Dryopithecins, Darwin, de Bonis, and the European origin of the African apes and human clade

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ABSTRACT
Darwin famously opined that the most likely place of origin of the common ancestor of African apes and humans is Africa, given the distribution of its living descendents. But it is infrequently recalled that immediately afterwards, Darwin, in his typically thorough and cautious style, noted that a fossil ape from Europe, *Dryopithecus*, may instead represent the ancestors of African apes, which dispersed into Africa from Europe. Louis de Bonis and his collaborators were the first researchers in the modern era to echo Darwin’s suggestion about apes from Europe. Resulting from their spectacular discoveries in Greece over several decades, de Bonis and colleagues have shown convincingly that African ape and human clade members (hominines) lived in Europe at least 9.5 million years ago. Here I review the fossil record of hominoids in Europe as it relates to the origins of the hominines. While I differ in some details with Louis, we are in complete agreement on the importance of Europe in determining the fate of the African ape and human clade. There is no doubt that Louis de Bonis is a pioneer in advancing our understanding of this fascinating time in our evolutionary history.

KEY WORDS
INTRODUCTION

In 1871, Charles Darwin published the first serious, comprehensive and well-informed analysis of human evolutionary history. In this work, “The Descent of Man, and Selection in Relation to Sex”, Darwin compares the morphology of extant great apes to humans, and he concludes that among other things humans and African apes are more closely related to one another than either are to orangutans. Here he was drawing heavily on the work of Thomas Henry Huxley and his most important publication, “Evidence as to Man’s Place in Nature” (Huxley 1863). While today we recognize the phyletic link between African apes and humans, based both on morphological and molecular evidence, it is often forgotten that for much of the 20th century Darwin and Huxley’s conclusions were rejected, and the great apes were routinely linked together, with humans set apart. In fairness to historically strong advocates of the Pongidae (great apes), such as Adolph Schultz (1936, 1950), the morphological evidence for a hominine clade (African apes and humans to the exclusion of orangutans) was not overwhelming, and the gradistic resemblances among extant great apes are undeniable. I think it is fair to say that Darwin and Huxley were not vindicated until genetic technology was able to establish with little doubt that chimpanzees are more closely related to humans than they are to gorillas, and that the group of African apes and humans as a whole is more closely related to each other than any of them are to orangutans.

During this time, researchers were trying to integrate fossil discoveries with our understanding of ape and human evolution. Darwin felt it most likely that African apes and humans evolved in Africa, stating the following: “In each great region of the world the living mammals are closely related to the extinct species of the same region. It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and as these two species are now man’s nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere.” (Darwin 1871: 199).
However, Darwin knew of a discovery in France of a fossil with close similarities to living great apes. Here is what he had to say about that fossil on the very next line: “But it is useless to speculate on this subject, for an ape nearly as large as a man, namely the *Dryopithecus* of Lartet, which was closely allied to the anthropomorphous *Hylobates*, existed in Europe during the upper Miocene period; and since so remote a period the earth has certainly undergone many great revolutions, and there has been ample time for migration on the largest scale.” (Darwin 1871: 199).

Lartet himself spoke of the similarities between *Dryopithecus* Lartet, 1856 and African apes, and these observations were repeated by later researchers commenting on newer discoveries in France and Germany (Lartet 1856; Gaudry 1890; Branco 1898; Harlé 1898; Schlosser 1901; Abel 1902). However, following impressive discoveries first in Asia and then in Africa, attention shifted away from Europe. “The *Dryopithecus* of Lartet” was eventually lumped in with most other fossil apes, which were distinguished from what were then taken to be the putative ancestors of humans, the ramapithecines (Simons & Pilbeam 1965). Attention was turned away from Europe until the early 1970’s, when discoveries from Greece and Hungary, and an emerging understanding of the evolutionary position of the Siwalik fossil apes, were leading to a renewal of interest in Europe (see Begun [2002] for a more detailed history). In 1974, a new species of *Dryopithecus*, *D. macedoniensis* (Bonis, Bouvrain, Geraads & Melentis, 1974), was recognized on the basis of fossil specimens from northern Greece. In the same year Kretzoi (1975) published an account of a genus of fossil ape, *Rudapithecus* Kretzoi,1969, from Hungary. In both cases, but based on very different lines of evidence, Europe was being repositioned as an area of great importance in interpretations of ape and human evolutionary history.

In the intervening 30 years or so, many new discoveries have been made in both Greece and Hungary, as well as in Spain, and these have shaped the debate on the relevance of Europe in the evolutionary history of the African apes and humans. For the remainder of this paper I will review the data from these three most important locations, along with isolated discoveries from Turkey and Bulgaria, to try to make some sense of the fossil evidence of hominids in the Miocene of Europe (see below for terminology used in this paper).

**ABBREVIATIONS**

**Institutions**

AU Ankara University;  
AUT Aristotle University of Thessaloniki;  
GMH Geological Museum of Hungary, Budapest;  
IPS Institut Paleontologic, Sabadell (Institut Català de Paleontologia);  
NMB Naturhistorisches Museum Basel.

**Localities**

CO Çorakyerler collection (in AU);  
RUD Rudabánya primate collection (in GMH);  
XIR Xirochori collection (in AUT).

