Miocene Hominids and the Origins of the African Apes and Humans

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Abstract

In the past 20 years, new discoveries of fossil apes from the Miocene have transformed our ideas about the timing, geography, and causes of the evolution of the African apes and humans. Darwin predicted that the common ancestor of African apes and humans would be found in Africa. Yet the majority of fossil great apes are from Europe and Asia. I briefly review the fossil record of great apes and then examine the main competing hypotheses of our origins, African or European, inspired by these recent discoveries, concluding that elements of both ideas are likely to be correct. Given current interpretations of the paleobiology of fossil apes and relationships among living hominids, I suggest that the last common ancestor of chimpanzees and humans was morphologically unique, but more chimpanzee-like than hominin-like: a knuckle-walker with a chimpanzee-sized brain, canine sexual dimorphism, and many probable behavioral similarities to living chimpanzees.

INTRODUCTION

The First 137 Years

The history of research on the origins of the great apes and humans is over 150 years old. In 1856 Edouard Lartet published an account of a new fossil ape from France that he called *Dryopithecus fontani* (Lartet 1856). By the end of the nineteenth century a handful of specimens had been recovered from Germany and France, and many authorities recognized evolutionary links between these fossils and living apes. Even Darwin, who predicted that the fossilized antecedents of African apes and humans would be found in Africa, speculated that *Dryopithecus* may in fact be that ancestor, despite being from Europe (Darwin 1871).

Darwin's African prediction nevertheless seemed to be validated by discoveries in Kenya in the 1920s, and much of the attention of researchers of great ape and human origins has been focused on Africa ever since. *Proconsul*, named by Arthur Hopwood in 1933, was widely accepted as a direct ancestor of Africa apes, and when *Kenyapithecus* was discovered and described by Louis Leakey in 1962, many believed that the earliest member of the human family had been found in Africa as well (Hopwood 1933, Leakey 1962). It was not until the 1970s that attention returned to Europe, with the discoveries of Louis de Bonis and colleagues in Greece and Miklós Kretzoi in Hungary. In both cases, the describers of these new taxa, *Ouranopithecus* and *Rudapithecus*, argued that these fossil great apes are closely related to African apes and humans, or even directly related to humans (Bonis et al. 1974, Kretzoi 1969).

Despite those new discoveries in Europe, most researchers continued to prefer Darwin's idea that the African ape and human clade originated in Africa, the European genera representing evolutionary dead ends that migrated to Europe at some point after the origin of the lineage (e.g., Szalay & Delson 1979). The discovery of more complete fossil specimens from Pakistan in the 1980s led most researchers to conclude that fossil apes referred to variously as *Kenyapithecus*, *Ramapithecus*, or *Rudapithecus* are

in fact not closely related to humans, as Leakey and Kretzoi had proposed. One of these taxa, *Ramapithecus*, was reinterpreted as a close relative of orangutans, and in fact the genus name was synonymized with the previously named *Sivapithecus* (Greenfield 1974, 1980; Pilbeam 1982). *Kenyapithecus* was soon reinterpreted as a basal (stem) ape without a direct relationship to any individual member of the great ape and human group, and *Rudapithecus* came to be viewed as synonymous with *Dryopithecus*, and was most commonly seen as an evolutionary dead end (Andrews & Martin 1987; Harrison 2010). It was not until the discovery of several very well-preserved specimens from Europe that a serious reexamination of the fossil record of apes in Europe took place, the "Renaissance of Europe's ape" (Martin & Andrews 1993). In the 17 years since then, many new discoveries in both Europe and Africa have contributed to a lively debate on the topic of the origins and evolution of the African ape and human clade.

The Past 17 Years

Most authorities accept the hypothesis that fossil apes from Asia are members of the lineage that includes the living orangutan, which is usually referred to the subfamily Ponginae (Kelley 2002) (**Table 1**). A much more animated debate characterizes interpretations of the fossil record of apes in Europe and Africa. There are three main points of view in the current literature. Some researchers support the idea that no known fossil ape has any specific evolutionary relationship to living great apes and humans. As noted, most authorities accept the evolutionary link between *Sivapithecus* and *Pongo*, but the idea that all Eurasian apes are evolutionary dead ends has some supporters (Benefit & McCrossin 1995, Pilbeam 1997, Pilbeam & Young 2004). However, most researchers view the fossil apes of Europe as close relatives of living great apes. Moyà-Solà and colleagues have suggested that *Dryopithecus*, like *Sivapithecus*, is a member of the orangutan clade (Moyà-Solà & Köhler 1995). This suggestion is based on the sample of fossil apes from Spain, which are now

Table 1   A classification of taxa discussed in the text

Magnafamily Hominidea[a]
Superfamily Proconsuloidea
   Proconsul
   Afropithecus
   Heliopithecus
Superfamily Hominoidea
  Family Hominidae
    Subfamily Griphopithecinae
      Griphopithecus
      Equatorius
      Nacholapithecus
      Kenyapithecus
    Subfamily Homininae
     Tribe Dryopithecini
      Dryopithecus
      Hispanopithecus
      Rudapithecus
      Ouranopithecus
     Tribe Hominini
      Subtribe Hominina
        Homo
        Australopithecus
        Paranthropus
        Ardipithecus
        Sahelanthropus
        Orrorin
        Pan
      Subtribe Gorillina
        Gorilla
    Subfamily Pongidae
      Pongo
     Tribe *Sivapithecini*[b]
      Sivapithecus
      Ankarapithecus
      Gigantopithecus
     Tribe Lufengpithecini[b]
      Lufengpithecus
      Khoratpithecus
  Family Hylobatidae

