

Last Common Ancestor of Apes and Humans: Morphology and Environment

Peter Andrews

Natural History Museum, London, UK

Keywords

Fossil ape · Chimpanzee · Palaeoanthropology · Terrestrial behaviour · Woodland · Environment · Palaeoecology · Miocene · Pliocene · Hominin

Abstract

For much of their history, fossil apes retained many monkey-like features in posture and body structure. They also occupied a range of habitats, of which tropical forest was only a part, and there is evidence of increasing terrestriality in the fossil record as it is known at present (2019). In the early Miocene (18–20 million years ago, Ma), fossil apes were pronograde arboreal slow climbers, associated mainly with forest environments and deciduous woodland and with some indications of terrestrial behaviour, particularly the larger species. Their hands had long and opposable thumbs, and the phalanges were curved. In the early middle Miocene (15–16 Ma), apes were still monkey-like in body plan and posture and were associated almost entirely with non-forest, deciduous woodland habitats, with increasing evidence of terrestrial adaptations. Hand proportions remained the same. Towards the end of the middle Miocene (12 Ma), some fossil ape species had broadened chests, long clavicles, medial torsion of the humerus and re-positioning of the scapula to the back. These adaptations may have been linked with more upright posture, as in the living apes, but unlike them, the hand phalanges were short, robust and less curved, and the thumb remained long. Associated environments were deciduous woodland rather than forest. This body plan was retained in part in some later Miocene apes (10 Ma), some of which also had more elongated limbs and hands (thumb length not known), and hind limbs modified for greater flexibility, analogous with the orang utan. Associated environments were subtropical deciduous woodlands and subtropical evergreen laurophyllous woodland in southern Europe. Other late Miocene European apes had adaptations for living on the ground, and some of these also shared characters of the skull with orang utans. They are associated with more open deciduous woodland habitats. This body plan and environment were retained in the early hominin, *Ardipithecus ramidus*, but with a more robust postcranial skeleton and

incipient bipedalism. Based on shared character states in fossil apes, living apes and early hominins, 27 characters are identified as probable attributes of the last common ancestor (LCA) of apes and humans. The likely environment of the LCA was tropical deciduous woodland with some evidence of more open habitats, and this remained unchanged in the transition from apes to early hominins.

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Introduction

There are three ways by which the last common ancestor (LCA) of apes and humans can be reconstructed: one is to work backwards from the known fossil history of humans (and ideally of chimpanzees except they have almost no known fossil history); second is to work forwards from the known history of fossil apes, spanning the Miocene; and third is to work with the end results of evolution at the present time, comparing living apes and humans. Descriptions and interpretations of the first of these, the hominin fossil record, have produced no clear consensus on the characters of the LCA [Wrangham and Peterson, 1997; McGrew, 2010; Wood and Harrison, 2011; Harrison, 2012], and I will not be taking this approach.

The second method of reconstructing the LCA, through a review of fossil apes insofar as they relate to the LCA, take up the first part of this paper [Andrews and Harrison, 2005; Andrews, 2015]. At the present time, 36 species of Miocene apes are known during the period leading up to the origin of the human lineage [Harrison, 2010b], but this can only be a fraction of the species that actually lived during this period from 20 to 5 million years ago (Ma). Compared with today, for example, there are 185 species of Old World higher primates [Groves, 2001; Mittermeier et al., 2013], and it is reasonable to suppose that in the past there may have been as many fossil species living at any one time so that the present fossil record falls far short of the species and morphological diversity present in the Miocene. There is no evidence that any one of these 36 species was ancestral to any of the living apes or humans, but what they can provide is an overview of the ranges of morphologies and environments from which both humans and chimpanzees may have evolved. The taxonomy used here for fossil apes is summarised in Table 1 [Andrews, 1996; Hartwig, 2002; Harrison, 2010b; Werdelin and Sanders, 2010].

In the second part of this paper, I will consider the third method of reconstructing the LCA by examining the shared morphologies and behaviours of humans with our closest living relative, the chimpanzee. Chimpanzees and humans have many characters and behaviours in common [McGrew, 1992, 2010, 2014]. It is a mistake, however, to imagine that the LCA looked anything like a chimpanzee, for it, like humans, has evolved from the common ancestor by “descent with modification” [Darwin, 1859]. It should have been no surprise that when fossil remains of early hominin ancestors such as *Australopithecus anamensis* were found [Leakey et al., 1995, 1998], this 4-million-year-old human ancestor looked nothing like a chimpanzee, while on the other hand it had similarities in its jaws and teeth to the Miocene apes [Andrews, 1995]. Similarly, the early hominin *Ardipithecus ramidus* has many similarities to fossil apes [White et al., 1994; Lovejoy et al., 2009a–c], but since both have human attributes such as incipient adaptations for bipedalism, they were already on the human lineage and could not themselves be the LCA.

Table 1. List of fossil taxa discussed in the text, taxonomy based on Hartwig [2002], with some amendments to bring it up to date

Family taxon	Genera of fossil apes	Geographic location	Age range
Proconsulidae	<i>Proconsul</i>	East Africa	Early Miocene
	<i>Ekembo</i>	East Africa	Early Miocene
	<i>Rangwapithecus</i>	East Africa	Early Miocene
	<i>Nyanzapithecus</i>	East Africa	Early Miocene
Dendropithecidae	<i>Dendropithecus</i>	East Africa	Early Miocene
Afropithecidae	<i>Afropithecus</i>	East Africa	Early Miocene
	<i>Equatorius</i>	East Africa	Early middle Miocene
	<i>Nacholapithecus</i>	East Africa	Early middle Miocene
	<i>Heliopithecus</i>	Saudi Arabia	Middle Miocene
Indeterminate	<i>Turkanapithecus</i>	East Africa	Early middle Miocene
	<i>Mabokopithecus</i>	East Africa	Early middle Miocene
Griphopithecidae	<i>Griphopithecus</i>	Turkey, Germany	Early middle Miocene
Kenyapithecidae	<i>Kenyapithecus</i>	East Africa	Early middle Miocene
Hominidae, Dryopithecinae	<i>Dryopithecus</i>	Europe	Late middle Miocene
	<i>Anoiapithecus</i>	Spain	Late middle Miocene
	<i>Pierolapithecus</i>	Spain	Late middle Miocene
	<i>Rudapithecus</i>	Hungary	Late Miocene
	<i>Hispanopithecus</i>	Spain	Late Miocene
Indeterminate	<i>Graecopithecus</i>	Greece	Late Miocene
Indeterminate	<i>Ouranopithecus</i>	Greece	Late Miocene
Indeterminate	<i>Oreopithecus</i>	Italy	Late Miocene
Pongidae	<i>Sivapithecus</i>	India, Pakistan, Nepal	Middle and late Miocene
	<i>Ankarapithecus</i>	Turkey	Late Miocene
	<i>Indopithecus</i>	India, Pakistan	Late Miocene
	<i>Gigantopithecus</i>	China	Pleistocene
	<i>Lufengpithecus</i>	China	Late Miocene
	<i>Khoratpithecus</i>	East Africa	Late Miocene
Hominidae, Homininae, Hominini	<i>Sahelanthropus</i>	Chad	Late Miocene
	<i>Orrorin</i>	Kenya	Pliocene
	<i>Ardipithecus</i>	Ethiopia	Pliocene
	<i>Australopithecus</i>	East and South Africa	Pliopleistocene

Hominidae is used here to denote the African ape and human clade, including those fossil apes identified with this clade; Homininae is used to denote the chimpanzee/human clade, and Hominini is used for the human clade.

Present estimates for the divergence of chimpanzees and humans based on DNA divergence are 9–5 Ma [Rogers and Gibbs, 2014], but dates estimated from different parts of the genome can vary by as much as 4 million years [Patterson et al., 2006]. These age estimates are close to the earliest fossils assigned to the chimpanzee/human clade, Homininae, and it is possible that gene flow continued for some time after the two lineages had diverged [Rogers and Gibbs, 2014]. The earliest fossils assigned at present to Hominini may in fact be part of hybridising subspecies or even morphologically similar sibling species, with gene flow between them still in place but ancestral respectively to the chimpanzee and human lineages. This raises the question as to the speciation process, and one possibility for this is chromosomal speciation [Groves, 1989], particularly for example in the Y chromosome [Hughes et al., 2010]. The chimpanzee Y chromosome differs in sequence structure and gene content from the human Y chromosome, implying rapid evolution [Hughes et al., 2010].

Evidence from Fossil Apes

Early Miocene

The Morphology of Early Miocene Proconsulids

The earliest good evidence of fossil apes comes from 18 Ma sites in East Africa. Two partial skulls and skeletons of *Ekembo heseloni* [McNulty et al., 2015 – formerly *Proconsul*] have a moderate degree of mid-facial prognathism and a low degree of alveolar prognathism, the opposite to what is present in the great apes. The skull is lightly built, lacks brow ridges and thickening of bone for the attachment of the jaw muscles. There is a broad incisive canal, which connects the nasal passage with the oral cavity, interpreted as the primitive condition for apes. The incisors are relatively large, broad and spatulate compared with most monkeys, and the canines are high crowned and projecting beyond the levels of the tooth rows. The lower third premolar is single cusped, and premolar honing is less strongly developed than in monkeys and *Proconsul africanus* but greater than in most later fossil apes. There is in fact little to identify any of the proconsulid species as apes based on skull and dentition alone [Andrews, 1978].

The forelimb of *Ekembo* indicates that this fossil ape was adapted to life in trees [Le Gros Clark and Leakey, 1951; Napier and Davis, 1959]. Amongst its many arboreal adaptations in the upper arm are the greater torsion of the head of the humerus compared with most monkeys, lack of curvature of the shaft and the morphology of the distal end [Napier and Davis, 1959; Rose, 1983; Gebo et al., 1988, 2009]. In the forearm, the neck of the radius is somewhat elongated, the styloid process of the ulna is elongated, and the brachial index is lower than is found in most living anthropoids. The patella is broad and flat and also rather thin, similar to chimpanzee patellas and different from the thicker bones present in monkeys [Ward et al., 1995], which suggests it was a slow climber in trees [Walker, 1997]. This morphology is seen also in other fossil apes for which the patella is known, and it seems to be an early ape condition.

Six lumbar vertebrae were present as in monkeys [Ward, 1993], with wedge-shaped bodies and transverse processes originating from the dorsal edge of the vertebral bodies [Nakatsukasa, 2008]. The scapulae are placed on the sides of the narrow chests, as in monkeys, and the narrow pelvis is monkey-like, indicating that these

fossil apes also had narrow bodies and that they were pronograde quadrupedal and largely arboreal. The head of the femur is angled upwards ($\pm 138^\circ$), more steeply than in monkeys, and this allows greater mobility at the hip joint, an adaptation for living in trees [MacLatchy and Bossert, 1996]. Preservation of cranial and postcranial remains is summarised in Table 2.

The bones of the hand are curved and gracile, and the thumb is long so that the hand has similar proportions to human hands [Napier and Davis, 1959; Beard et al., 1986; Lewis, 1989]. The morphology of the trapezium and its degree of medial rotation in the wrist indicates that the thumb was opposable, and the proximal phalanx of the thumb is long and cylindrical [Napier, 1960; Marzke, 1997]. However, the cylindrical articular surface limits movement and restricts the rotatory movement of the thumb seen in the human hand. The distal ends of the metacarpals are pinched posteriorly, limiting their capacity for weight bearing with extended digits [Napier and Davis, 1959; Begun et al., 1994]. These characters of the forelimb and the slender grasping feet indicate that proconsulids were primarily above-branch arboreal quadrupeds [Napier, 1964; Lewis, 1989]. Finally, the narrowing of the sacrum at the end of the spine shows that they lacked tails [Ward et al., 1991], but there are few other characters that link proconsulids with the apes so that the hominoid status of this group is still open to doubt [Harrison, 1993].

Functionally, this mix of characters shows that proconsulids were neither fully ape-like nor fully monkey-like, but it does show that they were powerful but relatively slow climbers [Rein, 2010; Rein et al., 2012], but with extensive limb mobility, using all four legs and moving in quadrupedal fashion [MacLatchy and Bossert, 1996; MacLatchy, 2004; Gebo et al., 2009]. They had a wide size range, from 8 to 14 kg, 28 to 46 kg and up to 80 kg [Rafferty et al., 1995]. The size of the brain for *E. heseloni* has been estimated as 167 cm³ [Walker et al., 1983], but a lower figure has been estimated based on regression of the foramen magnum area: 130 cm³ [Harrison, 2010a]. The encephalization quotient of the former overlaps the upper ranges of monkeys but the latter is close to the anthropoid mean [Rafferty et al., 1995; Harrison, 2010b]. Proconsulids were primarily fruit eaters, based on molar morphology [Kay, 1977; Ungar, 2007], incisor shape [Deane, 2009] and microwear [Beynon et al., 1998]. Root formation in the third molar was complete between 6 and 7 years so that their early life history was much shorter than in living apes [Dean, 2006].