**EUROPEAN HOMININE TAXONOMY**

Before reviewing the fossil record of European hominines it is necessary to explain the taxonomic usage adopted here. With regard to the sample from Greece, I recognize a genus level distinction between *Ouranopithecus* Bonis & Melentis, 1977 and *Graecopithecus* von Koenigswald, 1972 (Begun 2002, 2007a; Koufos & Bonis 2005). In *Graecopithecus* the M2 is close in size to male *Ouranopithecus*, but the mandible is the size of a female *Ouranopithecus*. In fact, the breadth of the M2 is greater than the mandibular breadth at that level. This suggests an important difference in relative tooth size between the two taxa. In addition, the symphysis in *Graecopithecus* is more vertical in orientation, and the M1 is smaller relative to the M2 (Begun 2002). While they are often lumped together by virtue of the fact that both appear to have thickly enameled teeth and both are found in Greece, it is worth noting that the shortest distance between an *Ouranopithecus* locality (Nikiti) and Pyrgos Vassilissis (*Graecopithecus*) is about 250 km as the crow flies today. In the late Miocene the Thermaikos Gulf and Aegean Sea intervened between the Chalkidiki Peninsula and mainland Greece as it does today, so the land distance between the two localities is even greater. In addition, Nikiti, the youngest *Ouranopithecus*
locality, is estimated to be about 9 Ma (Koufos 2003), and Pygros Vassilissis, though difficult to date, is likely to be MN 12, or 6-8 Ma, and the ecology of Greece during these different time periods was quite different (Solounias 1981; Bernor 1983; Bonis et al. 1994; Bernor et al. 1996; Mein 1999; Solounias et al. 1999; Steininger 1999; Agustí et al. 2003; Begun & Nargolwalla 2004; Begun 2005; Mercerén et al. 2005a; Agustí 2007; Strömberg et al. 2007). This taxonomic interpretation is consistent with Bonis & Melentis (1984).

A recent review of the taxa usually attributed to *Dryopithecus* has led to a revised taxonomy (Begun et al. 2008). With the discovery of a number of partial crania, diversity among the dryopithecins has become clearer. The large sample from the Vallès Penedès expanded dramatically with the discovery of a partial skeleton from Can Llobateres (Begun & Moyà-Solà 1992; Moyà-Solà et al. 1992; Moyà-Solà & Köhler 1993, 1995, 1996), a second partial skeleton from Hostalets de Pierola (Moyà-Solà et al. 2004), a palate from Can Mata (Moyà-Solà et al. 2009a) and a partial face from Can Mata (Moyà-Solà et al. 2009b). When compared to the postcranial sample and the three partial crania now known from Rudabánya, there are a sufficient number of differences to warrant the recognition of separate genera for each sample (Begun et al. 2008).

*Pierolapithecus catalaunicus* Moyà-Solà, Köhler, ALba, Casanovas-Villar & Galindo, 2004, from Barranc de Can Vila 1 in Catalonia, Spain, is known from a partial skeleton including much of the face and portions of the postcranial skeleton (Moyà-Solà et al. 2004). The locality is dated to MN 7/8, and is therefore older than Can Llobateres and Rudabánya, both of which are MN 9 or early Vallesian (Begun 2002). Barranc de Can Vila 1 is the same age as *Dryopithecus fontani* Lartet, 1856 from St-Gaudens and La Grive (France) and from Can Vila and Can Mata (Spain). *Pierolapithecus* Moyà-Solà, Köhler, ALba, Casanovas-Villar & Galindo, 2004 is distinct from and more primitive than the Can Llobateres and/or Rudabánya samples in that the lumbar vertebrae have somewhat more anteriorly positioned transverse processes (not known at Rudabánya) and the proximal hand phalanges are shorter, less curved with proximal articular surfaces oriented more dorsally. The face is difficult to compare to the Can Llobateres and Rudabánya samples because it is distorted. It is unlikely that the face of *Pierolapithecus* resembled *Afropithecus* Leakey & Leakey, 1986, as suggested by Moyà-Solà et al. (2004), after the distortion is corrected (Begun & Ward 2005; Begun 2007a). The teeth are quite similar to MN 9 dryopithecins but, interestingly, the I1 and M3 most closely resembles those attributed to *Dryopithecus fontani* from La Grive (Begun & Ward 2005) (Fig. 1). In addition, the canines are relatively large, as is the case for the lower canines of *Dryopithecus fontani* from St-Gaudens. Like MN 7/8 *Dryopithecus*, *Pierolapithecus* has partial molar cingula, short premolars and a smaller M1 relative to M2. The lower dentition of *Dryopithecus* from France also has relatively lower premolar talonids, a primitive character, compared to MN 9 European hominines. Two previously known isolated lower molars also from Can Vila share attributes with French *Dryopithecus*, including partial buccal cingula and a well-developed tuberculum sextum on the M3 (Fig. 1B) (Begun & Moyà-Solà 1990; Begun 2002). In summary, the samples from Can Vila and France are the same age and have many attributes in common, and they are generally more primitive than MN 9 hominines. I therefore recognize *Pierolapithecus* as a junior subjective synonym of *Dryopithecus* (Begun et al. 2008). This interpretation is further supported by the recent discovery of a *Dryopithecus fontani* palate, from the nearby MN 7/8 locality of Can Mata, and a partial face attributed to the new genus *Anioapithecus* Moyà-Solà, Alba, Almécija, Casanovas-Vilar, Köhler, Esteban-Trivigno, Robles, Galindo & Fortuny, 2009, also from Can Mata, which are both very similar dentally to *Pierolapithecus* (Moyà-Solà et al. 2009a, b). These new specimens are all attributed to *Dryopithecus* (Begun et al. in press).