[a]Follows Begun (2007).
[b]Follows the classification of Kelley (2002) except for *Khoratpithecus*, which was not known at the time, and *Ankarapithecus*, following Begun & Güleç (1998).

referred to the genus *Hispanopithecus*. Other researchers interpret the European fossil great apes to be more closely related to African apes and humans. De Bonis and Koufos offer the hypothesis that *Ouranopithecus* is more closely related to humans than to any great ape, and represents the ancestor of australopithecines and living humans (Bonis & Koufos 1994, Koufos 2007). They interpret *Dryopithecus* (today *Dryopithecus* is split into at least three genera, *Hispanopithecus*, *Rudapithecus*, and *Dryopithecus*) as closely related to African apes. Begun and Kordos have argued that all European fossil great apes are closely related to one another and are the sister group to the African apes and humans (Begun 2007, 2009; Begun & Kordos 1997). This interpretation is based mostly on the sample of fossil great apes from Hungary now attributed once again to *Rudapithecus*.

Most recently, new discoveries have refueled proponents of the African origins hypothesis. Suwa and colleagues describe new remains from Ethiopia that they interpret as early members of the African ape and human clade, possibly closely related to living gorillas (Suwa et al. 2007). Kunimatsu and colleagues describe a new genus of fossil ape from Kenya that they interpret as a close relative of *Ouranopithecus* (Kunimatsu et al. 2007). In both cases, these authors suggest that the African ape and human clade originated in Africa perhaps 12 to 13 Ma, and that some branches of this group moved to Europe, only to become extinct without leaving descendents a few million years later. Here I survey the evidence for both of these hypotheses and in the end I suggest that although both have merit, the preponderance of evidence today favors a European origin of the African ape and human clade and an African origin of the last common ancestor (LCA) of the African apes and humans.

HOMINID ORIGINS

Taxonomy

Before discussing the evidence for hominid origins, and the origins of all other lineages or clades covered in this review, I need to clarify the terminology used here (**Table 1**). By hominid I mean great apes and humans and all their fossil relatives. In other words,

anything more closely related to a living great ape or human than to a hylobatid (gibbons and siamangs). Hominids as defined here are genetically as similar to one another as are members of many other mammalian families (Begun 1999, Goodman et al. 1998). Furthermore, if we are to continue to use the traditional dichotomy of hominid (for humans and our ancestors) and pongid (for the great apes), we would run counter to the laws of biological classification, one of the principles of which is that members of a group (e.g., pongids) must be more closely related to each other than to members of any other group. Because, as traditionally defined, some pongids (African apes), are more closely related to non-pongids (humans) than to the other pongid (orangutans), the pongid-hominid dichotomy breaks the law. African apes must be classified with humans because they are more closely related to each other than either one is to orangutans. That being the case, we have two choices. We could continue to reify humans as hominids, in which case we would need a category for humans and African apes (somewhere between the family and the superfamily), a similar rank for orangutans and their fossil relatives, and another higher level taxonomic rank to unify great apes and humans to the exclusion of the hylobatids. It gets very complicated. The simple alternative is to recognize one family (consistent with the genetics) and two subfamilies (consistent with the genetics, morphology, and fossil evidence) (**Table 2**). To summarize, herein hominine refers to African apes and humans and their fossil relatives, pongine to orangutans and their fossil relatives, and hominin to humans and our fossil relatives. This is a widely recognized classification scheme (Begun 2007, Kelley 2002, Strait & Grine 2004, Wood & Richmond 2000), though there are prominent holdouts for the more traditional classification that excludes all but humans and our ancestors from membership in the Hominidae (White 2002). Nevertheless, here, hominid origin refers to the origin of the clade that includes all great apes and humans and all their fossil relatives, while excluding hylobatids.

Griphopithecus

In my view, the best candidate for the earliest hominid is *Griphopithecus*, a genus of thickly enameled, robust-jawed ape that first appeared approximately 16 to 16.5 Ma (Mega-annum, or millions of years ago) (Begun et al. 2003a, Heizmann & Begun 2001). *Griphopithecus* or *Griphopithecus*-like apes (griphopithecins) are known first from sites in Germany and Turkey (**Table 2**, **Figure 1**). One to 1.5 Ma later similar apes are found in Africa, again with robust jaws and thickly enameled teeth (Ishida et al. 2000, Ward et al. 1999). The teeth are more modern than those of older apes such as *Proconsul*, especially in the development of the cingulum, a ridge of enamel that rims the buccal or outer edge of lower molars and the lingual or inner edge of upper molars. The disappearance of cingula, which is beginning in *Griphopithecus* and related taxa such as *Equatorius*, may be related to the broadening and flattening of the enamel cusps and the substance that supports them from below, the dentine.

Although they are dentally more like living hominids than *Proconsul*, *Griphopithecus* and its relatives retain primitive postcrania. They are more monkey-like than ape-like, as is *Proconsul*, in having fore and hind limbs of roughly equal length, without any indications of the suspensory capabilities of all later fossil and living great apes (Begun 1992b, 2003; Ishida et al. 2004; Nakatsukasa et al. 1998, 2003; Rose 1988, 1997; Rose et al. 1996; Ward 1997a, 2007; Ward et al. 1999). The one big exception with regard to the monkey-like anatomy of these early apes is that they lacked a tail, or, more precisely, they had a coccyx, as in all living hominoids (hylobatids and hominids) (Nakatsukasa et al. 2003, Ward et al. 1991).