Proconsulid Environments in the Early Miocene

Some of the environments associated with proconsulid species are non-forest types of woodland. Since the larger proconsulid species (28–80 kg) were bigger than most arboreal monkeys living today, their body size would have limited their capacity for movement in trees, as seen today, for example, in terrestrial baboons. This leads to the conclusion that these species may have been partly terrestrial, with the larger species even more so. Palaeoecological reconstructions of early Miocene environments associated with proconsulids show that environments were moderately seasonal. The fossil soil profiles that formed on the Rusinga sediments [Bestland, 1990] had calcareous horizons, which form under conditions of seasonal drying of the soil but with a high water table [Bestland and Retallack, 1993]. Fossil leaves indicate the presence of wet forest, with predicted higher rainfall during this time [Maxbauer et al., 2013; Michel et al., 2014], but the geological evidence of a high water table may suggest that the forest could be a ground water forest existing under local, edaph-

Table 2. Summary of skeletal elements available for the fossil apes discussed in the text

Family taxon	Genera of fossil apes	Cranial elements	Postcrania
Proconsulidae	<i>Proconsul</i> <i>Ekembo</i> <i>Rangwapithecus</i> <i>Nyanzapithecus</i>	Jaws and isolated teeth Partial skulls Jaws and isolated teeth Partial skull, jaws, isolated teeth	Few, indeterminate Several skeletons None None
Dendropithecidae	<i>Dendropithecus</i>	Jaws and isolated teeth	Partial limb elements
Afropithecidae	<i>Afropithecus</i> <i>Equatorius</i> <i>Nacholapithecus</i> <i>Heliopithecus</i>	Skull Jaws and teeth Jaws and teeth, skull fragments Maxilla	Isolated postcrania Partial skeleton Incomplete skeleton Partial skeleton
Indeterminate	<i>Turkanapithecus</i> <i>Mabokopithecus</i>	Partial skull Jaws and isolated teeth	Isolated postcrania None
Griphopithecidae	<i>Griphopithecus</i>	Jaws and isolated teeth	Phalanges only
Kenyapithecidae	<i>Kenyapithecus</i>	Jaws and isolated teeth	Humerus
Hominidae, Dryopithecinae	<i>Dryopithecus</i> <i>Anoiapithecus</i> <i>Pierolapithecus</i> <i>Rudapithecus</i> <i>Hispanopithecus</i>	Partial skulls, jaws and teeth Skull Partial skull Partial skull, jaws and teeth Partial skull, jaws and teeth	Isolated limb bones None Partial skeleton Many isolated postcrania Partial skeletons
Indeterminate	<i>Graecopithecus</i>	Mandible	None
Indeterminate	<i>Ouranopithecus</i>	Partial skull, jaws and teeth	Few phalanges
Indeterminate	<i>Oreopithecus</i>	Crushed skull, jaws and teeth	Crushed skeleton
Pongidae	<i>Sivapithecus</i> <i>Ankarapithecus</i> <i>Indopithecus</i> <i>Gigantopithecus</i> <i>Lufengpithecus</i> <i>Khoratpithecus</i>	Partial skull, jaws and teeth Partial skull, jaws and teeth Mandibles only Partial skull, jaws and teeth Partial skull, jaws and teeth Several mandibles	Isolated postcrania Isolated postcrania None None Isolated postcrania None
Hominidae, Homininae, Hominini	<i>Sahelanthropus</i> <i>Orrorin</i> <i>Ardipithecus</i> <i>Australopithecus</i>	Distorted skull, jaws Isolated teeth Partial skull, jaws and teeth Skulls, jaws and teeth	Isolated postcrania Isolated postcrania Partial skeleton Partial skeletons

ic conditions, rather than high rainfall. Analysis of carbon isotopes indicates that the vegetation consisted of trees and shrubs probably growing under conditions of water stress [Bestland, 1990]. Chesters [1957] reconstructed the environment as forest margin woodland habitats or gallery forest along a river, and later excavations in the major plant-bearing horizon yielded woodland floor debris consisting of abundant small twigs, larger wood fragments and fruits and seeds [Collinson et al., 2009] interpreted as leaf litter accumulations over a period of about 100 years [Retallack, 1990]. The fruits and seeds come from species today growing in closed deciduous woodland, with trees, shrubs, lianas and climbers.

Table 3. Summary of fossil ape environments showing type of evidence for reconstructing environments and the environmental reconstructions

Family taxon	Genera of fossil apes	Evidence on environment	Environmental reconstructions
Proconsulidae	<i>Proconsul</i> <i>Ekembo</i>	Ecological diversity, fossil mammals Fossil soils, plants, mammals, gastropods	Lowland and montane forest Deciduous woodland and lowland forest
	<i>Rangwapithecus</i> <i>Nyanzapithecus</i>	Fossil soils, mammals, gastropods Fossil plants, mammals, gastropods	Lowland and montane forest Deciduous woodland and lowland forest
Dendropithecidae	<i>Dendropithecus</i>	Fossil soils, plants, mammals, gastropods	Lowland and montane forest
Afropithecidae	<i>Afropithecus</i>	Stable isotopes	Deciduous woodland
	<i>Equatorius</i>	Stable isotopes, fossil plants, mammals	Deciduous woodland
	<i>Nacholapithecus</i>	Stable isotopes, fossil plants, mammals	Deciduous woodland
	<i>Heliopithecus</i>	Fossil mammals	Deciduous woodland
Indeterminate	<i>Turkanapithecus</i>	Stable isotopes	Deciduous woodland
	<i>Mabokopithecus</i>	Fossil mammals	Deciduous woodland
Griphopithecidae	<i>Griphopithecus</i>	Sediments, soils, isotopes, mammals	Deciduous woodland
Kenyapithecidae	<i>Kenyapithecus</i>	Sediments, soils, isotopes, mammals	Deciduous woodland
Hominidae	<i>Dryopithecus</i>	Fossil mammals	Deciduous woodland
	<i>Anoiapithecus</i>	Fossil mammals	Deciduous woodland
	<i>Pierolapithecus</i>	Fossil mammals	Deciduous woodland
	<i>Rudapithecus</i>	Sediments, soils, fossil plants, fossil mammals	Deciduous and lauroid evergreen wood
	<i>Hispanopithecus</i>	Sediments, soils, fossil plants, fossil mammals	Deciduous and lauroid evergreen wood
Indeterminate	<i>Graecopithecus</i>	None	None
	<i>Ouranopithecus</i>	Sediments, soils, isotopes, mammals	Open deciduous woodland
	<i>Oreopithecus</i>	Sediments, soils, fossil mammals, palynology	Deciduous and lauroid evergreen wood
Pongidae	<i>Sivapithecus</i>	Sediments, soils, fossil mammals	Deciduous woodland, subtropical forest
	<i>Ankarapithecus</i>	Sediments, soils, fossil mammals	Open deciduous woodland
	<i>Indopithecus</i>	Sediments, soils, fossil mammals	Deciduous woodland, subtropical forest
	<i>Gigantopithecus</i>	None	None
	<i>Lufengpithecus</i>	Sediments, soils, fossil mammals	Deciduous and lauroid evergreen wood
	<i>Khoratpithecus</i>	Stable isotopes, sediments, fossil plants	Subtropical forest/woodland
Hominini	<i>Sahelanthropus</i>	Sediments, soils, fossil mammals	Deciduous woodland
	<i>Orrorin</i>	Fossil mammals	Deciduous woodland
	<i>Ardipithecus</i>	Sediments, soils, isotopes, fossil mammals	Deciduous woodland
	<i>Australopithecus</i>	Sediments, soils, isotopes, fossil mammals, fossil plants	Open woodland savanna

At one site on Rusinga Island (R3) the dense remains of tree stumps and roots in a brown soil indicate the presence of forest. There is leaf litter that suggests evergreen forest, and this evidence is associated with proconsulids and probably with earlier finds of dendropithecids [Michel et al., 2014]. Other evidence on environments associated with proconsulids on Rusinga Island has come from land gastropods, indicating mixed savanna and bush with gallery forest [Verdcourt, 1963] and fossil mammals indicating mixed environments on Rusinga Island, Songhor and Koru [Andrews and Van Couvering, 1975; Andrews et al., 1979; Lehman et al., 2012]. General

conclusions from all these lines of evidence are that proconsulids occupied a range of habitats, predominantly tropical rainforest and deciduous woodland. This variation is summarised in Table 3 at the family and genus level, as for Table 1.

Early Middle Miocene

The Morphology of Early Middle Miocene Apes

The proconsulids described in the previous section form a coherent group that had a limited (known) geographic distribution in eastern Africa. They were succeeded by a number of genera and species of fossil apes with a greater range across Africa and, for the first time, outside Africa. African and European apes are grouped in Afropithecidae and Griphopithecidae, but none have yet received the monographic descriptions available for proconsulids, and the nature of the differences suggests that this is a paraphyletic grouping (Table 1). Kenyapithecidae are distinguished from both by derived characters of the anterior dentition [Kelley et al., 2008].

The African afropithecids are represented by partial skeletons [Ishida and Pickford, 1997; Nakatsukasa et al., 1998, 2007; Ishida et al., 1999, 2004; Ward et al., 1999; Kunimatsu et al., 2004]. The skull has a strongly projecting face, low broad origin of the zygomatic root, greater robusticity of the jaws than is present in proconsulids, greater development of the inferior transverse torus of the mandible, relatively broad upper central incisors, lateral incisors highly asymmetrical with a broad but low lingual tubercle, lower crowned and relatively robust canines, enlarged premolars that are relatively long, molars with thick enamel and low dentine relief, lower molars with reduced cingulum and no upper molar cingulum [Rossie and MacLachy, 2013]. They also have a long flexible back as in proconsulids, large cervical vertebrae relative to presumed body mass, axis and atlas vertebrae are intermediate between monkeys and great apes, which suggests the beginnings of greater upright posture; lumbar vertebrae have long bodies with ventral keels but small body surface area relative to vertebral spine size and assumed body mass, similarly for thoracic vertebrae, transverse processes arising from vertebral bodies as in proconsulids [Nakatsukasa et al., 2007; Kikuchi et al., 2012]; neural spines of the lumbar vertebrae limit the bending of the lower back; the clavicle is relatively long; the head of the humerus is posteriorly directed; the anatomy of the lower arm bones and wrist is strikingly similar to the condition in proconsulids; the distal humerus medial epicondyle is long and bent backwards; the olecranon fossa is deep; the coronoid process is well developed and inclined distally; the ulna has a long and projecting olecranon process; the head of the femur has a high neck angle and projects above the level of the greater trochanter; there is a wide patellar surface, thick fibular shaft, metacarpal heads with well-developed transverse dorsal ridges and broad distal articular surfaces; the hallux is relatively long and stout; the phalanges are lightly built and are not curved. The forelimbs are adapted for both climbing and terrestrial locomotion [Patel et al., 2009]. Overall the afropithecids resemble proconsulids in their adaptations for slow climbing in trees, but with a greater emphasis on terrestrial locomotion.

Contemporaneous with the afropithecids, fossil apes assigned to Griphopithecidae are known from Europe [Heizman and Begun, 2001]. Engelswies in Germany is dated to 16–15 Ma, and slightly later in time is Paşalar in western Turkey [Alpagut et al., 1990] estimated at 15 Ma, although a later date has been proposed [Begun et al., 2003]. Griphopithecids share many features of morphology with afropithecids [Alpagut et al., 1990] that are probably primitive retentions from proconsulids, and as

such they provide an indication of geographic continuity between apes in Europe and East Africa, but they do not indicate a cladistic relationship between them. The only postcranial specimens are phalanges from Paşalar, and their expanded proximal articular surfaces indicate that the apes moved quadrupedally like monkeys [Ersoy et al., 2008]. The degree of curvature of the shafts, and the length indices between phalanges, are intermediate between arboreal and terrestrial species of monkey, showing that the fossil apes were not exclusively arboreal but moved both in trees and on the ground, probably in a manner like that of macaques. Unlike proconsulids, they were highly dimorphic in size; coefficients of variation for most teeth are greater than those in the living apes, and size distributions of several of the teeth have discreet distributions [Humphrey and Andrews, 2008], as are the indices of maximum/minimum dimensions. These data indicate a high level of sexual dimorphism as great or greater than is present today in extant great apes.

