relative cost of bent-hip bent-knee walking is reduced in water. Homo 60(6): 479–488. CrossRef

Kumar, S., Filipski, A., Swarna, V., Walker, A., and S.B. Hedges. 2005. Placing confidence limits on the molecular age of the human-chimpanzee divergence. Proceedings of the National Academy of Sciences USA 102(52):18842–18847. CrossRef

Kunimatsu, Y., Nakatsukasa, M., Sawada, Y., Sakai, T., Hyodo, M., Hyodo, H., et al. 2007. A new Late Miocene great ape from Kenya and its implications for the origins of African great apes and humans. Proceedings of the National Academy of Sciences USA 104(49): 19220–19225. CrossRef

Lamarck J.B. 1809. Zoological philosophy: An exposition with regard to the natural history of Animals. Bill Huth Publishers, Rosamond, CA.

Leakey, M.D. 1981. Discoveries at Laetoli in Northern Tanzania. Proceedings of the Geologists' Association 92(2): 81–86. CrossRef

Leakey, M.G., Feibel, C.S., Bernor, R.L., Harris, J.M., Cerling, T.E., Stewart, K.M., et al. 1996. Lothagam: A record of faunal change in the late Miocene of East Africa. Journal of Vertebrate Paleontology 16(3): 556–570. CrossRef

Liebenberg, L. 2006. Persistence hunting by modern hunter-gatherers. Current Anthropology 47: 1017. CrossRef

Lordkipanidze, D., Vekua, A., Ferring, R., Rightmire, G. P., Agusti, J., Kiladze, G., et al. 2005. Anthropology: the earliest toothless hominin skull. Nature 434(7034): 717–718. CrossRef

Lutz, H., Engel, T., Lischewsky, B., and A. Berg. 2017. A new great ape with startling resemblances to African members of the hominin tribe, excavated from the Mid-Vallesian Dinotheriensande of Eppelsheim. CARTA. First report.

Young, N., and L. MacLatchy. 2004. The phylogenetic position of *Morotopithecus*. Journal of Human Evolution 46: 163–184. CrossRef

Mailund, T., Halager, A.E., Westergaard, M., Dutheil, J.Y., Munch, K., Anderson, L.N., et al. 2012. A new isolation with migration model along complete genomes infers very different divergence processes among closely related Great Ape species. PLOS Genetics 8(12): e1003125. CrossRef

Malassé, A.D. 2016. The first Indo-French prehistorical mission in Siwaliks and the discovery of anthropic activities at 2.6 million years. Comptes Rendus Palevol 15(3-4): 281–294. CrossRef

McBrearty, S., and N. Jablonski. 2005. First fossil chimpanzee. Nature 437: 105–108. CrossRef

McNutt, E.J., Zipfel, B., and J.M. DeSilva. 2018. The evolution of the human foot. Evolutionary Anthropology 27(5): 197–217. CrossRef

Meldrum, J., and E. Sarmiento. 2018. Comments on possible Miocene hominin footprints. Proceedings of the Geologists' Association 129: 577–580. CrossRef

Merceron, G., Blondel, C., Viriot, L., Koufos, G. D., and L. de Bonis. 2007. Dental microwear analysis of bovids from the Vallesian (late Miocene) of Axios Valley in Greece: Reconstruction of the habitat of *Ouranopithecus macedoniensis* (Primates, Hominoidea). Geodiversitas 29(3): 421–433.

Messerli, F.H., Hofstetter, L., Syrogiannouli, L., Rexhaj, E., Siontis, G.C.M., Seiler, C., et al. 2021. Sodium intake, life expectancy, and all-cause mortality. European Heart Journal 42(21): 2103–2112. CrossRef

Meyer, M.R., Jung, J.P., Spear, J.K., Araiza, I. Fx., Galway-Witham, J., Williams, S. A., 2023. Knuckle-walking in *Sahelanthropus*? Locomotor inferences from the ulnae of fossil hominins and other hominoids. Journal of Human Evolution 179: 103355. CrossRef

Miga, K.H. 2017. Chromosome-specific centromere sequences provide an estimate of the ancestral chromosome 2 fusion event in hominin genomes. Journal of Heredity 108(1): 45–52. CrossRef

Mitchell, N., Shi, W., Yousif, I., and I. Stewart. 2020. Reconstructing the level of the central Red Sea evaporites at the end of the Miocene. Basin Research 33: 1266–1292. CrossRef

Morgan, E. 1972. The Descent of Woman. Souvenir Press.