Proconsul and middle Miocene hominoids show signs in the hip, wrist, and hand of greater ranges of mobility and more powerful grasping capabilities than those seen in a typical monkey (Beard et al. 1986; Begun et al. 1994; Ward 1993; Ward 1997a, 2007). However, the best-known middle Miocene taxon, *Nacholapithecus*, while having limb proportions closer to those of

Table 2   Fossil apes discussed in the text

Ma	Genera	Important localities (bold = type localities)	Country
19–17	*Proconsul*[a]	Rusinga, Songhor, **Koru**	Kenya
17.5	*Afropithecus*	**Kalodirr**	Kenya
17	*Heliopithecus*	**Ad Datiyah**	Saudi Arabia
16.5–14	*Griphopithecus*	Engelswies, **Děvínská Nová Ves**, Çandır, Paşalar	Germany, Slovakia, Turkey
15	*Equatorius*	**Maboko**	Kenya
15	*Nacholapithecus*	**Nachola**	Kenya
13.5	*Kenyapithecus*	Paşalar, **Fort Ternan**	Turkey, Kenya
12.5–7	*Sivapithecus*	Potwar Plateau	India, Pakistan
9–8	*Lufengpithecus*	**Lufeng**	China
?13.5–7	*Khoratpithecus*[b]	**Khorat**, Ba Sa	Thailand
10	*Ankarapithecus*	**Sinap**	Turkey
6.5	aff. *Gigantopithecus*[c]	Potwar Plateau	India
12	*Dryopithecus*[d]	**St. Gaudens**, Pierola, Can Vila, Can Mata, St. Stefan	France, Spain, Austria
10	*Hispanopithecus*	Can Llobateres, Can Ponsic, **La Tarumba**	Spain
10	*Rudapithecus*	**Rudabánya**	Hungary
9.5	*Ouranopithecus*	**Ravin de la Pluie**, Xirochori, Nikiti	Greece
?7–8	*Udabnopithecus*	**Udabno**	Georgia
?7–8	aff. *Ouranopithecus*[e]	**Çorakyerler**	Turkey
?7–8	aff. *Ouranopithecus*[e]	**Chirpan**	Bulgaria
9.8	*Nakalipithecus*	**Nakali**	Kenya
10	*Chororapithecus*	**Chorora**	Ethiopia
7-6	*Sahelanthropus*	**Toros-Menalla**	Chad
6	*Orrorin*	**Lukeino**	Kenya
5.8	aff. *Ardipithecus*[f]	**Alayla**	Ethiopia

[a]This is a simplified taxonomy. There may well be more than one genus present in this sample.
[b]The older age for *Khoratpithecus* is less certain.
[c]This material is sometimes attributed to *Indopithecus*.
[d]*Dryopithecus* includes the synonymous genera *Pierolapithecus* and *Anoiapithecus*.
[e]These fossils are most similar to *Ouranopithecus* from Greece but probably represent one or more new taxa.
[f]This material is much older and more primitive than *Ardipithecus ramidus* from Aramis, and probably represents a different genus. It may be more closely related to *Orrorin* and/or *Sahelanthropus*.

a monkey than of an ape, has much more powerfully built arms compared to its legs, suggesting the beginning of a shift in importance in locomotion to the forelimbs. Despite this shift in morphology, *Nacholapithecus* shows no signs of having been suspensory (Ishida et al. 2004).

Griphopithecins are the first cosmopolitan hominoid taxon, probably as a result of their powerful jaws and teeth that allowed them to exploit a wide variety of resources. They may have evolved from *Afropithecus*, which had morphologically different but also powerfully built jaws, and was distributed as far north as Saudi Arabia (**Figure 1**) (Begun 2002, Leakey & Walker 1997, Leakey et al. 1988). While moving more or less as a large arboreal monkey, griphopithecins may have been quite adept in the trees, perhaps slow-moving, with postures that would have allowed them access to terminal branches, where much of the food is, despite their relatively large body masses. I see the entire region from Germany and Turkey in the north to Kenya in the south as a potential core area in which early hominids could have
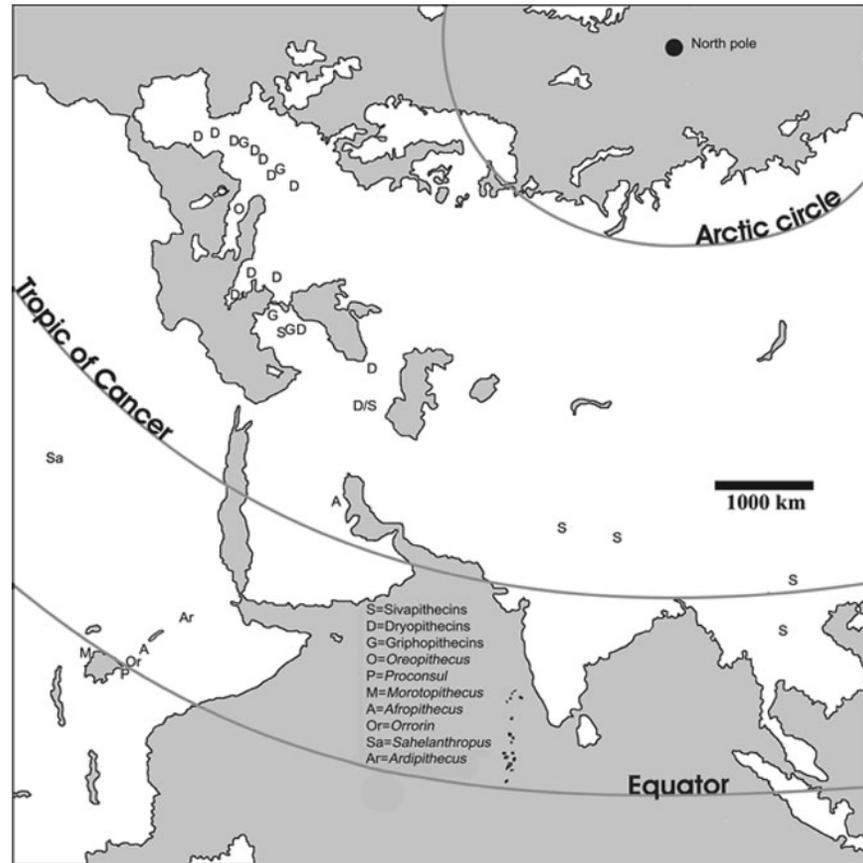
Figure 1