Living at the same time as the afropithecids was another group of fossil apes with an intercontinental distribution, being found in Kenya and Turkey, Kenyapithecidae [Andrews and Tobien, 1977; Kelley et al., 2008]. They have robust and deep maxillary alveolar processes; the incisive canal is broad and long, and the anterior teeth show a series of highly derived morphologies distinct from all other fossil apes [Andrews and Tobien, 1977; Kelley et al., 2008]. The teeth have high sexual dimorphism [Humphrey and Andrews, 2008]. Most of the lower molars from Paşalar have cingula either weakly or strongly developed, but 8% of the lower molars lack a buccal cingulum entirely, which may be a distinguishing feature of *Kenyapithecus kizili* molars.

Environments in Africa and Europe in the Early Middle Miocene

Carbon isotopes for afropithecid sites show that environments in Africa were extremely varied from the middle Miocene onwards [Kingston et al., 2002]. Carbon isotope records show that both forest and woodland savanna habitats were present, but even where forest floras are known, as in the Ngorora Formation, fossil apes came from a different member of the formation [Jacobs, 1987, 1992; Makishima, 2005]. Plant remains at Engelswies show the presence of an evergreen laurophyllous flora growing in a subtropical humid climate. This is a relic of the oak-laurel-palm forests that extended across southern Europe during the Paleogene and early Neogene supported by highly seasonal climates, with monsoonal warm, wet summers and frost-free winters [Axelrod, 1975; Axelrod and Raven, 1978; Kovar-Eder and Teodoridis, 2018]. The structure of these woodlands that still exist today, for example on Tenerife and Gomera [Izquierdo, 2011] and in California [Axelrod, 2000], is a single evergreen canopy. The community structure of the mammal fauna from Engelswies is dominated by terrestrial species [Andrews, 2015]. Arboreal species and frugivores are also relatively abundant, and browsing herbivores dominate the trophic niche, with few grazers.

Multiple soil formation occurred in the Paşalar deposits [Bestland, 1990]. Prolonged dry seasons are indicated by abundance of calcareous nodules in the soils, while gleying is present in the same deposits caused by periods of waterlogging of the soils during the wet seasons [Bestland, 1990]. This combination of gleying and calcareous nodule formation indicates strong seasonal changes in precipitation.

The community structure of the large Paşalar mammal fauna has a log series distribution (χ^2 5.71 for 7 degrees of freedom), with over half the species represented by only one or two individuals. Log series ecological models occur in environments

dominated by one or two factors, such as extreme aridity, monocultures or highly seasonal environments [Andrews, 1996]. The fauna is dominated by terrestrial browsing herbivores and frugivorous species [Andrews, 2015], and its community structure is closest to present day faunas from subtropical monsoon (summer rainfall) woodlands of India growing in highly seasonal climates [Andrews, 1990]. Finally, the ecomorphology of the carnivores from Paşalar showed the presence of four carnivore guilds together indicating tropical woodlands and subtropical forest/woodland [Viranta and Andrews, 1995], and the carbon isotopes on the teeth of 10 of the large herbivores from Paşalar indicate diets dominated by C_3 plants [Quade et al., 1995].

No postcrania are known from Paşalar that can be attributed to kenyapithecids. There is a single humerus from Fort Ternan that is attributed to *Kenyapithecus wickeri*, indicating that the Fort Ternan ape was also a pronograde quadruped with both arboreal and terrestrial adaptations [Andrews and Walker, 1976]. This evidence for some degree of ground living, however, continues the theme first encountered in the early Miocene apes.

The 9 kenyapithecid individuals from Paşalar are all young adult individuals at exactly the same stage of maturity [Kelley, 2008]. This age structure contrasts with that of the 94 griphopithecid individuals, for which all age classes are represented in a typical attritional mortality pattern [Kelley et al., 2008; Andrews, 2015]. Differences in hypoplasias show that the 9 kenyapithecid individuals had consistently different developmental histories and suggest that they could have been an immigrant population. How far they may have travelled, and from what type of environment, is not known.

The fossil fauna from Fort Ternan is dominated by just 2–3 species [Andrews, 1996]. The carbon isotopes from three of the palaeosols at Fort Ternan indicate vegetation with C_3 photosynthetic pathways [Cerling, 1992; Cerling et al., 1997]. Closed canopy tree cover is indicated by these results. Similarly, the carbon isotopes on the teeth of 9 herbivores from Fort Ternan, including the 2 bovids that constitute a large proportion of the fauna, also show the C_3 photosynthetic pathway, which indicates diets of browse or leaves of trees and bushes rather than grass [Cerling et al., 1997]. In contrast to this, the fossil soils in which the Fort Ternan fossil faunas were preserved have been compared with recent grassland soils [Retallack et al., 1990].

Taphonomic evidence shows that the fossil fauna from Fort Ternan was derived from two or more sources [Shipman, 1982, 1986], a proximal source from which the majority of the fauna was derived, including the kenyapithecids, and a more distal source. Combining this evidence with that from the sediments, palaeosols and isotopes, the general conclusion is that both open grassland and closed canopy woodland were present at or close to the fossil site.

Late Middle Miocene

The Morphology of Later Middle Miocene Apes

Fossil apes from southern Europe are known from several sites about 12 Ma and attributed to three different genera and species [Moyà-Solà and Köhler, 1995; Moyà-Solà et al., 2009b]. The face has a large triangular nasal aperture and a wide palate; most species have moderately strong mid-face prognathism, but alveolar prognathism is low. The face is also more muzzle-like in that the edge of the nasal aperture projects in front of the cheekbones, which is similar to the condition in proconsulids and afropithecids, probably a primitive character retained in dryopithecines. The or-

bits of the eyes are placed well above the top of the nasal aperture. The upper canines are high crowned and robust, with a distinct honing facet where they occlude against the lower third premolar. The premolars are relatively broad, and the molars are moderately broader than long, both of which are primitive characters. The front of the face is flat from side to side, with the cheekbones in the same plane as the nasal cavity [Pérez de los Ríos et al., 2012]. Some species have molars and premolars with thick enamel [Alba et al., 2010a, b; Beynon et al., 1998]. The maxillary sinus is restricted anteriorly but extends posteriorly towards the ethmoid, and this and the lack of a frontal sinus are both orang utan characters [Schwartz, 1987].

The shaft of a humerus from Saint Gaudens, the same site from which the type specimens of *Dryopithecus fontani* were recovered, is similar to the humerus of the bonobo in overall size and robusticity [Pilbeam and Simons, 1971]. Although the head of the humerus is missing, it is apparent that the head has some degree of medial torsion, unlike the arm bones of earlier fossil apes. The flattened and broad distal end of the humerus is also like that of chimpanzees and unlike monkeys. The head of the femur from Can Mata is large relative to the neck, and it is situated at a level with the greater trochanter. The neck is relatively short and at a low angle to the shaft (123°), which limits movement at the hip joint. The curvature of the ribs from a partial skeleton indicates that this dryopithecine had a broad chest; this is also indicated by the length of the clavicle, which places the shoulder on the back rather than the side of the rib cage [Moyà-Solà et al., 2004]. The single lumbar vertebra known is similar to great ape vertebrae in its robustness and reduced wedging angle, both of which indicate this fossil ape had a relatively rigid lower back. The wrist is similar to that of the great apes, but the phalanges are short and less curved than in other fossil apes [Begun, 1993]. This monkey-like hand is associated with apparent great ape characters linked supposedly with suspensory behaviour [Almécija et al., 2007, 2009].

Dryopithecine Environments in the Late Middle Miocene

Little is known of the environment for most middle Miocene dryopithecine sites [Marmi et al., 2012]. The regional environment of St. Gaudens during the middle Miocene has been described as warm temperate broad-leaved woodland [Kovar-Eder et al., 1996; Kovar-Eder, 2003]. The palaeobotanical evidence from the Vallès-Penedès region of Spain indicates laurophyllous forest, i.e. trees with laurel-like leaves, which was widespread across southern Europe during the middle Miocene [Axelrod, 1975; Casanovas-Vilar et al., 2008; Kovar-Eder and Teodoridis, 2018]. The large mammals indicate the presence of a warm humid evergreen forest based on the presence of several arboreal species.

Late Miocene

The Morphology of Late Miocene Dryopithecines

Two fossil apes from Europe are represented by a partial skeleton from Spain and a skull and several jaws and teeth from Hungary. The late Miocene dryopithecine skulls of *Hispanopithecus laietanus* and *Rudapithecus* are dramatically different from earlier dryopithecines. They are lightly built, with moderately developed brow ridges [Begun, 1992, 1993; Begun and Kordos, 1993; Moyà-Solà and Köhler, 1995; Kordos and Begun, 1997; Alba, 2012]. The nasal aperture is narrow and the distance between the eyes is broad. In these features it resembles proconsulids, but unlike these the

cheek region is flatter and directed more forwards, similar to the condition in orang utans [Andrews and Cronin, 1982; Pilbeam, 1982] and (probably) in *Kenyapithecus*. The anatomy of the floor of the nasal aperture and the incisive fossa in the palate retains the primitive condition and differs little from other fossil apes. Its cheek teeth are primitively small and have relatively thin enamel, unlike other fossil apes from the same period. The incisors are narrow and high crowned, the canines are relatively small, the premolars lack some of the honing function present in earlier apes and monkeys, the molars have no or reduced cingula, the lower molars are elongated with broad central basins and the third lower molar is reduced in size.

The postcranial anatomy of later dryopithecines is also dramatically different from that of earlier fossil apes, for many of the postcranial features of the forelimb, hindlimb and axial skeleton are functionally related to suspensory and arboreal climbing apes and more upright posture [Moyà-Solà and Köhler, 1996; Köhler et al., 1999]. The lumbar vertebrae are short and robust, the transverse processes originate above the vertebral body, although not as high on the pedicle as in living great apes, and both indicate reduced mobility in the lumbar region (stiffer back); the thoracic vertebrae indicate a broad chest, and similarly the clavicle is proportionately long. The distal humerus has a wide trochlea for articulation with the ulna and a prominent trochlear ridge, and a rounded capitulum for articulation with the radius [Kretzoi, 1975; Morbeck, 1983], combining to give stability and mobility to the elbow joint. The wrist bones show enhanced mobility at the wrist joint [Begun, 1993; Kivell and Begun, 2009]. The hand is large relative to body size. The phalanges in particular are greatly elongated. The thumb has a robust metacarpal, which indicates that the hand was adapted for powerful grasping, and fragments of phalanges show that the thumb is not reduced. In addition, the phalanges are curved with strong insertion markings for the flexor muscles. The large head of the femur extends beyond the greater trochanter, and the neck has a high angle with the femoral shaft as in the orang utan. These features are adaptations for extreme mobility at the hip joint, where the legs are almost as mobile as the arms. The distal tibia differs from the condition in orang utans, combining adaptations for above-branch quadrupedalism with adaptations for vertical climbing. Together this mixture of characters indicates a form of locomotion different from any living primate. Much of the same suite of dryopithecine characters is also present in the enigmatic fossil ape *Oreopithecus bambolii* [Harrison and Harrison, 1989; Harrison, 1991; Harrison and Rook, 1997; Moyà-Solà and Köhler, 1997]. These characters indicate suspensory and climbing activities to a greater degree than is seen in monkeys and the earlier Miocene apes.

Dryopithecine Environments in the Late Miocene

The dryopithecine deposits at Rudabánya in Hungary were laid down in a shallow valley running into the ancient Pannonian Lake [Kordos, 1985; Kordos and Begun, 2002]. Palaeoenvironments shifted up and down the valley due to rises and falls of lake level, giving rise to two cyclical events of swampy fossil soil topped by lignite and covered by grey marl lake beds and redeposited later as a red marl, with renewed swamp conditions leading to another lignite layer at the top of the sequence [Andrews and Cameron, 2010]. Fossil wood and swamp cypress (*Taxodiaceae*) pollen is ubiquitous in the subtropical flora [Kretzoi et al., 1974], and aerial roots from the swamp cypress are abundant in the lignite deposits of Rudabánya 2 [Andrews and Cameron, 2010]. Warmth-loving species such as *Zelkova*, *Celtis*, *Diospyros* and *Engelhardtia* are

also present [Kretzoi et al., 1974], indicating a rich and varied form of subtropical woodland.