Morimoto, N., Zollikofer, C.P., and M.S. Ponce de León. 2012. Shared human-chimpanzee pattern of perinatal femoral shaft morphology and its implications for the evolution of hominin locomotor adaptations. PLoS ONE 7(7): e41980. CrossRef

Morton, D.J. 1926. Evolution of man's erect posture (preliminary report). Journal of Morphology 43: 147–179. CrossRef

Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., and J. Galindo. 2004. *Pierolapithecus catalaunicus*, a new middle Miocene Great Ape from Spain. Science 306(5700): 1339–1344. CrossRef

Moyà-Solà, S., Alba, D.M., Almécija, S., Casanovas-Vilar, I., Köhler, M., Esteban-Trivigno, S., et al. 2009. A unique Middle Miocene European hominoid and the origins of the great ape and human clade. Proceedings of the National Academy of Sciences 106 (24): 9601–9606. CrossRef

Nargolwalla, M.C. 2009. Eurasian middle and late Miocene hominoid paleobiogeography and the geographic origins of the Homininae. PhD Dissertation, University of Toronto.

Odent, M. 2017. The Birth of Homo, the Marine Chimpanzee: When the Tool Becomes the Master. Pinter & Martin Limited.

Oxnard, C. 1975. The place of the *Australopithecines* in human evolution: Grounds for doubt? Nature 258: 389–395. CrossRef

Patterson, N., Richter, D., Gnerre, S., Lander, E.S., and D. Reich. 2006. Genetic evidence for complex speciation of humans and chimpanzees. Nature 441: 1103–1108. CrossRef

Perez-Caballero, D., Soll, S.J., and P.D. Bieniasz. 2008. Evidence for restriction of ancient primate Gammaretroviruses by APOBEC3 but not TRIM5α proteins. PLOS Pathogens 4 (10): e1000181. CrossRef

Senut, B., Pickford, M., Gommery, D., and L. Ségalen. 2017. Palaeoenvironments and the origin of hominid bipedalism. Historical Biology 30: 1–13. CrossRef

Pilbeam, D.R., and E.L. Simons. 1965. Some problems of hominid classification. American Scientist 53(2): 237–259. CrossRef

Polavarapu, N., Bowen, N.J., and J.F. McDonald. 2006. Identification, characterization and comparative genomics of chimpanzee endogenous retroviruses. Genome Biology 7(6): R51. CrossRef

Popadin, K., Gunbin, K., Peshkin, L., Annis, S., Fleischmann, Z., Franco, M., et al. 2022. Mitochondrial pseudogenes suggest repeated inter-species hybridization among direct human ancestors. Genes 13(5): 810. CrossRef

Poulakakis, N., Lymberakis, P., Valakos, E., Pafilis, P., Zouros, E., and M. Mylonas. 2005. Phylogeography of Balkan wall lizard (*Podarcis taurica*) and its relatives inferred from mitochondrial DNA sequences. Molecular Ecology 14(8): 2433–2443. CrossRef

Prang, T.C. 2019. The African ape-like foot of *Ardipithecus ramidus* and its implications for the origin of bipedalism. eLife 8: e44433 CrossRef

Rak, Y., Ginzburg, A., and E. Geffen. 2007. Gorilla-like anatomy on *Australopithecus afarensis* mandibles suggests *Au. afarensis* link to robust Australopiths. Proceedings of the National Academy of Sciences USA 104(16): 6568–6572. CrossRef

Rein, T.R., Harrison, T., Carlson, K.J., and K. Harvati. 2017. Adaptation to suspensory locomotion in *Australopithecus sediba*. Journal of Human Evolution 104: 1–12. CrossRef

Rodman, P.S., and H.M. McHenry. 1980. Bioenergetics and the origin of hominid bipedalism. American Journal of Physical Anthropology 52(1): 103–106. CrossRef