Hominoid localities discussed in this review article.

evolved. But there are major gaps in the record. For example, one species of *Kenyapithecus* is known from 16–16.5 Ma in Turkey and another from Kenya at about 13.5 Ma (Begun et al. 2003a, Kelley et al. 2008, Pickford 1986, Pickford & Morales 1994, Pickford et al. 2006). It was probably present elsewhere in the intervening interval of time but we have not yet found the fossils. This is likely the case for other members of this early radiation. From this core area these stem hominids (not specifically related to either living group of hominids, pongines, or hominines) eventually split, with one segment of the distribution of species dispersing to the north and east and another to the north and west. The causes of

this dispersal are unknown, but griphopithecins are the most primitive hominids we know. The later-occurring sivapithecins of Asia and dryopithecins of Europe are more modern, and strong cases can be made that they are related to living orangutans and African apes and humans, respectively.

ASIAN FOSSIL GREAT APES

As the focus here is on African ape and human origins, I only briefly cover the fossil record of the pongines. *Pongo*, the extant genus of orangutan, is thought by most researchers to be the end of a long and highly diverse radiation of great apes that originated at about

13–16 Ma (Kappelman et al. 1991, Kelley 2002). *Sivapithecus*, the best-known genus of fossil pongine, bears a remarkable resemblance to *Pongo* in its facial morphology, but is different in details of the structure of the jaws, teeth, and certain aspects of the postcranial skeleton (Kelley 2002; Madar et al. 2002; Pilbeam 1982; Rose 1986, 1989; Ward & Brown 1986; Ward 1997b; Ward & Pilbeam 1983). *Lufengpithecus* and *Khoratpithecus*, from south China and Thailand, respectively, more closely resemble *Pongo* in details of their tooth morphology, but less so in the face (only known for *Lufengpithecus*) (Chaimanee et al. 2003, 2004; Kelley 2002; Schwartz 1997). So it is not clear to which, if any, of these fossil apes *Pongo* is most directly related, but it is almost universally agreed that they are all pongines. *Ankarapithecus* from Turkey represents the most western of the sivapithecins and is the only one that overlaps with the geographic ranges of the griphopithecins and dryopithecins (Begun & Güleç 1998, Begun et al. 2003b) (**Figure 1**). I would be remiss in discussing fossil pongines without referring to the most impressive of all of them, *Gigantopithecus* and its relatives. This lineage of huge apes lived from about 6.5 Ma to 300,000 years ago, eventually attaining a size equivalent to two to three big male gorillas. Curiously, despite their huge size and, one would think, large, durable limb bones and skulls, *Gigantopithecus* is known only from isolated teeth (numbering in the thousands) and a small number of partial mandibles. The traditional Chinese apothecary market, which includes medicines made from the ground remains of fossil mammals, may account in large part for this dearth of specimen, given that the first teeth of *Gigantopithecus* known to western biologists came from these shops.

There is much to resolve in the details of the evolution of Asian great apes, but very few researchers doubt that they are pongines. On the other hand, the case for the European side of the dispersal of griphopithecins as members of the African ape/human clade has met with much more debate (**Table 3**).

Table 3   Shared derived characters of the hominines found in one or more dryopithecins

Character state	Fossil taxon[a]
Biconvex premaxilla	R, D, O
Stepped subnasal fossa	R, D, O
Patent incisive canals	R, D, O
Broad, flat nasal aperture base	R, D, O, H
Moderate alveolar prognathism	R, D, O, H
Shallow canine fossa	R, D, O, H
Supraorbital torus	R, D, O, H
Inflated glabella	R, D, O, H
Ethmoidal frontal sinus	R, H
Elongated neurocranium	R
Inclined frontal squama	R, D
Klinorhychy	R
Broad temporal fossa	R
Projecting entoglenoid process	R
Fused articular and tympanic temporal	R
Deep glenoid fossa	R

[a]R: Rudapithecus; D: Dryopithecus; H: Hispanopithecus; O: Ouranopithecus.

EUROPEAN GREAT APES

Dryopithecus

As noted in the introduction, *Dryopithecus* is one of the first described fossil apes, and the only one about which Darwin comments. But it was not until the mid 1970s when sufficiently well preserved fossils began to be found that the significance of *Dryopithecus* began to be more completely understood.

The older sample of *Dryopithecus* from Europe consists of three partial male mandibles and a humeral shaft from the type locality of St. Gaudens, France and a motley collection of isolated teeth and fragmentary jaws from sites in Spain, Germany, Austria, and the Republic of Georgia (Begun 2002) (**Table 2**, **Figure 1**). Other specimens that have at one time or another been attributed to *Dryopithecus* (Simons & Pilbeam 1965, Szalay & Delson 1979) from Europe, Asia, and Africa are now considered to represent different genera. With the discovery of more complete specimens from Greece, Spain, and Hungary, attention turned

back to Europe among those researchers interested in great ape and human origins (Martin & Andrews 1993).