Similarly, the Vallès-Penedès region in Spain, where the Spanish dryopithecines are from, had warm temperate evergreen woodland and forest. This type of sclerophyllous forest was common across southern Europe at that time [Axelrod and Raven, 1978]. Laurels were an important understory component of these laurophyllous and *Juniperus/Taxodium* woodlands [Elias et al., 2016] during the Miocene [Axelrod and Raven, 1978], with palms, deciduous tree species and figs [Marmi et al., 2012]. The mammal faunas have many aquatic species such as otters and beavers, and the small mammals include species like flying squirrels and several species of arboreal dormice. The mesowear and microwear on the mammal teeth show evidence of mixed feeders, engaging in both browsing and grazing [Merceron et al., 2007]. The ecomorphology of the single equid species with its elongated limbs indicates that it was adapted for running in open environments rather than moving through thick cover [Merceron et al., 2007], but the mammal evidence indicates subtropical swamp woodland. The habitat reconstructed by ecomorphology of the mammal fauna was one of swampy woodlands in humid warm conditions [Köhler, 1993; Kordos and Begun, 2002].

Other Late Miocene Hominid Apes and Pliocene Hominins

Three fossil apes are known from Africa during the period 9–10 Ma, but they are too fragmentary to be able to assign them either with each other or to any living or fossil ape [Pickford and Senut, 2005; Kunitatsu et al., 2007; Suwa et al., 2007]. Carbon isotope distribution associated with the fossil apes shows the presence of mainly C₃ plants, indicating some form of closed woodland or forest [Kingston et al., 2002].

Later Miocene apes from eastern Europe and western Asia have skulls similar to that of the orang utan. Their skulls have rounded vaults, deep jaws, gracile brow ridges, broad central incisors and enlarged molar teeth with thick enamel [Andrews and Cronin, 1982; Pilbeam, 1982; Brown and Ward, 1988; Alpagut et al., 1996; Begun and Güleç, 1998]. Their postcrania are distinct from both monkeys and great apes, with quadrupedal and pronograde adaptations in *Sivapithecus* [Rose, 1983, 1989, 1994] and terrestrial adaptations in *Ankarapithecus* [Kappelman et al., 2003].

A second group of fossil apes from Europe has skulls more similar to those of African apes, but with distinct postcrania, showing that they were quadrupedal, pronograde and mainly terrestrial (*Ouranopithecus*, *Graecopithecus*). They have more robust skulls, relatively slender jaws, broad central incisors, low-crowned canines and enlarged molar teeth with thick enamel [de Bonis and Melentis, 1977, 1978; de Bonis and Koufos, 2014]. Their taxonomic attribution is uncertain. The environment is deciduous woodland [de Bonis and Melentis, 1977, 1978; de Bonis et al., 1992]. A third group of fossil apes has teeth and mandibular morphology similar to those of the orang utan (*Lufengpithecus*, *Khoratpithecus*) [Chaimanee et al., 2003, 2004].

On the basis of apparent shared derived characters linking some European apes, e.g. dryopithecines and *Graecopithecus* (and *Ouranopithecus*), with the African ape and human clade, it has been suggested that one or other of the late Miocene African fossil apes evolved in Europe and migrated back to Africa [Andrews, 1992; Begun, 1992, 2009]. It has also been suggested further that there are characters linking *Graecopithecus* (and *Ouranopithecus*) with the hominins [Fuss et al., 2017], but it is not clear at present which characters are homoplasies and which homologues. Some

dryopithecines also have characters similar to derived characters in the orang utan [Begun and Kivell, 2011]. One thing that is clear from this is that characters were evolving in mosaic fashion long before the divergence of the species of great ape [Moyà-Solà et al., 2004, 2009a, b; Begun and Kivell, 2011; Begun et al., 2012; Begun, 2013].

There are four late Miocene species that appear to offer information on the LCA of chimpanzees and humans, all from Africa. They are all attributed at present to the hominin line. The skull of the earliest in time, *Sahelanthropus*, has many similarities with earlier fossil ape skulls such as *Pierolapithecus* [Moyà-Solà et al., 2004], and it is attributed to the human clade on the basis of small canines and the forward position of the foramen magnum [Brunet et al., 2002; but see Wolpoff et al., 2002]. The position of the foramen magnum may be evidence of more upright posture, as seen in some dryopithecine fossil apes, but it does not necessarily support bipedal locomotion. Also, the dating of this fossil is close to the estimated time of divergence of chimpanzees and humans [Patterson et al., 2006; Rogers and Gibbs, 2014].

Orrorin tugenensis has features of the femur that are similar to those of afropithecids and dryopithecines as well as with later hominins [Senut et al., 2001; Almécija et al., 2013], and they indicate adaptations for semi-terrestrial locomotion. The trabecular pattern of the neck of the femur is said to be adaptive for bipedalism [Senut et al., 2001; Galik et al., 2004], but the functional significance of this character may have more to do with weight bearing than specifically with bipedal locomotion, for such features are also present in terrestrial quadrupedal monkeys [Rafferty, 1998; Ruff and Higgins, 2013].

Slightly later in time are two species of *Ardipithecus*, *A. ramidus* from Pliocene deposits at Aramis and Gona (4–5 Ma) and *A. kadabba* from the middle Awash region (late Miocene, 5–6 Ma), all three sites in Ethiopia. The earlier species, *Ardipithecus kadabba*, is poorly known and has large ape-like canines and a P₃ with a mesial wear facet, implying at least some degree of functional honing as in apes and unlike early hominins [Haile Selassie, 2001, 2004].

The endocranial capacity of *Ardipithecus ramidus* is small, particularly relative to body size (approx. 350 cm³), and it has reduced lower face prognathism [Suwa et al., 2009] as in most fossil apes. The canines are low crowned, and the upper canine is broad and angular, so that P₃ honing is absent; molars and premolars are small; the base of the skull is short, the chest broad and the forelimbs robust [Lovejoy et al., 2009b]; hand proportions are similar to those seen in proconsulids and early dryopithecines [Almécija et al., 2015], and thumb proportions are also similar to those of fossil apes (where known); the pelvis has a broad ilium, shared with later hominins [Lovejoy et al., 2009d]; the ischium is long and ape-like; there is a divergent big toe as in most primates and an elongated mid-tarsal region of the foot [Lovejoy et al., 2009a]; phalanges are short and robust; leg length is relatively long as present in most fossil apes [Lovejoy et al., 2009c]. In sum, *A. ramidus* combines a unique blend of primitive characters of the skull and teeth with hominin morphological features of the postcrania [Leakey et al., 1995; Beynon et al., 1998].

Environments of Late Miocene and Pliocene Hominids

The environment in the Lukeino Formation associated with *Orrorin tugenensis* is interpreted as open woodland with patches of forest [Pickford and Senut, 2001]. The palaeoecology has not yet been studied in detail, but there are 38 species of mam-

mal in the associated fauna, dominated by impala, and possible woodland/forest indicators such as colobine monkeys are also present. However, non-forest equids, rhinos and some bovids are also present, and the presence of crocodiles, hippos and freshwater mussels (*Iridina* species) in the fauna [Munro, 2010] show that there was permanent fresh water nearby.

The site at Aramis, where *A. ramidus* comes from, was a low-relief flood plain. Calcareous palaeosols were developed in areas of low relief and could have had impeded drainage, and the deposits between the two dated tuffs indicate stable conditions [Woldegabriel, 1994, 2001]. This is in contrast to the same aged deposits at Gona, where similar faunas were recovered from what has been interpreted as mixed habitats [Louchart et al., 2009]. Analysis of soil carbon isotopes indicates intermediate values between the C₃ and C₄ photosynthetic pathways, with up to 70% C₄ plants present in the eastern part of the region. This is taken to indicate a range of vegetation types from woodland to wooded grassland [Woldegabriel et al., 2001, 2009]. The carbon isotope values of herbivore teeth from Aramis show a range of $\delta^{13}\text{C}$ values, with *Ardipithecus ramidus* linked with the tragelaphines, neotragines and giraffes with C₃ photosynthetic pathway and occupying woodland habitats, feeding both in trees and on the ground [Nelson, 2013]. Deciduous woodlands ranging from open to closed woodland are inferred from these data.

Evidence from Living Apes

For three quarters of their history, the fossil apes known at present differed greatly from living apes. The norm for fossil apes in the early and middle Miocene was of quadrupedal monkey-like adaptations, both arboreal and terrestrial. In the middle and late Miocene, the majority of known species did not live in tropical forest but in tropical to subtropical deciduous woodland savanna and evergreen single-canopy woodland. After about 10–12 Ma, apes with more upright posture and broad great-ape-like chests appeared, some with terrestrial adaptations and some with adaptations for below-branch arboreal adaptations. With one or two exceptions, fossil apes retained similar length limbs and human-like hand proportions and opposable thumbs, although without the rotatory thumb characteristic of modern humans. These aspects of fossil apes provide background for human origins to set against evidence from chimpanzee morphology for there are next to no morphological characters shared uniquely by chimpanzees and humans. The evidence for shared ancestry is based entirely on DNA evidence, with divergence dates of 9–5 Ma [Rogers and Gibbs, 2014] but with a potential range of dates up to 4 million years because of variations in divergence in different parts of the genome [Patterson et al., 2006].

The near-absence of fossil apes sharing derived characters with any of the extant apes makes it almost impossible to show their morphological history. Humans have lost a pair of chromosomes relative to chimpanzees and other apes so that the ancestral condition was probably $2n = 48$, as in the living great apes and the LCA. In addition, the sequence structure and gene content of the chimpanzee Y chromosome differs from both humans and other apes, implying rapid evolution in the chimpanzee lineage [Hughes et al., 2010]. The chimpanzee Y chromosome has both added and lost nucleotide sequences, and its gene repertoire is considerably smaller and simpler than that of the human and great ape Y chromosomes and by implication the LCA

[Hughes et al., 2014]. Chromosomal speciation may have been the trigger that led to the divergence of chimpanzees and humans from the LCA, even though there appear to be no differences in their environmental preferences. For comparisons with chimpanzees, therefore, we have to rely on comparisons between living chimpanzees and humans.

The great range of diets in chimpanzee populations has been demonstrated through the analysis of carbon isotopes. Both diet and isotopes differ from those of leaf-eating and fruit-eating monkeys and are similar to human diets [Smith et al., 2010]. Chimpanzee diet includes less than 10% meat products [Goodall, 1986; Foley, 2001], and the killing and eating of vertebrate prey ranks low in chimpanzee (*Pan troglodytes*) carnivory [Goodall, 1986; Stanford and Bunn, 2001]. Insect prey makes up a far larger proportion of their diet than vertebrate prey [Nishida and Kawanaka, 1985; Arcadi and Wrangham, 1999; Newton-Fisher, 1999; Watts, 2008; Nelson, 2013; O'Malley and McGrew, 2014]. Animal protein has high nutritional value, and it has been observed that chimpanzees eat meat more frequently during the dry season when their staple diet of fruit is most difficult to come by [Nelson, 2013]. Common chimpanzees engage in cooperative hunts, for example of colobus monkeys. They eat the whole of the animals, including gnawing on bones leaving marks similar to human chewing [Pobiner et al., 2007; Fernandez-Jalvo and Andrews, 2011]. The sharing of meat-eating and hunting, at least to the same extent as chimpanzees, are probably shared characters in the human and chimpanzee lineages. As seen today for chimpanzees, wood and stones were used as tools long before hominins were making stone tools [Blumenschine, 1987; Blumenschine and Cavallo, 1988; Watts, 2008]. Such material left no trace, either as modified tools or cut marks on bones, but there is every reason to believe that meat-eating and tool-making were present in the LCA of chimpanzees and humans.

The use of sticks by the Gombe chimpanzees when fishing for termites [Goodall, 1986] was only the first of a series of studies showing both tool use and cultural differences in tool manufacture [Boesch and Boesch, 1990; McGrew, 1992; Boesch, 1996]. A summary of tool types used by the chimpanzee populations in Gombe, Mahale, Tai, Bossou and Goulougo includes 15–25 different types of tools, from using sticks to catch termites or stones for cracking open hard nuts [Boesch, 1996; Boesch and Boesch-Ackermann, 2000], to using stones with a hammer and anvil technique to break open nuts, to using “weapons” such as spears when hunting, to using sticks to dig for underground plant storage organs [Hockings et al., 2010]. The differences between chimpanzee and human use of tools is not so much qualitative as quantitative, and the transition from ape to human was a shift in emphasis rather than something completely new. For example, the ability to learn from others of the same species, and to make technological improvements, is partly dependent on group size [Barrett et al., 2002]. Large social networks allow humans to learn from others to a degree far greater than is possible with small groups, and it may be that chimpanzee social groups have never been big enough, or cohesive enough, to achieve this ability to learn and improve by imitation of other group members. Moreover, intergroup rivalry between adjacent groups of chimpanzees can lead to extreme violence [Goodall, 1986], with apparent targeted death of individuals or groups in some cases [Mitani et al., 2010].