As noted above, MN 9 dryopithecins are derived relative to *Dryopithecus* as defined here. The best samples of MN 9 dryopithecins are from Can Llobateres and Rudabánya. Here I recognize separate genera for each of these two samples, *Hispanopithecus* Villalta & Crusafont, 1944 at Can Llobateres and *Rudapithecus* at Rudabánya, as originally suggested by Kretzoi (1969) and Villalta & Crusafont (1944). The best preserved and most informative specimens from Can Llobateres are a face and partial skeleton,
IPS 18000 and IPS 18800 (Moyà-Solà & Köhler 1993, 1995; Begun 1994; Almécija et al. 2007). These fossils were originally attributed to the same individual. In the cranial specimen the frontal squama of *Hispanopithecus* is strongly biconcave transversely and anteroposteriorly, while in *Rudapithecus* it is smoothly bi-convex. In *Hispanopithecus* there is a groove separating the supraorbital ridge from the supraorbital torus. The anterior temporal lines in *Hispanopithecus* are very strongly developed and raised above the cranial surface immediately anterior and medial to it. IPS 18000 is a male, as is RUD 44. The latter is larger than IPS 18000 but with less strongly developed temporal ridges. The surface of the zygomatic process of the frontal (the superolateral corner of the orbit) in *Hispanopithecus* also differs from the three *Rudapithecus* specimens in being more anteriorly oriented. In *Hispanopithecus* the body of the zygomatic bone is flat and faces more anteriorly than in *Rudapithecus*, in which all three specimens have more convex zygoma facing more laterally (Begun 1994). Although highly variable in extant hominoids, the position, size and number of the zygomaticofacial foramina also differ between the two taxa, with those in *Hispanopithecus* being relatively large, more numerous, and higher on the zygomatic frontal process (Begun 1994; Moyà-Solà & Köhler 1995).
The palate of \textit{Rudapithecus} is narrower than that of \textit{Hispanopithecus}, and the zygomaticoalveolar crests are thicker anteroposteriorly. The mandible of \textit{Rudapithecus} is generally more robust and oval in cross section. The only identifiable male mandible of \textit{Hispanopithecus} (IPS 1764) has a triangular shaped cross section between P4-M1. Dentally, the upper incisor crowns are narrow compared to \textit{H. laietanus} Villalta & Crusafont, 1944, with concave lingual surfaces and single central pillars. \textit{Hispanopithecus laietanus} I1s have complicated cresting on their lingual surfaces, and \textit{H. crusafonti} Begun, 1992 I1s are extremely narrow with very prominent mesial, distal and central labial pillars (Begun 1992a, 1994). In \textit{Rudapithecus} the canines are smaller and more compressed buccolingually and the upper postcanine teeth tend to be more elongated relative to breadth. The upper and lower M3s are elongated, strongly tapered, and are smaller than the M2s in \textit{Rudapithecus}. Males of \textit{Rudapithecus} differ from males of \textit{Hispanopithecus} in having large lower premolars, strongly triangular (beaked) P3, large P3 fovea of equal height with buccal crista of equal length, and broad, wrinkled lower molar basins with marginalized cusps (Begun & Kordos 1993; Begun 1994).

Postcranially, \textit{Rudapithecus} differs from \textit{Hispanopithecus} in having much less robust manual proximal phalanges with a more proximally oriented proximal articular surface and broader trochlea. The metacarpal is also less robust transversely. The femoral neck in \textit{Rudapithecus} is larger superoinferiorly relative to head diameter compared to \textit{Hispanopithecus} (MacLatchy et al. 2001; Köhler et al. 2002; and pers. obs.). Table 1 lists the most important European hominine taxa and their main diagnostic characters.