New, more informative *Dryopithecus* have been recovered over the past five years from a cluster of localities near the village of Els Hostalets de Pierola (Catalonia, northern Spain). The Hostalets de Pierola locality has produced a partial skeleton, and two sites at Can Mata yielded an upper and lower jaw, a proximal femur, and a fragmentary facial skeleton (Moyà-Solà & Köhler 1995; Moyà-Solà et al. 2004, 2009a,b). These specimens have attributed to three different genera (*Pierolapithecus*, *Anoiapithecus*, and *Dryopithecus*). I have argued elsewhere that they are most likely to be the same genus and very possibly the same species, *Dryopithecus fontani*, and that is how they are treated here (Begun 2009; Begun et al. 2006, 2008).

Dryopithecus from Spain closely resembles *Dryopithecus fontani* from France in details of its dental anatomy. In both cases the dentitions are more primitive than in later-occurring dryopithecins (**Table 1**) and are to some extent intermediate between these and more ancient genera such as *Kenyapithecus* (Begun 2009; Begun et al. 2006, 2008; Moyà-Solà et al. 2009a). The most obvious differences from later dryopithecins are the slightly more pronounced expression of molar cingula, the more robust male canines, and the relatively small size of the first molars (Begun 2009). *Anoiapithecus* is said to be primitive in the shortness of its face, but the specimen is too poorly preserved to make an accurate measurement, and dryopithecins in general have short faces below the nose, most closely resembling those of gorillas (Begun 1994, 2007, 2009). *Pierolapithecus* is said to be primitive in the orientation of its face relative to the tooth row, but in my view, the upward rotation of the face is due to distortion in the fossil, and with that corrected it would closely resemble the faces of other dryopithecins (Begun 2009).

The appearance of *Dryopithecus* at about 12 Ma parallels the first appearance of *Sivapithecus* at nearly the same time, suggesting that they diverged from a common ancestor possibly 13 to 16 Ma. *Dryopithecus* from St. Gaudens, Hostalets de Pierola, and Can Mata is known from postcranial remains, which are dramatically different from those of the griphopithecins and *Proconsul*. They show unambiguous indications of the importance of highly mobile limbs and suspensory positional behavior (Begun 1992b; Deane & Begun 2008; Moyà-Solà et al. 2004, 2009b; Pilbeam & Simons 1971; Rose 1997). This represents a significant departure from previous fossil apes, and provides clear evidence that *Dryopithecus* is an early great ape of modern aspect, with a broad thorax, stiff lower back, a well-developed capacity for powerful grasping and climbing and the ability to move about in the trees below the branches, though perhaps less efficiently than in later dryopithecins and living apes. I interpret this change to be extremely important in the evolution of the African and human clade. It allowed *Dryopithecus* to remain relatively large and yet retain the capacity to exploit terminal branch resources, by spreading its weight among the branches and by hanging below them to conserve energy, as do other larger highly arboreal animals (e.g., sloths). It also represents the evolutionary origins of human mobile and highly dexterous upper limbs.

In addition to being relatively primitive compared to later species, the teeth of *Dryopithecus* differ from those of the griphopithecins in having a thin layer of enamel and less rounded cusps. They more closely resemble the teeth of chimpanzees and have been interpreted as adaptations to a soft fruit diet, as in modern chimpanzees (Begun 1994, Deane 2007, Kay & Ungar 1997, Ungar 1996, Ungar & Kay 1995). The later occurring dryopithecins *Hispanopithecus*, *Rudapithecus*, and *Ouranopithecus* share even more postcranial derived characters with living great apes, and cranial characters with African apes.

Hispanopithecus

Hispanopithecus is now known from a partial skeleton that reveals numerous details of its anatomy unknown to previous researchers. The trunk and limbs of *Hispanopithecus* are even

better preserved than in the Pierola *Dryopithe-cus* specimen, and show that the limb proportions were not only great ape-like (long arms, short legs), but even extreme in this regard, being most similar to the limb proportions of *Pongo* (Moyà-Solà & Köhler 1996). The lower back has more strongly developed adaptations for stiffness than in *Dryopithecus*, and the hands are huge, with phalanges (finger bones) that closely resemble those of living orangutans in terms of their length and structure (Almécija et al. 2007, Deane & Begun 2008, Moyà-Solà & Köhler 1996). This was an ape with a fully developed adaptation to suspensory positional behavior, with hooks for hands and highly flexible, mobile limbs for clambering among the branches. It is likely that *Hispanopithecus* was as arboreal as living *Pongo* and, given its size—roughly that of a modern female *Pongo*, it may rarely have ventured to the ground. The teeth of *Hispanopithecus* are very similar to those of *Dryopithecus* and *Rudapithecus* (see below), in being basically chimpanzee-like and indicative of a broad-based soft fruit diet (Ungar 1996).

The cranial morphology of *Hispanopithecus* reveals its evolutionary relationship to the African ape and human clade (**Table 3**). *Hispanopithecus* has an incipient supraorbital torus, which distinguishes African apes and humans from *Pongo*, and it has a large frontal sinus positioned low between the orbits, which, once again, is seen only in African apes and humans (Begun 2009). However, the cranium of *Hispanopithecus* is not as well preserved as in another late Miocene great ape, *Rudapithecus*. This sample consists of three cranial specimens including one skull (cranium and mandible) and two brain cases, and provides many more details of the anatomy of the face and the brain case (Kordos & Begun 2001a,b).