Few mammal species are known that can live successfully in both forest and non-forest habitats in tropical Africa. This begs the question as to the environment of

origin for chimpanzees: was it forest, with chimpanzees hanging on in marginal woodland habitats? Or were they originally woodland-adapted species, managing to survive in forest as the African woodlands have declined, as suggested for the okapi [Kingdon, 2002]? Chimpanzees are able to survive in arid savanna habitats [McGrew et al., 1996] beyond the range of most forest-adapted mammals, and a common element to both forest and savanna habitats occupied by chimpanzees is the presence of fig trees [Makishima, 2005]. Fig trees have high species richness [Harrison, 2010a], and their success is based on their symbiotic relationship with fig wasps, many species having their own particular species of wasp that both pollinates the fig flowers and eats their fruits [Cook and Rasplus, 2003]. The life cycle of fig wasps in tropical environments is to a large extent independent of climatic seasons so that in a large enough area there are always fruiting figs supplying a constant supply of fruit on which chimpanzees and other frugivorous animals depend for survival, particularly in savanna habitats.

The LCA of Chimpanzees and Humans

The characters by which fossil members of the human lineage might be recognised have been documented as follows by Wood and Harrison [2011]: shortening of the face, forward position of the zygomatic process, enlarged brain, forward position of the foramen magnum (where the spinal column connects with the skull), vertically implanted incisors, reduced canines, loss of premolar shearing function with the upper canine, enlarged molars, and bipedal specialisations of the hip, legs and feet. This is an impressive list, but as Wood and Harrison point out, every one of these characters, except brain enlargement (and this occurs later in human evolution and not in early hominins), is present in one or other fossil ape or other primate. In some fossil apes, several of these characters are present in combination, with the result that they have even been proposed as hominin ancestors. All this highlights the subject of homoplasy and the importance of determining whether characters are the result of common ancestry or convergence, and with such a limited perspective it does little to reconstruct the LCA.

Combining the evidence available for fossil apes [Andrews, 2015] and chimpanzees [McGrew, 2010], I have put together another list of characters present in the LCA of apes and humans (Fig. 1). This is based on characters present in fossil apes before the LCA, those present in the early hominins soon after the LCA, and those shared by great apes, particularly chimpanzees, and humans (top, Fig. 1). In some cases, the same character states are present in all three categories, for example projecting canines and P_3 honing (Fig. 1). The distribution of character states in these three groups is the basis for reconstructing the probable character states present in the LCA of chimpanzees and humans (Fig. 1). It is taken as axiomatic that no character state in the LCA can be identical to any uniquely derived character state in either the post-LCA hominin lineage or in any of the great apes: e.g. adaptations for bipedality are unique to the human lineage and by definition could not have been present in the LCA.

Character states present in the earliest hominins but after the LCA are based in the first instance on the two species of *Ardipithecus* and *Australopithecus anamensis*, which are the earliest Pliocene hominins that are undisputedly on the human lin-

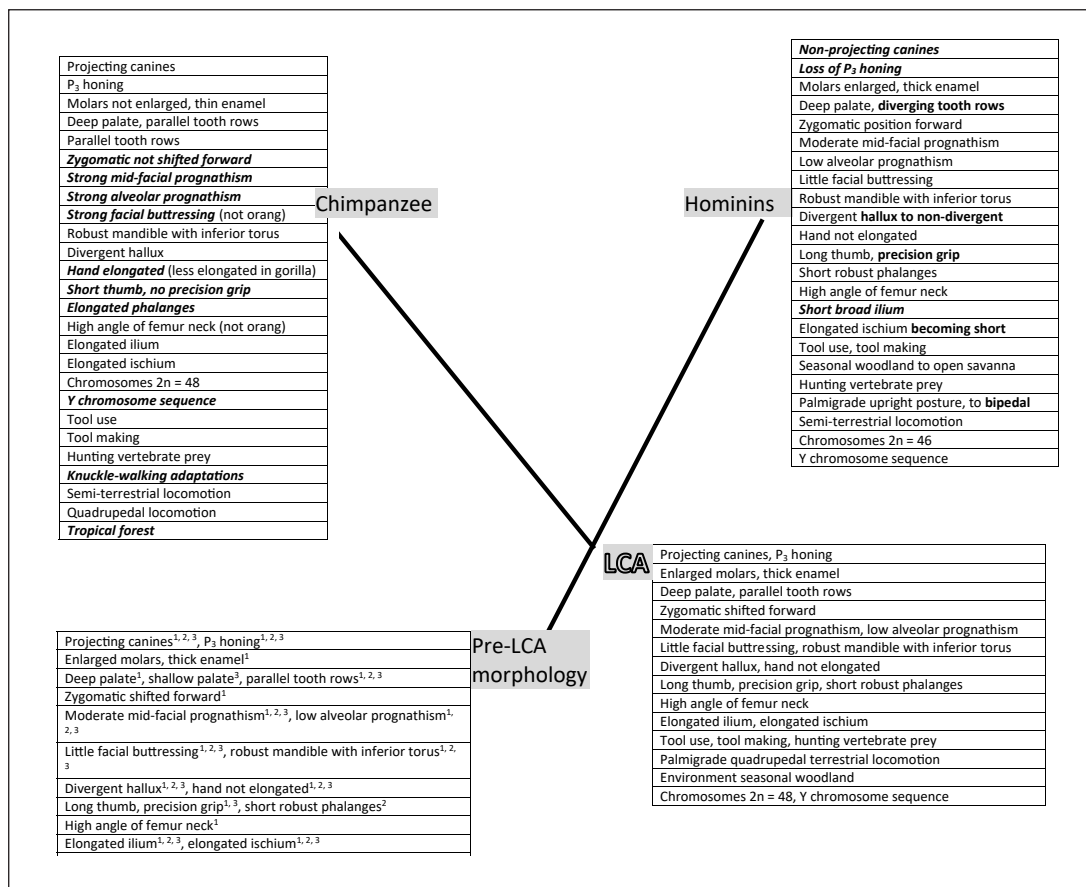


Fig. 1. Character states in four stages of hominid evolution. Character states in the fossil apes (pre-LCA) are distinguished by superscript figures: ¹ characters present in the latest fossil ape; ² characters present in the most terrestrial fossil apes; ³ characters present in the majority of fossil apes. Character states in undisputed early hominins are based on characters present in *Ardipithecus ramidus* and *Australopithecus anamensis*, with derived character states present in later stages of human evolution shown in bold. The same list of character states is shown for chimpanzees, with inferred derived characters for chimpanzees in bold and italics. Based on these distributions of character states, the morphology of the LCA is shown on the lower right.

age. Additional confirmation is based on later Pliocene and early Pleistocene species of *Australopithecus*. For example, projecting canines and P₃ honing are still present in *Ardipithecus kadabba* but altered to non-projecting and non-P₃ honing in *Ardipithecus ramidus* and *A. anamensis* and in all later hominins. The latter character states are assumed to be derived with respect to the LCA and fossil apes, and they are depicted in bold in Figure 1, top right. Note that these fossils cannot themselves be considered common ancestors to apes and humans since they are already on the hominin lineage.

Character states present in extant great apes are well attested, and, for example, they retain the projecting canines and honing P₃ present in nearly all fossil apes. Where gorillas or orang utans differ from chimpanzees the differences are noted, sometimes as primitive retentions and sometimes as separately derived character states. Character states assumed to be derived with respect to the LCA and fossil apes are depicted in bold italics.

The presence in the LCA of projecting canines, P₃ honing, enlarged molars and parallel tooth rows are all predicted from their distribution in fossil apes and earliest hominins (Fig. 1). The deep palate is present in early hominins and a few fossil apes. The forward position of the zygomatic, moderate mid-facial and low alveolar prognathism are present on the more terrestrial fossil apes and in most hominins. Absence of facial buttressing is present on most fossil apes and early hominins. Divergent hallux is present on most apes and at least one early hominin (*A. ramidus*), and similarly the short hand with relatively short and robust phalanges but long thumb are present in most fossil apes (where known) and most early hominins. The elongated ilium and ischium are present on fossil apes (where known) and living apes, and the latter is also present in *A. ramidus*. The shared presence of tool use, tool making or hunting in chimpanzees and humans makes it likely that all were present in their LCA or even earlier in ape evolution. Several fossil apes for which evidence is available had hand proportions more similar to human hands than to those of great apes, and it is possible, if not probable, that they too were tool makers. Palmigrade semi-terrestrial locomotion is based on similar hand proportions in most fossil apes and earliest hominins (*A. ramidus*), and quadrupedal locomotion was the norm for fossil apes and probably still present in early hominins as the precursor to bipedalism. Chromosome number was probably $2n = 48$ in living great apes and 46 in humans, and in the LCA it was probably 48, while the Y chromosome probably retained the human condition.

Floras and faunas show a change in environment for fossil apes from tropical forest and deciduous woodland in the early Miocene to tropical and subtropical woodland habitats in the middle and late Miocene. Fossil apes in Africa are found associated with woodland habitats throughout the middle Miocene, and although fossil floras show the presence of forests, no apes have been found associated with them. A shift in fossil ape environments occurred after immigration into Europe in the middle Miocene: summer rainfall (monsoonal) woodland is associated with apes in Turkey and Germany during the middle Miocene; deciduous coniferous swamp woodland (*Taxodium*) combined with laurophyllous (lauroid) evergreen woodland was associated with fossil apes in the late Miocene and laurel-palm-Taxodiaceae evergreen woodlands in wet areas also in the late Miocene. Although called forest by common usage, these subtropical floras have the structural attributes of woodland, such as low species richness, single tree canopies and relatively open canopies, contrasting with the African tropical forests [White, 1983]. These later Miocene ape habitats are similar to those reconstructed for early hominin habitats [Pickford and Senut, 2001; Kingston and Harrison, 2007; Andrews and Bamford, 2008; Woldegabriel et al., 2009; Kingston, 2011]. The environment of the LCA is therefore taken to be some form of woodland, probably deciduous and with single canopy structure, and there was little environmental shift from ape to hominin line.

Conclusions

The list of 27 character states for the LCA in Figure 1 is based in part on ancestral characters in fossil apes. Some of these are derived in chimpanzees and others derived in the hominin lineage, in both cases shown in bold in their respective boxes. Thus, projecting canines and P₃ honing are characteristic of apes generally but derived in hominins. The position of the zygomatic and degree of alveolar prognathism, on the other hand, are characteristic of fossil apes and hominins but derived in chimpanzees. Some other character states in the hominins retain the fossil ape condition in the earliest representatives of the lineage but alter to hominin character states very soon after, for example the long ischium.

In addition, there are some behavioural traits that are shared between chimpanzees and humans living today that are likely to have been present in their common ancestor. Tool use is present in many living animals, and there is no reason to suppose that the ancestor of both chimpanzees and humans did not also make tools. Tool making is not so common in primates or other animals, but the wide range of different types of tool made and used by chimpanzees suggests strongly that the LCA of chimpanzees and humans also made tools and by inference also hunted small vertebrate prey.

Palmigrade upright locomotion, in the LCA is inferred from its presence in later Miocene fossil apes, associated with short phalanges, its presence in the earliest hominins and the absence of knuckle-walking adaptations in the fossil record. Semi-terrestrial locomotion in seasonal woodland environments is based on their ubiquity (and interconnection) in middle and late Miocene apes and early hominins. Finally, the chromosomal character states inferred for the LCA are based on the probable derived states of chromosome number in hominins and the Y chromosome in chimpanzees.