\begin{table}
\centering
\begin{tabular}{|l|p{0.7\textwidth}|}
\hline
\textbf{Taxa} & \textbf{Characters} \\
\hline
\textit{Dryopithecus} & Short, vertical premaxilla with evidence of a subnasal step (associated with maxillary overlap), biconvex premaxilla, modest supraorbital tori and supratoral sulcus, broad interorbital space, robust lateral orbital margins, square orbits, subvertical nasal aperture margins, high zygomaticoalveolar crest, relatively broad canines, short premolars and small M1, low lower premolar talonids, partial molar cingula, thin occlusal enamel, tall crowned postcanines, M3 tuberculum sextum, somewhat robust mandibles, mesio-distally short, tall crowned I1, peg-shaped I2 \\
\hline
\textit{Hispanopithecus} & Short, vertical premaxilla with evidence of a subnasal step (associated with maxillary overlap), biconvex premaxilla, modest supraorbital tori and supratoral sulcus, strongly developed anterior temporal lines, biconcave vertical frontal squama, reduced subarcuate fossa, robust lateral orbital margins, square orbits, broad interorbital space, ethmoidal frontal sinus, subvertical nasal aperture margins, high zygomaticoalveolar crest, more anteriorly oriented zygoma, thin enamel, mesio-distally short, tall crowned I1, peg-shaped I2 \\
\hline
\textit{Rudapithecus} & Short, vertical premaxilla with some maxillary overlap, relatively narrow, posteriorly divergent palate, biconcave premaxilla, modest supraorbital tori and supratoral sulcus, vertical frontal squama, elongated, klinorhynch crania, inion high on the skull, reduced subarcuate fossa, fused tympanic and articular temporal, large brain, robust lateral orbital margins, square orbits, broad interorbital space, ethmoidal frontal sinus, subvertical nasal aperture margins, high zygomaticoalveolar crest, convex and more laterally facing zygoma, more compressed canines and elongated postcanines, strongly tapered M3, more peripheral cusp positions, mesio-distally short, tall crowned I1, peg-shaped I2 \\
\hline
\textit{Ouranopithecus} & Short, vertical premaxilla with some maxillary overlap, modest supraorbital tori and supratoral sulcus, vertical frontal squama, elongated, klinorhynch crania, inion high on the skull, reduced subarcuate fossa, long zygomaticoalveolar crest, strongly heteromorphic upper incisors, reduced canine size and premolar sectoriality, hyperthick occlusal enamel, tall crowned and megadont postcanines, broad rounded cusps, robust to very robust mandibles \\
\hline
\textit{Çorakyerler hominine} & Very short premaxilla, upper canines nearly aligned with incisors transversely, homomorphic upper premolars, extremely large postcanine teeth, teeth, narrow palate, thick, diamondshaped upper canines cervix reduced in size relative to the molars, thin palatine process, low crowned I1, peg-shaped I2 \\
\hline
\end{tabular}
\caption{Principle taxa discussed in this paper and their most important diagnostic craniodental characters.}
\end{table}
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The classification of European hominines followed here is as follows:

Subfamily **HOMININAE** Gray, 1825
Tribe **DRYOPITHECINI** Gregory & Hellman, 1939
Subtribe **DRYOPITHECINA**
Gregory & Hellman, 1939

**DIAGNOSIS.** — The Dryopithecina is diagnosed as follows: medium to large bodied hominines (20-45 kg) with thinly enameled teeth, robust and generally mesiodistally short upper incisors, tall crowned lower incisors, compressed canines, large, elongated premolars, M1 close in size to M2, peripheralized molar cusps, seven day cross striation periodicity, short premaxilla, stepped subnasal fossa, short, large caliber incisive canal, larger incisive foramen and fossa, robust palatine process, broad, flat inferior margin of the nasal aperture, high zygomatic root, large maxillary sinus, large ethmoid sinus continuous with a well-developed frontal sinus, thick interorbital space, weakly developed supraorbital tori, prominent anterior temporal lines, elongated brain case, inion slightly above glabella, large brain, fused articular and tympanic temporal, deep temporal fossa, prominent entoglenoid process, robust mandible, large ramus, posteriorly diverging tooth rows, elongated, tapered M3s.

Genus **Dryopithecus** Lartet, 1856
*Dryopithecus fontani* Lartet, 1856
*Dryopithecus catalaunicus* Moyà-Solà & Köhler, 2004
*Dryopithecus carinthiacus* Mottl, 1957

Genus **Rudapithecus** Kretzoi, 1969
*Rudapithecus hungaricus* Kretzoi, 1969

Genus **Hispanopithecus**
Villalta & Crusafont, 1944
*Hispanopithecus crusafonti* Begun, 1992
*Hispanopithecus laietanus* Villalta & Crusafont, 1944

Subtribe **OURANOPITHECINA** new subtribe

**DIAGNOSIS.** — The Ouranopithecina is diagnosed as follows: Large bodied hominines (45+ kg) with thickly enameled teeth, low, rounded cusps, broad, shallow occlusal basins, enlarged M3’s, anterior teeth and dental proportions as in Dryopithecina, except small male canine crown dimensions, premaxilla and maxilla as in Dryopithecina except low, thick zygomaticoalveolar crest, periorbital region as in Dryopithecina.

Genus **Ouranopithecus** Bonis & Melentis, 1977
*Ouranopithecus macedoniensis* Bonis & Melentis, 1977

Genus **Graecopithecus** von Koenigswald, 1972
*Graecopithecusfreybergii* von Koenigswald, 1972
Gen. et sp. nov. (Çorakyerler) (see below)

**Macedonia, Greece**
As noted above, in 1974 de Bonis and colleagues named a new species of *Dryopithecus* in Macedonia, from the locality of Ravin de la Pluie. Although from Europe, this fossil is strikingly different from other European fossil apes known at the time, particularly in the robust morphology of the mandible and the large and thickly enameled postcanine teeth (Bonis & Melentis 1976, 1977a, b, 1978, 1980; Begun & Kordos 1997). The canines are also unusually small, although the type specimen is a female, and over the years, the relative canine size in this taxon even in males has proven to be a difficult issue to resolve (Bonis & Koufos 2001; Kelley 2001). More discoveries of the same taxon at Ravin de la Pluie as well as two other localities in Macedonia, Xirochori and Nikiti, have made clear the differences from other European and African Miocene fossil apes from the same time period and before as well.