Rudapithecus

Rudapithecus provides the earliest evidence of a major reorganization of the skull, klinorhychy, which distinguishes African apes and humans from all other hominoids. A klinorhychous skull has the face tilted downwards relative to the long axis of the brain case. An airorhynchous skull has the face rotated upwards, as in *Pongo* and to a lesser extent *Hylobates* among extant apes (Begun 2007, 2009; Kordos & Begun 2001a; Shea 1985,1988). *Rudapithecus* is distinctly African ape-like in this regard. This fundamental reorganization of the skull is, in my view, a very important shared derived characteristic linking *Rudapithecus*, and by extension, other dryopithecins, with the African ape and human clade.

In addition, two of the *Rudapithecus* crania preserve portions of the anterior part of the palate, the premaxilla in most primates (Ashley-Montagu 1935; Krogman 1930a,b; Schultz 1926,1936). The morphology of the premaxilla and its position and orientation with regard to the maxilla clearly distinguishes genera among extant apes (Begun 2007, Ward & Kimbel 1983, Ward & Pilbeam 1983). African apes have moderate (*Gorilla*) to elongated (*Pan* and *Australopithecus*) premaxilla that overlap the roof of the palate, forming a step into the nasal fossa. In two *Rudapithecus* specimens the position, length, and orientation of the premaxilla are most similar to the condition in *Gorilla*. From what is preserved in *Dryopithecus* from Can Mata and *Ouranopithecus*, the same can be said for these taxa (**Table 3**).

Another striking similarity between dryopithecins and African apes and humans is the configuration of the frontal sinus, one of the paranasal sinuses that are ubiquitous among mammals (Begun 1994, 2007, 2009; Begun & Kordos 1997; Cave 1949, 1961; Cave & Haines 1940; Rossie 2005). In African apes, humans, and dryopithecins there is a large and direct connection between the sinuses of the ethmoid region, between the orbits, and the frontal sinuses. Therefore, it appears that dryopithecins grew their frontal sinuses directly from the ethmoid, as in African apes and humans, representing another important shared derived character of this clade (Cave & Haines, 1940). **Table 3** lists a total of 16 shared derived characters that serve to link dryopithecins to extant African apes and humans. It is noteworthy that they are spread across many different areas

of the cranium, from the premaxilla to the neurocranium and basicranium, and are very unlikely to have evolved in parallel.

Ouranopithecus

Ouranopithecus is a larger great ape from slightly younger sites in Greece (**Table 1**). It shares a number of characters with australopithecines that have led de Bonis and colleagues to conclude that it is an early hominin (Bonis 1983; Bonis et al. 1990; Bonis & Koufos 1993, 1994, 1997; Koufos 2007) (**Table 1**). These include enlarged and thickly enameled molars with broad, flat cusps, small male canines with apical (tip) wear, a robust maxilla and especially zygomatic region of the face, and a comparatively flat condylar process of the mandible. In *Ouranopithecus* all of the similarities to fossil humans can be attributed to selection for a single functional complex, powerful mastication, which has produced parallel adaptations in many fossil and extant primates (*Cebus*, *Pongo*, *Australopithecus*, *Sivapithecus*, *Gigantopithecus*) (Begun & Kordos 1997). Other than the characters that appear to be directly related to powerful chewing, *Ouranopithecus* is very similar to other dryopithecins, and it is for this reason that I place them in the same tribe (Begun 1994,1996, 2002, 2007, 2009) (**Table 1**).

Ouranopithecus has a premaxilla that closely resembles that of other dryopithecins and gorillas, and it has large, flat cusped, very thickly enameled molars resembling those of australopithecines. In *Ouranopithecus* males the lower canines are similar to those of other dryopithecins, though perhaps smaller relative to body size, but the male upper canines are undeniably reduced in size and in height. Whereas this attribute is one of the principle reasons that *Ouranopithecus* is attributed to the hominin clade by some, the pattern is different from that seen in any hominin, given that the obvious reduction in canine crown height is restricted to the upper dentition.

In the final analysis, *Ouranopithecus* probably evolved from a more typical dryopithecin such as *Rudapithecus*, following selection for more robust masticatory adaptations in an environment that was more open than for other dryopithecins (Begun 2009; Bonis et al. 1986; Bonis & Koufos 1994; Fortelius et al. 1996; Koufos 2003, 2007; Solounias et al. 1999).

Recently, two more European hominines have been added to the list, both most strongly resembling *Ouranopithecus* (**Table 2**). A very large hominine, dentally the size of Miocene *Gigantopithecus*, has been described from the site of Çorakyerler in Turkey. It is similar to *Ouranopithecus*, but differs in details of the morphology of the incisors, canines, and premolars and in the structure of the premaxilla and palate (Begun 2009, Begun et al. 2003b, Güleç et al. 2007). The paleoecology of the locality suggests that it was even more open, that is, less forested, than the *Ouranopithecus* localities from Greece (Güleç et al. 2007). The association of mammals from the site also suggests that it is younger that any *Ouranopithecus* locality, possibly by as many as two million years (Güleç et al. 2007). Another site in Bulgaria has yielded a hominoid upper premolar that looks very similar to *Ouranopithecus*, and a specimen of *Mesopithecus*, a primitive colobine monkey (Spassov 2009, Spassov & Geraads 2008). The significance of these new hominines is that they occur at a time and place where hominines were thought to have gone extinct, owing to the widely documented drying out of late Miocene Eurasia (Agustí 2007, Agustí et al. 2003, Begun 2009, Bernor 2007). That an ape from Turkey and another from Bulgaria managed to survive and adapt to these dramatic climatic fluctuations is a strong indication of the adaptability of the European hominines and anticipates the diversification of hominines in Africa. If confirmed, the co-occurrence of an Old World monkey and a fossil ape in Bulgaria would be a first in Eurasia.