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References

- Alba DM (2012). Fossil apes from the Vallès-Penedès Basin. *Evolutionary Anthropology* 21: 254–269.
- Alba DM, Fortuny J, Moyà-Solà S (2010a). Enamel thickness in the middle Miocene great apes *Anoiapithecus*, *Pierolapithecus* and *Dryopithecus*. *Proceedings of the Royal Society B* 277: 2237–2245.
- Alba DM, Fortuny J, Perez de los Rios M, Zanolli C, Almécija S, Casanovas-Vilar I, Robies JM, Moyà-Solà S (2010b). New dental remains of *Anoiapithecus* and the first appearance datum of hominoids in the Iberian Peninsula. *Journal of Human Evolution* 65: 573–584.
- Almécija S, Alba DM, Moyà-Solà S (2009). *Pierolapithecus* and the functional morphology of Miocene ape hand phalanges: paleobiological and evolutionary implications. *Journal of Human Evolution* 57: 284–297.
- Almécija S, Alba DM, Moyà-Solà S, Köhler M (2007). Orang-like manual adaptations in the fossil hominoid *Hispanopithecus laietanus*: first steps towards great ape suspensory behaviours. *Proceedings of the Royal Society B* 274: 2375–2384.
- Almécija S, Smaers JB, Jungers WL (2015). The evolution of the human and ape hand proportions. *Nature Communications* 6: 7717.
- Almécija S, Tallman M, Alba DM, Pina M, Moyà-Solà S, Jungers WL (2013). The femur of *Orrorin tugenensis* exhibits morphometric affinities with both Miocene apes and later hominins. *Nature Communications* 4: 2888.
- Alpagut B, Andrews P, Fortelius M, Kappelman J, Temizsoy I, Celebi H, Lindsay W (1996). A new specimen of *Ankarapithecus meteai* from the Sinap Formation of central Anatolia. *Nature* 382: 349–351.
- Alpagut B, Andrews P, Martin L (1990). New hominoid specimens from the middle Miocene site at Paşalar, Turkey. *Journal of Human Evolution* 19: 397–422.
- Andrews P (1978). A revision of the Miocene Hominoidea of East Africa. *Bulletin of the British Museum of Natural History (Geology)* 30: 85–224.
- Andrews P (1990). Palaeoecology of the Miocene fauna from Paşalar, Turkey. *Journal of Human Evolution* 19: 569–582.
- Andrews P (1992). Evolution and environment in the Hominoidea. *Nature* 360: 641–646.
- Andrews P (1995). Ecological apes and ancestors. *Nature* 376: 555–556.
- Andrews P (1996). Palaeoecology and hominoid palaeoenvironments. *Biological Reviews* 71: 257–300.
- Andrews P (2015). *An Ape's View of Human Evolution*. Cambridge, Cambridge University Press.
- Andrews P, Bamford M (2008). Past and present vegetation ecology of Laetoli, Tanzania. *Journal of Human Evolution* 58: 78–98.
- Andrews P, Cameron D (2010). Rudabanya: taphonomic analysis of a fossil hominid site from Hungary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 297: 311–329.
- Andrews P, Cronin J (1982). The relationships of *Sivapithecus* and *Ramapithecus* and the evolution of the orang utan. *Nature* 297: 541–546.
- Andrews P, Harrison T (2005). The last common ancestor of apes and humans. In *Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam* (Lieberman DE, Smith RJ, Kelley J, eds.), pp 103–121. Boston, Brill Academic Publishers.
- Andrews P, Tobien H (1977). New Miocene locality in Turkey with evidence on the origin of *Ramapithecus* and *Sivapithecus*. *Nature* 268: 699–701.
- Andrews P, Van Couvering JH (1975). Palaeoenvironments in the East African Miocene. In *Approaches to Primate Paleobiology* (Szalay FS, ed.), pp 62–103. Basel, Karger.
- Andrews P, Walker AC (1976). The primates and other fauna from Fort Ternan, Kenya. In *Human Origins* (Isaac G, ed.), pp 279–304. Menlo Park, Benjamin.
- Andrews P, Lord J, Evans EMN (1979). Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society* 11: 177–205.
- Arcadi AC, Wrangham RW (1999). Infanticide in chimpanzees: review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. *Primates* 40: 337–351.
- Axelrod DI (1975). Evolution and biogeography of the Madrean-Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden* 62: 280–334.
- Axelrod DI (2000). *A Miocene (10–12 Ma) Evergreen Laurel-Oak Forest from Carmel Valley, California*. University of California Publications in Geological Sciences 145. Berkeley, University of California Press.
- Axelrod DI, Raven PH (1978). Cretaceous and Tertiary vegetation history in Africa. In *Biogeography and Ecology of Southern Africa* (Werger MJA, ed.), pp 77–130. The Hague, Junk.
- Barrett L, Dunbar RIM, Lycett J (2002). *Human Evolutionary Psychology*. Basingstoke, Palgrave.
- Beard KC, Teaford MF, Walker A (1986). New wrist bones of *Proconsul africanus* and *P. nyanzae* from Rusinga Island, Kenya. *Folia Primatologica* 47: 97–118.
- Begun DR (1992). Miocene fossil hominids and the chimp-human clade. *Science* 257: 1929–1933.
- Begun DR (1993). New catarrhine phalanges from Rudabánya (Northeastern Hungary) and the problem of parallelism and convergence in hominoid postcranial morphology. *Journal of Human Evolution* 24: 373–402.

- Begun DR (1994). Relations among the great apes and humans: new interpretations based on the fossil great ape *Dryopithecus*. *Yearbook of Physical Anthropology* 37: 11–63.
- Begun DR (2002). European hominoids. In *The Primate Fossil Record* (Hartwig WC, ed.), pp 339–368. Cambridge, Cambridge University Press.
- Begun DR (2009). Dryopithecins, Darwin, de Bonis and the European origin of the African apes and human clade. *Geodiversitas* 31: 789–816.
- Begun DR (2013). The Miocene hominoid radiations. In *A Companion to Paleoanthropology* (Begun DR, ed.), pp 398–416. Oxford, Wiley-Blackwell.
- Begun DR, Güleç E (1998). Restoration of the type and palate of *Ankarapithecus metei*: taxonomic and phylogenetic implications. *American Journal of Physical Anthropology* 105: 279–314.
- Begun DR, Kivell TL (2011). Knuckle-walking in *Sivapithecus*? The combined effects of homology and homoplasy with possible implications for pongine dispersals. *Journal of Human Evolution* 60: 158–170.
- Begun DR, Kordos L (1993). Revision of *Dryopithecus brancoi* Schlosser, 1910, based on the fossil hominid material from Rudabánya. *Journal of Human Evolution* 25: 271–286.
- Begun DR, Geraads D, Güleç E (2003). The Çandır hominoid locality: implications for the timing and pattern of hominoid dispersal events. *Courier Forschungsinstitut Senckenberg* 240: 251–265.
- Begun DR, Nargolwalla MC, Kordo L (2012). European Miocene hominids and the origin of the African ape and human clade. *Evolutionary Anthropology* 21: 10–23.
- Begun DR, Teaford MF, Walker A (1994). Comparative and functional anatomy of *Proconsul* phalanges from the Kaswanga primate site, Rusinga Island, Kenya. *Journal of Human Evolution* 26: 89–165.
- Bestland E (1990). Sedimentology and paleopedology of Miocene alluvial deposits at the Paşalar hominoid site, western Turkey. *Journal of Human Evolution* 19: 363–377.
- Bestland EA, Retallack GI (1993). Volcanically influenced calcareous palaeosols from the Miocene Kiahira Formation, Rusinga Island, Kenya. *Journal of the Geological Society* 150: 293–310.
- Beynon AD, Dean MC, Leakey MG, Reid DJ, Walker A (1998). Comparative dental development and microstructure of *Proconsul* teeth from Rusinga Island, Kenya. *Journal of Human Evolution* 35: 163–209.
- Blumenschine R (1987). Characteristics of an early hominid scavenging niche. *Current Anthropology* 28: 383–407.
- Blumenschine RJ, Cavallo JA (1988). Scavenging and human evolution. *Scientific American* 267: 90–96.
- Boesch C (1996). Three approaches for assessing chimpanzee culture. In *Reaching into Thought* (Russon A, Bard K, Parker S, eds.), pp 404–429. Cambridge, Cambridge University Press.
- Boesch C, Boesch H (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica* 54: 86–99.
- Boesch C, Boesch-Achermann H (2000). *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford, Oxford University Press.
- Brown B, Ward SC (1988). Basicranial and facial topography in *Pongo* and *Sivapithecus*. In *Orang Utan Biology* (Schwartz J, ed.), pp 247–260. New York, Plenum Press.
- Brunet M, Guy F, Pilbeam D, Zollikofer C (2002). A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418: 145–151.
- Casanovas-Vilar I, Alba DM, Moyà-Solà S, Galindo J, Cabrera L, Garces M, Furia M, Robles JM, Köhler M, Angelone C (2008). Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). *Journal of Human Evolution* 55: 589–603.
- Cerling TE (1992). Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology Palaeoecology* 97: 241–247.
- Cerling TE, Harris JM, Ambrose S, Leakey MG, Solounias NJ (1997). Dietary and environmental reconstruction with stable isotope analyses of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya. *Journal of Human Evolution* 33: 635–650.
- Cerling TE, Wynn JG, Andanje SA, Bird MI, Korir DK, Levin NE, Mace W, Macharia AN, Quade J, Remien CH (2011). Woody cover and hominin environments in the past 6 million years. *Nature* 476: 51–56.
- Chaimanee Y, Jolly D, Benammi M, Tafforeau P, Duzer D, Moussa I, Jaeger J-J (2003). A middle Miocene hominoid from Thailand and orangutan origins. *Nature* 422: 61–65.
- Chaimanee Y, Suteethorn V, Jintsakul P, Vidthayanon C, Marandat B, Jaeger J-J (2004). A new orang-utan relative from the late Miocene of Thailand. *Nature* 427: 439–441.
- Chesters KI (1957). The Miocene flora of Rusinga Island, Lake Victoria, Kenya. *Palaeontographica* 101: 30–71.
- Collinson ME, Andrews P, Bamford M (2009). Taphonomy of the early Miocene flora, Hiwegi Formation, Rusinga Island, Kenya. *Journal of Human Evolution* 57: 149–162.
- Cook JM, Rasplus JY (2003). Mutualists with attitude: coevolving fig wasps and figs. *Trends in Ecological Evolution* 18: 241–248.
- Darwin C (1859). *On the Origin of Species by Means of Natural Selection*. London, John Murray.