De Bonis and Melentis attributed the new taxon from Greece to *Dryopithecus*, but they later revised their taxonomic conclusions in light of the similarities they saw with *Sivapithecus* Pilgrim, 1910, *Gigantopithecus* von Koenigswald, 1935 and australopithecines (Bonis & Melentis 1977b). These include the large, robust jaws and thickly enameled teeth that distinguish *Ouranopithecus* from *Dryopithecus*, but also details of canine and premolar morphology and the structure of the palate (Bonis & Melentis 1977b, 1978; Bonis 1983). Additional preparation of the palate of *Ouranopithecus* would lead de Bonis and Melentis to interpret it as a direct link between Miocene apes and australopithecines, sharing synapomorphies with the tribe Hominini Grey, 1825, in which they include *Homo* Linnaeus, 1758 and *Australopithecus* Dart, 1925 (Bonis 1983; Bonis & Melentis 1984). In effect, they are attributing *Ouranopithecus* to the Hominini,
though they do not say this directly. Bonis (1983) also attributes Dryopithecus and Hispanopithecus to the Dryopithecini Gregory & Hellman, 1939, in which he includes Pan Oken, 1816 and Gorilla Geoffroy-Saint-Hilaire, 1852, which is very close to the phylogeny followed here.

Begun & Kordos (1997) make the case for a slightly different interpretation of Ouranopithecus and Dryopithecus, but one that still places them firmly among the hominines (African apes and humans in both Bonis [1983] and Begun [1992b]). Whether the African apes and humans have separate origins in Africa during the early/middle Miocene (Bonis & Melentis 1977a, b; Bonis 1983; Bonis & Koufos 1993) or a common origin in the middle Miocene of Europe (Bonis 1987; Bonis & Koufos 1994; Begun & Kordos 1997; Begun 2000, 2002, 2003, 2005, 2007a; Begun & Nargolwalla 2004), in both scenarios Europe is central to hominine origins as the place in which they evolved and presumably acquired their diagnostic characteristics before returning to Africa.

Louis de Bonis and George Koufos have made a strong case for the phylectic link between Ouranopithecus and Australopithecus (Bonis & Koufos 1993, 1994, 1997, 2001, 2004; Koufos 1993, 1995, 2007; Bonis et al. 1998; Koufos & Bonis 2004). Important characters interpreted as synapomorphies of an Ouranopithecus-Australopithecus clade include a relatively vertical face, narrow and convex mandibular condyle, distal accessory cusps on the upper and lower M3, rounded P3 lacking a buccal honing facet, relatively small male upper canine more rounded in cross section at the cervix, small deciduous canines, and molarized deciduous premolars (Koufos 2007). This hypothesis is represented in Figure 2A.

Begun (2007b) and Begun & Kordos (1997) argue that all of the similarities between Ouranopithecus and Australopithecus are homoplasies because, 1), this is consistent with the most parsimonious cladogram (Begun et al. 1997; Begun 2001), and 2), they are all related to a single functional complex, powerful mastication. Interestingly, Bonis & Melentis (1977a, 1978) suggested that Ouranopithecus might be closely related to Gigantopithecus based on many of the same characteristics. Reduction in the relative size of the canine, changes in canine-premolar relationships, postcanine megadontia and increases in gnathic robusticity and enamel thickness characterize several lineages of fossil hominids (Sivapithecus, Ankanapithecus Ozansoy, 1965, Griphopithecus Abel, 1902, Gigantopithecus, Paranthropus Broom, 1939, Paraustralopithecus Arambourg & Coppens, 1968). These features leave an overwhelming impression on facial and dental morphology, though they are all closely interrelated and essentially constitute a single trait complex that results from selection for more powerful mastication. As noted, the history of interpretation is quite revealing in this regard. At one time or another, all thickly enameled middle and late Miocene hominoids were grouped into the same genus (Sivapithecus) and linked phyletically to one another and to other similar taxa such as Gigantopithecus (Andrews & Tobien 1977; Bonis & Melentis 1977a, b, 1978; Andrews & Tekkaya 1980; Andrews 1983, 1985). However, when all available characters are considered, Ouranopithecus consistently falls out among the hominines as the sister clade of the African ape and human clade (Begun et al. 1997; Begun 2001, 2002, 2005, 2007a) (Fig. 2B).