There are no hominines known from Africa between 13.5 and 10 Ma, and there are many characteristics shared by dryopithecins and extant African apes. Nevertheless, two newly described samples have led some to call into question the hypothesis that the African apes and humans evolved and experienced their first radiation in Europe.

AFRICAN FOSSIL GREAT APES

Chororapithecus

A handful of isolated teeth discovered at the 10 Ma site of Chorora in Ethiopia have been attributed to the Homininae (Suwa et al. 2007). Suwa and colleagues speculate that *Chororapithecus* may represent an ancestor of gorillas given the presence of a ridge on one molar that appears to them to be the precursor of a slicing crest on the teeth of modern gorillas. However, the ridge in question is only partially developed, and is mainly visible on the enamo-dentine junction, the surface directly below the enamel (visualized using microCT scans). There is no way to be confident that this very subtle character is a homology with *Gorilla*, especially given the fact that the anatomy of the dentition of *Chororapithecus* overall is distinctly unlike gorillas both in terms of morphology and functional anatomy. Suwa and colleagues also indicate that the presence of a hominine or a gorilla ancestor as represented by *Chororapithecus* effectively falsifies the hypothesis that the African ape and human clade originated or even existed for any time in Eurasia (see also Harrison 2010). However, even if *Chororapithecus* is a hominine, which is far from certain, it is still 2 Ma younger than the earliest hominine, *Dryopithecus*, and nothing about the anatomy of *Chororapithecus* calls into question the hominine affinities of the dryopithecins (Begun 1992a, 2007, 2009; Hill & Ward 1988; Moyà-Solà et al. 2009b).

Nakalipithecus

Another possible hominine from Africa is *Nakalipithecus*, from Nakali in Kenya (Kunimatsu et al. 2007). The sample includes a partial mandible with worn teeth and several isolated teeth. The female upper canine bears a strong resemblance to the same tooth in *Ouranopithecus*, lending support to the hypothesis that *Nakalipithecus* is related to *Ouranopithecus* (Kunimatsu et al. 2007). These authors have argued that because *Nakalipithecus* is slightly older than *Ouranopithecus* (9.8 versus 9.5 Ma) it

might be ancestral to the latter, and that European great apes in general represent extinct side branches of the hominines. However, as with *Chororapithecus*, *Nakalipithecus* is about 2 million years younger than *Dryopithecus* (Begun 2009, Moyà-Solà et al. 2009b). Even if *Nakalipithecus* is ancestral to *Ouranopithecus* it has no direct bearing on the question of hominine origins.

THE PALEOBIOGEOGRAPHY OF HOMININE ORIGINS

In this review I have emphasized the evidence for a European origin of the Africa ape and human clade. In contrast to the simplistic interpretation that hominines could not have evolved in Europe (Bernor 2007, Harrison 2010), the fossil record shows that the circumstances of hominine origins are very complex. The fossil and molecular evidence of the other Old World catarrhine radiation, the cercopithecoids, shows a similar pattern of complexity, with genetic and fossil evidence of multiple dispersals starting in the late Miocene (Jablonski 2002, Stewart & Disotell 1998). The earliest hominines are European and there are no fossil hominines in Africa for at least two million years after they first appear in Spain and France. Although it has been argued that the absence of evidence is not evidence of absence, and that Africa is vast and relatively unexplored, the bottom line is that we have to base hypotheses on actual data and not on expectations of future discoveries. The absence of hominines in Africa does not explain the large number of hominine characters found in the European sample (**Table 3**).

Hominids first occur in Europe at about 16.5 Ma, as represented by *Griphopithecus* in Germany and Turkey (Begun 2002, Begun et al. 2003a, Heizmann & Begun 2001). Hominids were not alone in dispersing into Europe in the middle Miocene and eventually expanding their range to Africa. Numerous lineages of mammals including ungulates, carnivores, proboscideans, aardvarks, and small mammals disperse and expand their ranges between Europe and Africa at this time

(Begun 2009; Begun et al. 2003a,b; Begun & Nargolwalla 2004, 2009; Nargolwalla et al. 2006). Europe from the Mediterranean to northern France, Germany, and Central Europe was subtropical in climate, and these conditions appear to have favored the evolution of the early great apes.

It is not clear where the ancestor of hominines originated, in Europe, Anatolia, or Africa, but by about 12.5–13 Ma hominines are present in Spain, France, and Austria. They thrive in Europe and expand their range east over the next two to three million years. At first they are always found in contexts that indicate densely forested conditions, and often in proximity to the shores of the ancient inland sea, the Central Parathethys (Nargolwalla et al. 2006).