- Dean MC (2006). Tooth microstructure tracks the pace of human life-history evolution. *Proceedings of the Royal Society B* 273: 2799–2808.
- Deane AS (2009). Early Miocene catarrhine dietary behaviour: the influence of the Red Queen effect on incisor shape and curvature. *Journal of Human Evolution* 56: 275–285.
- De Bonis L, Koufos GD (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.
- De Bonis L, Melentis J (1977). Un nouveau genre de primate hominoïde dans le Vallesien (Miocène supérieur) de Macédoine. *Comptes Rendus de l'Académie des Sciences, Paris* 284: 1393–1396.
- De Bonis L, Melentis J (1978). Les primates hominoïdes du Miocène supérieur de Macédoine. *Annales de Paléontologie* 64: 185–202.
- De Bonis L, Bouvrain G, Geraads D, Koufos G (1992). Diversity and palaeoecology of Greek late Miocene mammalian faunas. *Comptes Rendus de l'Académie des Sciences, Paris* 291: 99–121.
- Elias RB, Gil A, Silva L, Fernández-Palacios JM, Azevedo B, Reis F (2016). Natural zonal vegetation of the Azores Islands: characterization and potential distribution. *Phytocoenologia* 46: 107–123.
- Ersoy A, Kelley J, Andrews P, Alpagut B (2008). Hominoid phalanges from the middle Miocene site of Paşalar, Turkey. *Journal of Human Evolution* 54: 518–529.
- Fernandez-Jalvo Y, Andrews P (2011). When humans chew bones. *Journal of Human Evolution* 60: 117–123.
- Foley RA (2001). The evolutionary consequences of increased carnivory in hominids. In *Meat-Eating and Human Evolution* (Stanford CB, Bunn HT, eds.), pp 305–331. Oxford, Oxford University Press.
- Fuss J, Spassov N, Begun DR, Bohm M (2017). Potential hominin affinities of *Graecopithecus* from the late Miocene of Europe. *PLoS One* 12: e0177127.
- Galik K, Senut B, Pickford M, Gommery D, Treil J, Kupervage AJ, Eckhardt RB (2004). External and internal morphology of the BAR 1002'00 *Orrorin tugenensis* femur. *Science* 305: 1450–1453.
- Gebo DL, Beard KC, Teaford MF, Walker A, Larson SG, Jungers WL, Fleagle JG (1988). A hominoid proximal humerus from the early Miocene of Rusinga Island, Kenya. *Journal of Human Evolution* 17: 393–401.
- Gebo DL, Malit NR, Nengo IO (2009). New proconsuloid postcranials from the early Miocene of Kenya. *Primates* 50: 311–319.
- Goodall J (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Harvard University Press.
- Groves CP (1989). *A Theory of Human and Primate Evolution*. Oxford, Oxford Scientific Publications.
- Groves CP (2001). *Primate Taxonomy*. Washington, The Smithsonian Institution.
- Haile-Selassie Y (2001). Late Miocene hominids from the Middle Awash. *Nature* 412: 178–181.
- Haile-Selassie Y (2004). Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science* 303: 1503–1505.
- Harrison RD (2010a). Figs and the diversity of tropical rainforests. *Ecography* 33: 148–158.
- Harrison T (1991). The implications of *Oreopithecus* for the origins of bipedalism. In *Origine(s) de la bipédie chez les hominidés* (Coppens Y, Senut B, eds.), pp 235–244. Paris, Cahiers de Paléanthropologie, CNRS.
- Harrison T (1993). Cladistic concepts and the species problem in hominoid evolution. In *Species Concepts and Primate Evolution* (Kimbel WH, Martin LB, eds.), pp 345–371. New York, Plenum Press.
- Harrison T (2002). Late Oligocene to middle Miocene catarrhines from Afro-Arabia. In *The Primate Fossil Record* (Hartwig WC, ed.), pp 311–338. Cambridge, Cambridge University Press.
- Harrison T (2010b). Dendropithecoidea, Proconsuloidea and Hominoidea. In *Cenozoic Mammals of Africa* (Werdelin L, Sanders WJ, eds.), pp 429–469. Berkeley, University of California Press.
- Harrison T (2012). Apes among the tangled branches of human origins. *Science* 327: 532–534.
- Harrison TS, Harrison T (1989). Palynology of the late Miocene *Oreopithecus*-bearing lignite from Bacinello, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 76: 45–65.
- Harrison T, Rook L (1997). Enigmatic anthropoid or misunderstood ape? The phylogenetic status of *Oreopithecus bambolii* reconsidered. In *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations* (Begun DR, Ward CV, Rose MD, eds.), pp 327–362. New York, Plenum Press.
- Hartwig WC (2002) (ed.). *The Primate Fossil Record*. Cambridge, Cambridge University Press.
- Heizmann E, Begun DR (2001). The oldest Eurasian hominoid. *Journal of Human Evolution* 41: 463–481.
- Hockings KJ, Anderson AR, Matsuzawa T (2010). Flexible feeding on cultivated underground storage organs by rainforest-dwelling chimpanzees at Bossou, West Africa. *Journal of Human Evolution* 58: 227–233.
- Hughes JF, Skaletsky H, Pynitkova T, Graves TA, van Daalen KM, Minx PJ, Fulton RS, McGrath SD, Locke DP, Friedman C, Trask BJ, Mardis ER, Warren WC, Repping S, Rozen S, Willson RK, Page C (2010). Chimpanzee and human Y chromosomes are remarkably divergent in structure and gene content. *Nature* 463: 536–539.
- Humphrey LT, Andrews P (2008). Metric variation in the postcanine teeth from Pasalar, Turkey. *Journal of Human Evolution* 54: 503–517.

- Ishida H, Pickford M (1997). A new late Miocene hominoid from Kenya: *Samburupithecus kiptalami* gen. et sp. nov. *Comptes Rendus de l'Académie des Sciences, Paris* 325: 823–829.
- Ishida H, Kunitatsu Y, Nakatsukasa M, Nakano Y (1999). New hominoid genus from the middle Miocene of Nachola. *Anthropological Science* 107: 189–191.
- Ishida H, Kunitatsu Y, Takano T, Nakano Y, Nakatsukasa M (2004). *Nacholapithecus* skeleton from the Middle Miocene of Kenya. *Journal of Human Evolution* 46: 69–103.
- Izquierdo T (2011). Vegetation indices changes in the cloud forest of La Gomera Island (Canary Islands) and their hydrological implications. *Hydrological Processes* 25: 1531–1541.
- Jacobs BF (1987). A middle Miocene (12.2 my old) forest in the East African Rift Valley, Kenya. *Journal of Human Evolution* 16: 147–155.
- Jacobs BF (1992). Taphonomy of a middle Miocene autochthonous forest assemblage, Ngorora Formation, central Kenya. *Palaeogeography, Palaeoclimatology, Palaeoecology* 99: 31–40.
- Kappelman J, Richmond BG, Seiffert ER, Maga AM, Ryan TM (2003). Hominoidea (Primates). In *Geology and Paleontology of the Miocene Sinap Formation* (Fortelius M, Kappelman J, Sen S, Bernor R, eds.), pp 90–124. New York, Columbia University Press.
- Kay RF (1977). Diet of early Miocene African hominoids. *Nature* 268: 628–630.
- Kelley J (2008). Identification of a single birth cohort in *Kenyapithecus kizili* and the nature of sympatry between *K. kizili* and *Griphopithecus alpani* at Paşalar. *Journal of Human Evolution* 54: 530–537.
- Kelley J, Andrews P, Alpagut B (2008). A new hominoid species from the middle Miocene site of Paşalar, Turkey. *Journal of Human Evolution* 54: 455–479.
- Kikuchi Y, Nakano D, Nakatsukasa M, Kunitatsu Y, Shimizu D, Ogihara N, Tsujikawa H, Takano T, Ishida H (2012). Functional morphology and anatomy of cervical vertebrae in *Nacholapithecus kerioi*, a middle Miocene hominoid from Kenya. *Journal of Human Evolution* 62: 677–695.
- Kingdon J (2002). *Lowly Origin*. Princeton, Princeton University Press.
- Kingston JD (2011). Stable isotope analyses of Laetoli fossil herbivores. In *Palaeontology and Geology of Laetoli, Tanzania* (Harrison T, ed.), pp 367–380. New York, Springer.
- Kingston JD, Harrison T (2007). Isotopic dietary reconstructions of Pliocene herbivores at Laetoli. Implications for early hominin paleoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243: 272–306.
- Kingston JD, Jacobs BF, Hill A, Deino A (2002). Stratigraphy, age and environments of the late Miocene Mpesida Beds, Tugen Hills, Kenya. *Journal of Human Evolution* 42: 95–116.
- Kivell TL, Begun DR (2009). New primate carpal bones from Rudabánya (late Miocene, Hungary): taxonomic and functional implications. *Journal of Human Evolution* 57: 697–709.
- Köhler M (1993). Skeleton and habitat of recent and fossil ruminants. *Münchner Geowissenschaftliche Abhandlungen* 25: 1–88.
- Köhler M, Moyà-Solà S, Andrews P (1999). Order Primates. In *Land Mammals of Europe* (Rossner G, Heissig K, eds.), pp 91–104. Munich, Pfeil.
- Kordos L (1985). Environmental reconstruction for prehomínids of Rudabánya, NE Hungary. *Akadémia der Wissenschaften der DDR Zentralinstitut für alte Geschichte und Archäologie* 41: 82–85.
- Kordos L, Begun DR (1997). A new reconstruction of RUD 77, a partial cranium of *Dryopithecus brancoi* from Rudabánya, Hungary. *American Journal of Physical Anthropology* 103: 277–294.
- Kordos L, Begun DR (2002). Rudabánya: a late Miocene subtropical swamp deposit with evidence of the origin of the African apes and humans. *Evolutionary Anthropology* 11: 45–57.
- Kovar-Eder J (2003). Vegetation dynamics in Europe during the Neogene. *Deinsea* 10: 373–392.
- Kovar-Eder J, Teodoridis V (2018). The middle Miocene Central European plant record revisited: widespread subhumid sclerophyllous forests indicated. *Fossil Imprint* 74: 115–134.
- Kovar-Eder J, Kvacek J, Zastawniak E, Givulescu R, Hably L, Mihajlovic D, Teslenko J, Walther H (1996). Floristic trends in the vegetation of the Paratethys surrounding areas during Neogene times. In *The Evolution of Western Eurasian Neogene Mammal Faunas* (Bernor RL, Fahlbusch V, Mitmann H-W, eds.), pp 395–413. New York, Columbia University Press.
- Kretzoi M (1975). New ramapithecines and *Pliopithecus* from the lower Pliocene of Rudabánya in north-eastern Hungary. *Nature* 257: 578–581.
- Kretzoi M, Krolpp E, Lorincz H, Palfalvy I (1974). A Rudabányai Alsopannonai prehomínidas lelohely flórája, faunája es retegáni helyzete. M. All. *Foldtani Intezet Evi Jelentezi* 1974: 365–394.
- Kunitatsu Y, Ishida H, Nakatsukasa M, Nakano Y, Sawada Y, Nakayama K (2004). Maxillae and associated gnathodontal specimens of *Nacholapithecus kerioi*, a large-bodied hominoid from Nachola, northern Kenya. *Journal of Human Evolution* 46: 365–400.
- Kunitatsu Y, Nakatsukasa M, Sawada Y, Sakai T, Hyodo M, Itaya T, Nakaya H, Saegusa H, Mazurier A, Saneyoshi M, Tsujikawa H, Yamamoto A, Mbua E (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 of the United States of America* 104: 19220–19225.
- Leakey MG, Feibel CS, MacDougall I, Walker A (1995). New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376: 565–571.

- Leakey MG, Feibel CS, MacDougall I, Walker A (1998). New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* 393: 62–66.
- Le Gros Clark WE, Leakey LSB (1951). *The Miocene Hominoidea of East Africa*. London, British Museum (Natural History).
- Lehmann T, Manthi FK, McNulty KP (2012). Early Neogene environments in East Africa: evidence from dental microwear of tragulids. *Palaeogeography, Palaeoclimatology, Palaeoecology* 342: 84–96.
- Lewis OJ (1989). *Functional Morphology of the Evolving Hand and Foot*. Oxford, Clarendon Press.
- Louchart A, Wesselman H, Blumenschine RJ, Hlusko LJ, Njau JK, Black MT, Asnake M, White TS (2009). Taphonomic, avian and small-vertebrate indicators of *Ardipithecus ramidus* habitat. *Science* 326: 66–70.
- Lovejoy CO, Latimer B, Suwa G, Asfaw B, White TD (2009a). Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. *Science* 326: 72–80.
- Lovejoy CO, Simpson SW, Whit TD, Asfaw B, Suwa G (2009b). Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science* 326: 70–78.
- Lovejoy CO, Suwa G, Simpson SW, Matternes JH, White T (2009c). The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. *Science* 326: 100–106.
- Lovejoy CO, Suwa G, Spurlock L, Asfaw B, White TD (2009d). The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking. *Science* 326: 71–77.
- MacLatchy L (2004). The oldest ape. *Evolutionary Anthropology* 13: 90–103.
- MacLatchy L, Bossert WH (1996). An analysis of the articular surface distribution of the femoral head and acetabulum in anthropoids, with implications for hip function in Miocene hominoids. *Journal of Human Evolution* 31: 425–453.
- Makishima H (2005). Flora and vegetation of Nachola, Samburu District, northern Kenya: a study of vegetation in an arid land. *African Study Monographs, Supplement* 32: 63–78.
- Marmí J, Casanovas-Vilar I, Robles JM, Moyà-Solà S, Alba M (2012). The paleoenvironment of *Hispanopithecus laietanus* as revealed by paleobotanical evidence from the late Miocene of Can Llobateres 1 (Catalonia, Spain). *Journal of Human Evolution* 62: 412–423.
- Marzke MW (1997). Precision grips, hand morphology and tools. *American Journal of Physical Anthropology* 102: 91–110.
- Maxbauer DP, Peppe DJ, Bamford M, McNulty KP, Harcourt-Smith WEH, Davis LE (2013). A morphotype catalog and paleoenvironmental interpretations of early Miocene fossil leaves from the Hiwengi Formation, Rusinga Island, Lake Victoria, Kenya. *Palaeontologia Electronica* 16.3.28A.
- McGrew WC (1992). *Chimpanzee Material Culture*. Cambridge, Cambridge University Press.
- McGrew WC (2010). In search of the last common ancestor: new findings on wild chimpanzees. *Philosophical Transactions of the Royal Society* 365: 3267–3276.
- McGrew WC (2014). The “other faunivory” revisited: insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution* 71: 4–11.
- McGrew WC, Marchant LF, Nishida T (1996). *Great Ape Societies*. Cambridge, Cambridge University Press.
- McNulty KP, Begun DR, Kelley J, Manthi FK, Mbua EN (2015). A systematic revision of *Proconsul* with the description of a new genus of early Miocene hominoid. *Journal of Human Evolution* 84: 42–61.
- Merceron G, Schulz E, Kordos L, Kaiser TM (2007). Paleoenvironment of *Dryopithecus brancoi* at Rudabánya, Hungary: evidence from dental meso- and micro-wear analyses of large vegetarian mammals. *Journal of Human Evolution* 53: 331–349.
- Michel LA, Peppe DJ, Lutz JA, Driese SG, Dunsworth HM, Harcourt-Smith WEH, Horner WH, Lehmann T, Nightingale S, McNulty KP (2014). Remnants of an ancient forest provide ecological context for early Miocene fossil apes. *Nature Communications* 5: 3236.
- Mitani JC, Watts DP, Amsler SJ (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology* 20: 507–508.
- Mittermeier RA, Wilson DE, Rylands AB (2013). *Handbook of Mammals of the World: Primates*. Barcelona, Conservation International, Lynx Edicions.
- Morbeck ME (1983). Miocene hominoid discoveries from Rudabánya: implications from the postcranial skeleton. In *New Interpretations of Ape and Human Ancestry* (Ciochon RL, Corruccini RS, eds.), pp 369–404. New York, Plenum Press.
- Moyà-Solà S, Köhler M (1995). New partial cranium of *Dryopithecus lartet*, 1863 (Hominoidea, Primates) from the upper Miocene of Can Llobateres, Barcelona, Spain. *Journal of Human Evolution* 29: 101–139.
- Moyà-Solà S, Köhler M (1996). The first *Dryopithecus* skeleton: origins of great ape locomotion. *Nature* 379: 156–159.
- Moyà-Solà S, Köhler M (1997). The phylogenetic relationships of *Oreopithecus bambolii* Gervais, 1872. *Comptes Rendus de l'Académie des Sciences, Paris* 324: 141–148.
- Moyà-Solà S, Alba DM, Almecija S, Casanovas-Vilar I, Köhler M, de Esteban-Trivigno S, Robles JM, Galindo J, Fortuny J (2009a). A unique middle Miocene European hominoid and the origins of the great ape and human clade. *Proceedings of the National Academy of Sciences of the United States of America* 106: 1–6.