Most significantly, Ouranopithecus lacks several characters shared between chimpanzees and early fossil humans such as Australopithecus. These include the structure of the premaxilla, which is more similar to that of Gorilla and Rudapithecus than Australopithecus and Pan (Bonis & Melentis 1987; Bonis & Koufos 1993; Begun 2001, 2002; Koufos 2007). Ouranopithecus shares the primitive condition for hominines, a relatively short and vertical premaxilla, a strongly stepped subnasal fossa and a large incisive fossa and canal. The nasal border of the premaxilla overlaps minimally with the palatine process of the maxilla. In Pan and Australopithecus the premaxilla is longer and more horizontally oriented, and its nasal border overlaps the maxillary palatine process to a considerably greater degree, which produces a reduced subnasal step, a smaller incisive fossa and a longer, narrower incisive canal (Ward & Kimbel 1983; Begun et al. 1997; Begun 2001, 2002). It could be argued that these premaxillary features also constitute a single character (Schwartz 1997). However, this complex actually cross cuts functional...
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**Fig. 2.** — Cladograms depicting alternative hypotheses discussed in the text. Modified from Begun et al. (1997) and Begun (2001, 2002, 2007). *Griphopithecus alpani* Tekkaya, 1974 and *Kenyapithecus kizili* Kelley, Andrews & Alpagut, 2008 are thickly enameled middle Miocene hominoids from Paşalar (Turkey). *Griphopithecus darwini* Abel, 1902 is the type species, from Děvínštá Nová Ves (Slovakia). *Neopithecus brancoi* Schlosser, 1901 is an isolated M3 that is most similar to *Rudapithecus* Kretzoi, 1969 but with insufficient anatomy preserved to justify synonymy. Other taxa are discussed in the text. In A, *Ouranopithecus* is a hominin; in B, it is a dryopithecin.
and phylogenetic boundaries. The very similar morphology of the Pan and Australopithecus lower face exists despite dramatic differences in functional morphology and probably diet. In addition, there is evidence of de-coupling of premaxillary length/orientation and incisive fossal/canal morphology in Ankarapithecus, which shares the former with Sivapithecus and the latter with hominines (Begun & Güleç 1998). Ouranopithecus also lacks the spatulate upper lateral incisor of Pan and all Hominini, and in this way also shares the primitive morphotype with Gorilla, other dryopithecins and all other anthropoids (Begun et al. 1997). Begun (2002) lists a number of additional characters shared between Pan and Hominini that are not found in Ouranopithecus, and would have to have evolved independently if Ouranopithecus were more closely related to hominins than Pan. These include lower crowned, flared molars, less robust lateral orbital pillars, more strongly developed supraorbital tori and sulci, a more horizontal frontal squama, and better developed supraorbital and glabellar pneumatization. Unlike the characters that are shared by Ouranopithecus and Australopithecus that are all seemingly related to a single functional constraint (heavy mastication), the characters shared by Pan and hominins that are not found in Ouranopithecus are not obviously related to a single functional complex, and cannot easily be explained as a consequence of a single, simple and common adaptive response. For these reasons, I consider Ouranopithecus to be in the outgroup of the extant hominines (Fig. 2B). In the phylogenetic analysis on which Figure 2B is based (Begun et al. 1997; Begun 2001), it is equally parsimonious to place Ouranopithecus as the sister clade to the African apes and humans as it is to link it with dryopithecins as a group that is the sister clade to African apes and humans, as represented in Figure 2B.

RUDABÁNYA, HUNGARY

In 1967 an anonymous newspaper announcement was made describing the discovery of an ape jaw from deposits surrounding the large open pit ore mine at Rudabánya, in northern central Hungary. In the same year the discovery was covered in a popular science magazine article (Tasnádi Kubacska 1967). In both cases the nomen Rudapithecus hungaricus was used, but without a diagnosis or type specimen designated, and with no taxonomically useful characters described. In 1969 a publication appeared with a short diagnosis (Kretzoi 1969). Thus the first available nomen for the sample from Rudabánya in my view is Rudapithecus hungaricus Kretzoi, 1969 (Kords & Begun 2001). In Kretzoi (1975) a new taxon, Bodvapithecus altipalatus Kretzoi, 1975 is named. Kretzoi interpreted Bodvapithecus Kretzoi, 1975 to be related to Sivapithecus, and Rudapithecus to Ramapithecus (Kretzoi 1975), and this hypothesis was widely accepted (Pilbeam 1979; Szalay & Delson 1979; Wolpoff 1980). Kay & Simons (1983) were the first, to my knowledge, to recognize that the smaller of the two hominid taxa from Rudabánya, Rudapithecus, had close affinities to Dryopithecus. In subsequent years most researchers have interpreted Rudapithecus and Bodvapithecus to be females and males respectively of the same taxon, Dryopithecus brancoi Schlosser, 1901 (Begun & Kords 1993). As noted earlier, here this sample is now returned to Rudapithecus.

The Rudabánya hominid sample includes three partial crania, two of which preserve significant portions of the brain case. One of these specimens, RUD 200, preserves the connection between the brain case and face, and provides our only glimpse of the architecture of the cranium of a European hominid. This specimen is associated with a mandible, RUD 212, making it the only well preserved skull (cranium and mandible) of a Eurasian hominid (a facial skeleton and mandible is known for Sivapithecus, but no neurocranium, and a crushed and distorted skull of Oreopithecus is also known).