The best-known samples of late Miocene European hominines are about 10 to 9.5 Ma in age (Rudabánya, Can Llobateres, Ravin de la Pluie). By this time hominines had diversified substantially and in some ways mimic the diversity that existed among Pliocene hominins. *Ouranopithecus* was substantially larger, with much more robust jaws, thickly enameled teeth, and many other adaptations to a diet that must have emphasized the consumption of hard or tough food objects, like australopithecines. *Rudapithecus* and *Hispanopithecus* were highly suspensory, arboreal soft fruit frugivores, with cheek teeth closely resembling those of living chimpanzees. The brain of *Rudapithecus* is known to have been as large as that of modern chimpanzees, and it is possible that this fossil ape had cognitive capabilities similar to those of chimpanzees (Begun & Kordos 2004). *Ouranopithecus* inhabited areas that were more open compared with the habitats of *Rudapithecus* and *Hispanopithecus*, and newly discovered *Ouranopithecus*-like apes probably inhabited even more open habitats (Güleç et al. 2007, Spassov 2009, Spassov & Geraads 2008). These discoveries effectively falsify the hypothesis that apes could not have lived in Europe after the beginning of the climatic deterioration that characterizes the late Miocene, and that they could not have dispersed from Europe into Africa at this time (Bernor 2007, Bernor & Rook 2003,

Rook & Bernor 2004). In fact, there is much evidence to show that forested conditions persisted locally in various areas of Europe and the eastern Mediterranean that could very well have accommodated both the more forest-adapted and more open country–adapted dryopithecins (Begun 2009).

Nevertheless, by about 9 Ma fossil hominines from Europe have all but disappeared, with remnants remaining in Turkey and Bulgaria. A taxon that I have not mentioned before, *Oreopithecus*, survives until about 8 Ma, but in my view this genus is not a hominine but rather evolved from a distinct ancestor (Begun 2001, 2002, 2007). A dryopithecin with teeth closely resembling those of *Rudapithecus*, *Udabnopithecus*, survives in Georgia until about 9 Ma (Begun 2007, Burchak-Abramovitsch & Gabashvili 1950). Despite their adaptability, most late Miocene European hominines disappear from Europe following ecological changes that led to much more open and seasonal conditions (Agustí et al. 2003). As in the middle Miocene, faunal exchanges between Europe and Africa are ubiquitous in the late Miocene, and many modern African mammals disperse from Eurasia into Africa at this time (Begun 2001, 2005, 2009; Nargolwalla 2009). A hominine was very probably among those taxa that moved south into Africa sometime between about 9 and 10 Ma, but whether it more closely resembled *Ouranopithecus* and *Australopithecus* or *Rudapithecus* and chimpanzees is impossible to say at this time.

Darwin was almost certainly correct in his hypothesis that the LCA of the living African apes and humans evolved in Africa. There is no evidence that this clade had already split by 10 Ma before entering Africa. However, a very substantial body of evidence from the morphology of European fossil hominines as well as dispersal patterns of other mammals and the paleoecology of the circum-Mediterranean region in the late Miocene all strongly suggest that hominines first evolve in Europe, or at least that they radiate and acquire their most significant adaptations there. As it stands today, the preponderance of evidence indicates that the

hominine clade originates and experiences its initial radiation in Europe, but that after dispersing back to Africa, the LCA of living African apes and humans splits to form the modern clades of hominines in Africa sometime after 10 Ma.

Finally, with regard to the nature of the LCA of humans and chimpanzees, it has recently been suggested that it was very much unlike either living taxa, being instead a palmigrade quadruped, like monkeys, with no anatomical specializations for suspension (White et al. 2009). This suggestion is based on the analysis of *Ardipithecus ramidus*, the oldest and most primitive Pliocene hominin (Lovejoy 2009; Lovejoy et al. 2009a,b,c,d; Suwa et al. 2009a,b; White et al. 2009). *Ardipithecus* is clearly a hominin, as indicated by its small canines, more centrally positioned foramen magnum, and probably by its pelvic morphology, although the bone is horribly distorted (Lovejoy et al. 2009b,d; Suwa et al. 2009a,b; White et al. 2009). However, it also had very powerfully built upper limbs, was about the same size and had similar levels of sexual dimorphism as in modern chimpanzees, and had a brain about the same size as a modern chimp's. The feet have highly divergent, mobile, powerful grasping big toes and the hand and foot phalanges are long and curved, as in all suspensory hominoids (Lovejoy et al. 2009b,d; Suwa et al. 2009a,b; White et al. 2009). *Ardipithecus* lived about three million years after the LCA of chimpanzees and humans. Speculations about the morphology of that ancestor should not be based exclusively on the evidence of this one partial skeleton, without considering the anatomy of Miocene apes, australopithecines, and the living descendents

as well. There are in fact numerous hallmarks of a suspensory ancestry in the skeleton of *Ardipithecus*. If it is correct that *Ardipithecus* and chimpanzees evolved from a palmigrade quadruped (Lovejoy 2009, White et al. 2009), then all of the characters related to suspensory positional behavior present in all living apes and all of the similarities between living apes and humans would have to have evolved in parallel, as would those of the numerous Miocene taxa that show the same adaptations. Although this is possible, it would represent a spectacular amount of homoplasy, unlike anything we see in any other lineage of vertebrates, and it would also call into question the very premise that it is possible to reconstruct evolutionary history and behavior using the fossil evidence.

From the perspective of the Miocene and its diversity of taxa, *Ardipithecus* actually fits in well as an intermediate genus between arboreal, suspensory, knuckle-walking chimpanzee-like common ancestors and our fully bipedal more direct ancestors. In my opinion, there is nothing to exclude the possibility that *Ardipithecus* is a surviving relict of an early branch of the hominins without a direct relationship to later taxa. Chimps are neither living fossils nor are they our ancestors. Nevertheless, the evidence from *Ardipithecus* does not falsify the most parsimonious hypothesis about the basically chimp-like nature of the common ancestor of chimpanzees and humans (Begun 2004, Richmond et al. 2001). As the search continues for additional sites with new hominines in both Europe and Africa (hopefully in the period between 10 and 8 Ma), further discoveries will surely shed light on many of the hypotheses presented herein.

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