Rogers, J., and R. Gibbs. 2014. Comparative primate genomics: Emerging patterns of genome content and dynamics. Nature Reviews, Genetics 15: 347–359. CrossRef

Rosen, K.H., Jones, C.E., and J.M. DeSilva. 2022. Bipedal locomotion in zoo apes: Revisiting the hylobatian model for bipedal origins. Evolutionary Human Sciences 4: e12. CrossRef

Sant, K., Palcu, D.V., Turco, E., Di Stefano, A., Baldassini, N., Kouwenhoven, T., et al. 2019. The mid-Langhian flooding in the eastern Central Paratethys: Integrated stratigraphic data from the Transylvanian Basin and SE Carpathian Foredeep. International Journal of Earth Sciences (Geol Rundsch) 108: 2209–2232. CrossRef

Schultz, A.H. 1925. Embryological evidence of the evolution of man. Journal of the Washington Academy of Sciences 15(12): 247–263.

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., and Y. Coppens. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). Comptes Rendus de l'Académie des Sciences – Series IIA – Earth and Planetary Science 332(2): 137–144. CrossRef

Senut, B. 2003. Palaeontological approach to the evolution of hominid bipedalism: the evidence revisited. Cour Forsch-Inst Senkenberg 243: 125–134.

Senut, B. 2016. Morphology and environment in some fossil Hominoids and Pedetids (Mammalia). Journal of Anatomy 228: 700–715. CrossRef

Sevim-Erol, A., Begun, D.R., Yavuz, A. Tarhan, E., Sönmez Sözer, C., Mayda, S., et al. 2023. A new ape from Türkiye and the radiation of late Miocene hominines. Communications Biology 6: 842. CrossRef

Shibata, H. 2001. Nutritional factors on longevity and quality of life in Japan. Journal of Nutrition, Health, and Aging 5(2): 97–102.

Simpson, S.W., Latimer, B., and C.O. Lovejoy. 2018. Why do knuckle-walking African apes knuckle-walk? The Anatomical Record 301: 496–514. CrossRef

Spassov, N., Geraads, D., Hristova, L., Markov, G.N., Merceron, G., Tzankov, T., et al. 2012. A hominid tooth from Bulgaria: The last pre-human hominid of continental Europe. Journal of Human Evolution 62(1): 138–145. CrossRef

Stankiewicz, P. 2016. One pedigree we all may have come from—did Adam and Eve have the chromosome 2 fusion? Molecular Cytogenetics 9: 72. CrossRef

Stauffer, R.L., Walker, A., Ryder, O.A., Lyons-Weiler, M., and S.B. Hedges. 2001. Human and ape molecular clocks and constraints on paleontological hypotheses. Journal of Heredity 92(6): 469–474. CrossRef

Stewart, C.B., and T.R. Disotell. 1998. Primate evolution—in and out of Africa. Current Biology 8(16): R582-R588. CrossRef

Suwa, G., Kono, R.T., Katoh, S. Asfaw, B., and Y. Beyene. 2007. A new species of great ape from the late Miocene epoch in Ethiopia. Nature 448: 921–924. CrossRef

Suwa, G., Sasaki, T., Semaw, S., Rogers, M.J., Simpson, S.W., Kunimatsu, Y., et al. 2021. Canine sexual dimorphism in *Ardipithecus ramidus* was nearly human-like. Proceedings of the National Academy of Science 118(49): e2116630118. CrossRef

Suwa, G., Asfaw, B., Kono, R.T., Kubo, D., Lovejoy, C. O., and T.D. White. 2009. The *Ardipithecus ramidus* skull and its implications for hominid origins. Science 326(5949): e68. CrossRef

Tallman, M. 2016. Shape ontogeny of the distal femur in the Hominidae with implications for the evolution of bipedality. PLoS ONE 11(2): e0148371. CrossRef

Thorpe, S.K.S., McClymont, J.M., and R.H. Crompton. 2014. The arboreal origins of human bipedalism. Antiquity 88: 906–926. CrossRef

Tobias, P.V. 1995. Daryll Forde Memorial Lecture. University College London, UK. *Cited in*: Vaneechoutte, M. 2000. Report of the Symposium 'Water and Human Evolution'. Human Evolution 15(3-4): 243–251. CrossRef