- Moyà-Solà S, Köhler M, Alba DM, Casanovas-Vilar I, Galindo J (2004). *Pierolapithecus catalaunicus*, a new middle Miocene great ape from Spain. *Science* 306: 1339–1344.
- Moyà-Solà S, Köhler M, Alba DM, Casanovas-Vilar I, Galindo J, Robles JM, Cabrera L, Garces M, Almecija S, Beamud E (2009b). First partial face and upper dentition of the middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Valles-Penedes Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. *American Journal of Physical Anthropology* 139: 126–145.
- Munro SJ (2010). *Molluscs as Ecological Indicators in Palaeoanthropological Contexts*. PhD thesis, Australian National University, Canberra.
- Nakatsukasa M (2008). Comparative study of Moroto vertebral specimens. *Journal of Human Evolution* 55: 581–588.
- Nakatsukasa M, Kunimatsu Y, Nakano Y, Ishida H (2007). Vertebral morphology of *Nacholapithecus keiroi* based on KNM-BG 35250. *Journal of Human Evolution* 52: 347–369.
- Nakatsukasa M, Yamanaka A, Kunimatsu Y, Shimizu D, Ishida H (1998). A newly discovered *Kenyapithecus* skeleton and its implications for the evolution of positional behaviour in Miocene East African hominoids. *Journal of Human Evolution* 34: 657–664.
- Napier JR (1960). Studies of the hands of living primates. *Proceedings of the Zoological Society of London* 134: 647–657.
- Napier JR (1964). The evolution of bipedal walking in the hominids. *Archives de Biologie, Liège* 75: 673–708.
- Napier JR, Davis PR (1959). *The Fore-Limb Skeleton and Associated Remains of Proconsul africanus*. London, British Museum (Natural History).
- Nelson SV (2013). Chimpanzee fauna isotopes provide new interpretations of fossil ape and hominin ecologies. *Proceedings of the Royal Society B* 280: 20132324.
- Newton-Fisher N (1999). Infant killers of Budongo. *Folia Primatologica* 70: 167–169.
- Nishida T, Kawanaka K (1985). Within-group cannibalism by adult male chimpanzees. *Primates* 26: 274–284.
- O'Malley RC, McGrew WC (2014). Primates, insects and insect resources. *Journal of Human Evolution* 71: 1–3.
- Patel BA, Susman RL, Rossie JB, Hill A (2009). Terrestrial adaptations in the hands of *Equatorius africanus* revisited. *Journal of Human Evolution* 57: 763–772.
- Patterson N, Richter DJ, Gnerre S, Lander ES, Reich D (2006). Genetic evidence for complex speciation of humans and chimpanzees. *Nature* 441: 1103–1108.
- Pérez de los Ríos M, Moyà-Solà S, Alba DM (2012). The nasal and paranasal architecture of the middle Miocene ape *Pierolapithecus catalaunicus* (Primates: Hominidae): phylogenetic implications. *Journal of Human Evolution* 63: 497–506.
- Pickford M, Senut B (2001). The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. *Comptes Rendus de l'Académie de Sciences, Paris* 332: 145–152.
- Pickford M, Senut B (2005). Hominoid teeth with chimpanzee- and gorilla-like features from the Miocene of Kenya: implications for the chronology of ape-human divergence and biogeography of Miocene hominoids. *Anthropological Science* 113: 95–102.
- Pilbeam DR (1982). New hominoid skull material from the Miocene of Pakistan. *Nature* 295: 232–234.
- Pilbeam DR, Simons EL (1971). Humerus of *Dryopithecus* from Saint Gaudens, France. *Nature* 229: 406–407.
- Pobiner BL, DeSilva J, Sanders WJ, Mitani JC (2007). Taphonomic analysis of skeletal remains from chimpanzee hunts at Ngogo, Kibale National Park, Uganda. *Journal of Human Evolution* 52: 614–636.
- Quade J, Cerling TE, Andrews P, Alpagut B (1995). Palaeodietary reconstruction of Miocene fauna from Paşalar, Turkey, using stable carbon and oxygen isotopes of fossil tooth enamel. *Journal of Human Evolution* 28: 373–384.
- Rafferty KL (1998). Structural design of the femoral neck in primates. *Journal of Human Evolution* 34: 361–383.
- Rafferty KL, Walker A, Ruff C, Rose M, Andrews P (1995). Postcranial estimates of body weight in *Proconsul*, with a note on a distal tibia of *P. major* from Napak, Uganda. *American Journal of Physical Anthropology* 97: 391–402.
- Rein TR (2010). *Locomotor Function and Phylogeny: Implications for Interpreting the Hominoid Fossil Record*. PhD thesis, New York University.
- Rein TR, Harrison T, Zollikofer PE (2012). Skeletal correlates of quadrupedalism and climbing in the anthropoid forelimb: implications for inferring locomotion in Miocene catarrhines. *Journal of Human Evolution* 61: 564–574.
- Retallack GJ (1990). *Soils of the Past: An Introduction to Paleopedology*. Boston, Unwin Hyman.
- Retallack GJ, Dugas DP, Bestland EA (1990). Fossil soils and grasses of a middle Miocene East African grassland. *Science* 247: 1325–1328.
- Rogers J, Gibbs RA (2014). Comparative primate genomics: emerging patterns of genome content and dynamics. *Nature Reviews* 15: 347–359.

- Rose MD (1983) Miocene hominoid postcranial morphology: monkey-like, ape-like, neither, or both? In *New Interpretations of Ape and Human Ancestry* (Ciochon RL, Corruccini RS, eds.), pp 405–417. New York, Plenum Press.
- Rose MD (1989). New postcranial specimens of catarrhines from the middle Miocene Chinji Formation, Pakistan: descriptions and a discussion of proximal humeral functional morphology in anthropoids. *Journal of Human Evolution* 18: 131–162.
- Rose MD (1994). Quadrupedalism in some Miocene catarrhines. *Journal of Human Evolution* 26: 387–411.
- Rossie JB, MacLatchy L (2013). Dentognathic remains of an *Afropithecus* individual from Kalodirr. *Journal of Human Evolution* 65: 199–208.
- Ruff CB, Higgins R (2013). Femoral neck structure and function in early hominins. *American Journal of Physical Anthropology* 150: 512–525.
- Schwartz JH (1987). *The Red Ape: Orang-Utans and Human Origins*. London, Elm Tree Books.
- Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y (2001). First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus de l'Académie de Sciences, Paris* 332: 137–144.
- Shipman P (1982). Reconstructing the paleoecology and taphonomic history of *Ramapithecus wickeri* at Fort Ternan, Kenya. Museum Briefs 26. Columbia, Museum of Anthropology.
- Shipman P (1986). Paleoecology of Fort Ternan reconsidered. *Journal of Human Evolution* 15: 193–204.
- Smith CC, Morgan ME, Pilbeam DR (2010). Isotopic ecology and dietary profiles of Liberian chimpanzees. *Journal of Human Evolution* 58: 43–55.
- Stanford CB, Bunn HT (2001). *Meat Eating and Human Evolution*. Oxford, Oxford University Press.
- Suwa G, Asfaw B, Kono RT, Kubo D, Lovejoy CO, White TD (2009). The *Ardipithecus* skull and its implications for hominid origins. *Science* 326: 100–106.
- Suwa G, Kono RT, Katoh S, Asfaw B, Beyene Y (2007). A new species of great ape from the late Miocene epoch in Ethiopia. *Nature* 448: 921–924.
- Ungar PS (2007) (ed.). *Evolution of the Human Diet*. Oxford, Oxford University Press.
- Verdcourt B (1963). The Miocene non-marine Mollusca of Rusinga Island, Lake Victoria and other localities in Kenya. *Palaeontographica* 121: 1–37.
- Viranta S, Andrews P (1995). Carnivore guild structure in the Palarar Miocene fauna. *Journal of Human Evolution* 28: 359–372.
- Walker AC (1997). *Proconsul* function and phylogeny. In *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation* (Begun DR, Ward CV, Rose MD, eds.), pp 209–224. New York, Plenum Press.
- Walker AC, Falk D, Smith R, Pickford M (1983). The skull of *Proconsul africanus*: reconstruction and cranial capacity. *Nature* 305: 525–527.
- Ward CV (1993). Torso morphology and locomotion in *Proconsul nyanzae*. *American Journal of Physical Anthropology* 92: 291–328.
- Ward CV, Ruff CB, Walker AC, Teaford MF, Rose MD, Nengo IO (1995). Functional morphology of *Proconsul* patellas from Rusinga Island, Kenya, with implications for other Miocene-Pliocene catarrhines. *Journal of Human Evolution* 29: 1–19.
- Ward CV, Walker A, Teaford MF (1991). *Proconsul* did not have a tail. *Journal of Human Evolution* 21: 215–220.
- Ward SC, Brown B, Hill A, Kelley J, Downs W (1999). *Equatorius*: a new hominoid genus from the middle Miocene of Kenya. *Science* 285: 1382–1386.
- Watts DP (2008). Scavenging by chimpanzees at Ngogo and the relevance of chimpanzee scavenging to early hominin behavioural ecology. *Journal of Human Evolution* 54: 125–133.
- Werdelin L, Sanders WJ (2010) (eds.). *Cenozoic Mammals of Africa*. Berkeley, University of California Press.
- White F (1983). *The Vegetation of Africa. A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa*. Paris, UNESCO.
- White TD, Suwa G, Asfaw B (1994). *Australopithecus ramidus*: a new species of early hominid from Aramis Ethiopia. *Nature* 371: 306–312.
- Woldegabriel G, Ambrose SH, Barboni D, Bonnefille R, Bremond L, Currie B, DeGusta D, Hart WK, Murray AM, Renne PR, Jolly-Saad MC, Steward KM, White TD (2009). The geological, isotopic, botanical, invertebrate, and lower vertebrate surroundings of *Ardipithecus ramidus*. *Science* 326: 65e1–5.
- Woldegabriel G, Hailie-Selassie Y, Renne PR, Hart WK, Ambrose SH, Asfaw B, Heiken G, White TD (2001). Geology and palaeontology of the late Miocene middle Awash valley, Afar rift, Ethiopia. *Nature* 412: 175–178.
- Woldegabriel G, White TD, Suwa G, Renne P, De Heinzelin J, Hart WK, Heiken G (1994). Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature* 371: 330–333.
- Wolpoff MH, Senut B, Pickford M, Hawks J (2002). *Sahelanthropus* or “*Sahelpithecus*”? *Nature* 419: 581–582.
- Wood B, Harrison T (2011). The evolutionary context of the first hominins. *Nature* 470: 347–352.
- Wrangham R, Peterson D (1997). *Demonic Males: Apes and the Origins of Human Violence*. London, Bloomsbury Press.