The craniodental sample of Rudapithecus is critical in interpretations of hominine relations. Begun (2005) and Kords & Begun (2001) list 16 characters of the dentition and cranium shared between Rudapithecus and extant great apes, and 15 additional characters shared exclusively with extant hominines. In contrast to the characters shared between Ouranopithecus and Australopithecus, these 31 characters come from throughout the cranium and dentition. There is no obvious functional inter-relationship among such hominine characters as a biconvex premaxilla, supraorbital torus, frontal sinus,
fused articular and tympanic temporal, elongated neurocranium and klinorhynchy. Where known, these characters are for the most part also shared with *Ouranopithecus*. One significant exception is the position of the root of the zygomatic process of the maxilla, which is low in *Ouranopithecus* and primitive hominoids such as *Proconsul* Hopwood, 1933, and high in *Rudapithecus* and most other hominids (Begun & Kordos 1997). However, this is a good example of the exception that proves the rule. The low position of the root of the zygomatic process in *Ouranopithecus* is not only shared with *Proconsul* and *Hylobates*, but also with robust australopithecines (Begun & Kordos 1997b; Begun 2007b). In the case of *Ouranopithecus* and *Pananthropus*, the morphology of the zygomatic has been related to elevated levels of stress generated by their greatly enlarged masticatory apparatus (Rak 1983; Begun & Kordos 1997b; Begun 2007b). While low on the alveolar process, the zygomatic bone in robust australopithecines and *Ouranopithecus* is very different in morphology from the same bone in *Proconsul* and *Hylobates*. I would interpret the apparently primitive position of the zygomatic root in *Ouranopithecus* as a clear homoplasy, given the known phylogeny of extant hominoids, the inferred phylogeny of fossil apes, and the probable functional integration of this character within the heavy mastication morpho-functional complex (Begun 2007b).

The postcrania of *Rudapithecus* also reveal a suite of great ape affinities. The distal end of a humerus and the proximal end of an ulna show the typical suite of great ape characters (large trochlea and capitulum well differentiated from each other by a deep zona conoidea, well-developed coranoid, radial and olecranon fossae, large, medial oriented medial epicondyle, strong ulnar trochlear keel, large radially oriented radial notch, robust ulnar shaft [Morbeck 1983; Begun 1992c]). Several carpal bones are known from Rudabánya. The scaphoid most closely resembles *Pongo* Lacépède, 1799, and like *Pongo* and nearly all non-hominine primates, it is not fused to the os centrale (Kivell & Begun 2009). The capitate is also *Pongo*-like but retains primitive characters found in some cercopithecoids (Kivell & Begun 2009). The distal end of a metacarpal closely resembles those of *Hispanopithecus* in being strongly constricted dorsally, with large collateral ligament pits. A talus has a typical hominid morphology with a broad, shallow body and an elongated neck, most reminiscent of *Pongo*. The phalanges are typical of suspensory hominoids and are long and strongly curved, with well-developed flexor sheath ridges and a proximally oriented proximal articular surface (Begun 1993; Deane & Begun 2008).

**Valles Penedés, Spain**

In 1944 Villalta & Crusafont described a new genus of hominoid from the Valles Penedes of Catalonia, northeastern Spain. The type specimen of *Hispanopithecus laietanus* comes from La Tarumba, but the vast majority of the sample attributed to this taxon comes from Can Llobateres (Begun & Moyà-Solà 1990; Golpe Posse 1993). A number of other taxa have been recognized based on the Can Llobateres sample (reviewed in Simons & Pilbeam [1965]), but only *Hispanopithecus* is recognized today.

As noted earlier, a major advance in our understanding of European hominine phylogeny and adaptation occurred with the discovery and analysis of a craniofacial specimen and partial skeleton of *Hispanopithecus* from Can Llobateres (Begun & Moyà-Solà 1992; Moyà-Solà et al. 1992; Moyà-Solà & Köhler 1993, 1995, 1996; Begun 1994; Köhler et al. 2002). Details of the differences between *Hispanopithecus* and *Rudapithecus* are listed above. In general, *Hispanopithecus* is smaller than *Rudapithecus*, though they overlap in size. Males of *Hispanopithecus* are intermediate in size between males and females of *Rudapithecus*. The vertebral column is known only in *Hispanopithecus*. The lumbar vertebrae show the important hominid character of a dorsal position of the transverse process, a feature that is associated with the short, stiff lower backs and orthogrady of great apes (Ward 1993, 1997, 2007; MacLatchy et al. 2000). Other great ape characters of the postcranium of *Hispanopithecus* include a large lunate and robust hamate, the latter with a well-developed hamulus, and large, long and curved manual proximal phalanges with well-developed flexor sheath ridges. Although the important great ape character of a reduced ulnar styloid process, resulting in the absence of ulnar...
triquetral contact, is not known for either *Hispanopithecus* or *Rudapithecus*, the absence of a facet for the ulnar styloid on the triquetrum of *Dryopithecus catalaunicus* strongly suggests that the same was true for the Vallesian taxa.

Moyà-Solà and colleagues have concluded that *Hispanopithecus* is a member of the *Sivapithecus* and *Pongo* clade (Moyà-Solà & Köhler 1993, 1995, 1996; Köhler et al. 2001). They base this conclusion on a small number of characters of the face, including the size and position of the zygomatico-facial foramina, the shape and orientation of the zygomatic bone, the position of the frontozygomatic suture, the size of the frontal sinus and the presence of supraorbital costae.