Tobias, P.V. 1998. Ape-like *Australopithecus* after seventy years: Was it a hominid? The Journal of the Royal Anthropological Institute 4(2): 283–308. CrossRef

Tobias, P.V. 2011. Revisiting water and hominin evolution. Pages 3–15 *In* Vaneechoutte, M., editor. Was Man More Aquatic in the Past? Fifty Years after Alister Hardy. Bentham Books. CrossRef

Vaks, A., Woodhead, J., Bar-Matthews, M., Ayalon, A., Cliff, R.A., Zilberman, T., et al. 2013. Pliocene-Pleistocene climate of the northern margin of Saharan-Arabian Desert recorded in speleothems from the Negev Desert, Israel. Earth and Planetary Science Letters 368: 88–100. CrossRef

van Hinsbergen, D. J. J., and J. Meulenkamp. 2006. Neogene supradetachment basin development on Crete (Greece) during exhumation of the South Aegean core complex. Basin Research 18(1): 103–124. CrossRef

van Hinsbergen, D.J.J., and S.M. Schmid. 2012. Map view restoration of Aegean-West Anatolian accretion and extension since the Eocene. Tectonics 31(5): TC5005. CrossRef

Vanarsdale, A. 2020. Human Fossil Record and Classification. Bookbaby, Philadelphia, USA.

Vaneechoutte, M., Kuliukas, A., and M. Verhaegen, editors. 2011. Was Man More Aquatic in the Past? Fifty years after Alister Hardy, Waterside Hypotheses of Human Evolution. Bentham E Books. CrossRef

Vaneechoutte, M., Mansfield, F., Munro, S., and M. Verhaegen. 2024. Have we been barking up the wrong ancestral tree? Australopithecines are probably not our ancestors. Nature Anthropology 2(1): 10007. CrossRef

Vekua, A., Lordkipanidze, D., Rightmire, G.P., Agusti, J., Ferring, R., Maisuradze, G., et al. 2002. A new skull of early *Homo* from Dmanisi, Georgia. Science 297 (5578): 85–89. CrossRef

Vekua, A., and D. Lordkipanidze. 2010. Dmanisi (Georgia) - Site of discovery of the oldest hominid in Eurasia. Bulletin of the Georgian National Academy of Sciences 4(2): 158–164.

Venkadesan, M., Yawar, A., Eng, C.M., Dias, M.A., Singh, D.K., Tommasini, S.M., et al. 2020. Stiffness of the human foot and evolution of the transverse arch. Nature 579: 97–100. CrossRef

Ventura, M., Catacchio, C., Sajjadian, S., Vives, L., Sudmant, P., Marques-Bonet, T., et al. 2012. The evolution of African great ape subtelomeric heterochromatin and the fusion of human chromosome 2. Genome research 22: 1036–1049. CrossRef

Venugopal, V., and K. Gopakumar. 2017. Shellfish: Nutritive value, health benefits, and consumer safety. Comprehensive Reviews in Food Science and Food Safety 16: 1219–1242. CrossRef

Verhaegen, M.J.B. 1990. African ape ancestry. Human Evolution 5: 295–297. CrossRef

Verhaegen, M.J.B. 1994. Australopithecines: Ancestors of the African Apes? Human Evolution 9: 121–139. CrossRef

Verhaegen, M.J.B. 1996. Morphological distance between australopithecine, human and ape skulls. Human Evolution 11: 35–41. CrossRef

Verhaegen, M.J.B. 2013. The Aquatic Ape evolves: Common misconceptions and unproven assumptions about the so-called Aquatic Ape Hypothesis. Human Evolution 28: 237–266.

Verhaegen, M., Puech P-F, and S. Munro. 2002. Aquarboreal ancestors? Trends in Ecology & Evolution 17(5): 212–217. CrossRef

Verhaegen, M.J.B., Puech, P-F., Munro, S., and M. Vaneechoutte. 2011. Early Hominoids: Orthograde aquarboreals in flooded forests? Pages 67 – 81 *In* Vaneechoutte, M., editor. Was Man More Aquatic in the Past? Fifty Years after Alister Hardy. Bentham ebooks. CrossRef

von Koenigswald, G.H.R. 1972. Ein Unterkiefer eines fossilen Hominoiden aus dem Unterpliozän Griechenlands. Proceedings of the Koninklijke

Nederlandse Akademie van Wetenschappen Series B. 75(5): 385–394.

Ward, C.V., Leakey, M.G., and A. Walker. 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. Journal of Human Evolution 41(4): 255–368. CrossRef

Ward, C.V., Hammond, A.S., Plavcan, J.M., and D.R. Begun. 2019. A late Miocene hominid partial pelvis from Hungary. Journal of Human Evolution 136: 102645. CrossRef

Wheeler, P.E. 1985. The loss of functional body hair in man: The influence of thermal environment, body form and bipedality. Journal of Human Evolution 14: 23–28. CrossRef

White, T., Ambrose, S., Suwa, G., Su, D., DeGusta, D., Bernor, R., et al. 2009. Macrovertebrate Paleontology and the Pliocene Habitat of *Ardipithecus ramidus*. Science 326(5949): 67–93. CrossRef

White, T.D., Lovejoy, C.O., Asfaw, B., Carlson, J.P., and G. Suwa. 2015. Neither chimpanzee nor human, *Ardipithecus* reveals the surprising ancestry of both. Proceedings of the National Academy of Science USA 112(16): 4877–4884. CrossRef

WoldeGabriel, G., Haile-Selassie, Y., Renne, P.R., Hart, W.K., Ambrose, S.H., Asfaw, B. et al. 2001. Geology and palaeontology of the Late Miocene Middle Awash valley, Afar rift, Ethiopia. Nature 412(6843): 175–178. CrossRef

Woldegabriel, G., Ambrose, S., Barboni, D., Raymonde, B., Bremond, L., Currie, B., et al. 2009. The geological, isotopic, botanical, invertebrate, and lower vertebrate surroundings of *Ardipithecus ramidus*. Science 326: e65. CrossRef

Wolpoff, M.H., Hawks, J., Senut, B., Pickford, M., and J. Ahern. 2006. An ape or the ape: Is the Toumaï Cranium TM 266 a Hominid? PaleoAnthropology 36-50.

Wood, B. 2011. Did early *Homo* migrate "out of" or "in to" Africa? Proceedings of the National Academy of Science USA 108(26): 10375–10376. CrossRef

Wood, B., and M. Collard. 1999. The human genus. Science 284(5411): 65–71. CrossRef

Wood, B., and T. Harrison. 2011. The evolutionary context of the first Hominins. Nature 470: 347–352. CrossRef

Yamori, Y., Liu, L., Mori, M., Sagara, M., Murakami, S., Nara, Y., et al. 2009. Taurine as the nutritional factor for the longevity of the Japanese revealed by a world-wide epidemiological survey. Advances in Experimental Medicine and Biology 643: 13–25. CrossRef

Yang, Z. 2002. Likelihood and Bayes estimation of ancestral population sizes in hominoids using data from multiple loci. Genetics 162(4): 1811–1823. CrossRef

Yohn, C.T., Jiang, Z., McGrath, S.D., Hayden, K.E., Khaitovich P., Johnson, M.E., et al. 2005. Lineage-specific expansions of retroviral insertions within the genomes of African Great Apes but not humans and orangutans. PLOS Biology 3(4): e110. CrossRef

Zachariasse, W., and L. Lourens. 2022. About the age and depositional depth of the sediments with reported bipedal footprints at Trachilos (NW Crete, Greece). Scientific Reports 12: 18471. CrossRef

Zhu, R.X., Potts, R., Pan, Y.X., Yao, H.T., Lü, L.Q., Zhao, X., et al. 2008. Early evidence of the genus *Homo* in East Asia. Journal of Human Evoultion 55(6): 1075–1085. CrossRef

Zhu, Z., Dennell, R., Huang, W., Wu, Y., Qiu, S., Yang, S., et al. 2018. Hominin occupation of the Chinese Loess Plateau since about 2.1 million years ago. Nature 559: 608–612. CrossRef