The number and size of the zygomaticofacial foramina are highly variable in extant anthropoids (Msuya & Harrison 1996). *Pongo* does tend to have a higher number of foramina than other great apes, but there is significant overlap. In addition, it is difficult to say exactly how many foramina are present in IPS 18000 given preservation in the area (Fig. 3). As Figure 3 shows, the position and orientation of the zygomatic bone is unclear as it is not attached to either the maxilla or the frontal bone. The small part of the body of the zygomatic bone that is preserved inferolateral to the orbital margin is flattened, and resembles *Pongo* in this regard, but so little of the bone is preserved that it is not possible to describe it reliably as overall *Pongo*-like. In addition, in the case of both the zygomaticofacial foramina and the orientation of the zygomatic bone, three specimens of *Rudapithecus* lack the *Pongo*-like morphology that has been suggested for IPS 18000. RUD 44, 77 and 200 all preserve more of the zygomatic bone, and they have neither large and supernummary zygomaticofacial foramina nor a flat and anteriorly facing zygomatic body.

Inset a in Figure 3 is a view of the partially preserved frontal sinus of IPS 18000. It is not reduced, as described in Köhler et al. (2001). In fact, it is quite large, and occupies most of the interorbital space and indeed it does invade the space between the endocranial and orbital plates. In dryopithecins this is the typical pattern, which is only found in African apes and humans. It departs most markedly from the pattern in *Pongo* and *Sivapithecus*.

The key is the size and position of the sinus. In dryopithecins, African apes, and humans, the sinus occupies most of the interorbital space from below nasion to glabella, and has a variable pneumatization into the frontal squama. This has been interpreted as a true ethmoidal frontal sinus, given the large involvement of the interorbital space and hence the ethmoidal air cells (Begun 1994, 2007a). *Sivapithecus* and *Pongo* lack expansion of the ethmoidal air cells, which invade neither the interorbital region nor the frontal squama. On the other hand, there are many taxa in which the frontal is pneumatized from behind, by the sphenoidal air sinus (Cave & Haines 1940). There are differing interpretations of the significance of various paranasal sinus configurations (Begun 1994; Rossie et al. 2002; Rossie 2005), but researchers agree that the loss of the ethmoidal and frontal sinus expansion in *Pongo* and *Sivapithecus* is an important synapomorphy of that clade (Ward & Brown 1986). *Hispanopithecus* clearly does not share this synapomorphy with Asian great apes (Fig. 3).

The frontozygomatic suture in IPS 18000 is said to be in a depressed position relative to the superior orbital margin, which is a tendency seen in *Pongo* (Moyà-Solà & Köhler 1995; Köhler et al. 2001). In Moyà-Solà & Köhler (1995: 123, fig. 17) it is clear that there is very substantial overlap between *Pan* and *Pongo*, with *Hispanopithecus* values falling in the range of overlapping values. Furthermore, they use internal biorbital breadth to standardize for body mass, despite the fact that *Pongo* and *Sivapithecus* have relatively smaller biorbital breadths given their narrow interorbital regions and their tall, narrow orbits. Figure 3 shows a more likely position of the zygomatic relative to the frontal in IPS 18000. Insets b and c show views of the frontozygomatic suture surfaces. On the zygomatic bone the surface is nearly complete. On the frontal it is preserved but somewhat eroded. This corresponds to the description of the bones in Moyà-Solà & Köhler (1995). When the mirror imaged frontal with its frontozygomatic suture surface is matched to the right zygomatic with its suture surface, the position of the suture itself is clear. It is relatively high on the orbit as in most anthropoids, and lacks the condition found in *Sivapithecus* and some *Pongo*. The interorbital region is occupied by the maxilla in IPS 18000 given preservation in the area (Fig. 3).
The orbits are also squared and the interorbital space large, unlike *Sivapithecus* and *Pongo*.

The presence of supraorbital costae is also said to unite *Hispanopithecus* with the *Sivapithecus/Pongo* clade (Moyà-Solà & Köhler 1995). Figure 3 shows the disposition of ridges or costae in the midfrontal region. Supraorbital costae appear on *Pongo* crania, and in *Sivapithecus*, and consist of ridges that rim the superior orbital margin and the upper part of the medial orbital margins. They do not meet in the midline, nor do they reach glabella or attach to any eminence at glabella. In contrast, supraorbital tori meet in the midline at glabella, and are usually continuous with an eminence at glabella (Begun 1994). In Figure 3 highlights mark the path of two tori emanating from a mildly inflated glabella, both running superolaterally. Superior to the glabella-tori complex is a deep biconcave depression, which is unique to *Hispanopithecus* (although such a depression is suggested by the morphology of Xir-1 [*Ouranopithecus*], this is not clear due to damage). In addition to the supraorbital tori, there are superior orbital margins but they are not thickened and do not project anteriorly from the supraorbital surface as they do in *Pongo* and *Sivapithecus*. This plus the fact that they do not rim the orbits as described above means that they are unlikely to be homologous to the supraorbital costae of Asian great apes. In the end there are no characters shared uniquely between *Hispanopithecus* and Asian great apes.

![Image](image-url)

**Fig. 3.** — Views of IPS 18000 from Can Llobateres: **A**, frontal view of the periorbital region with the right side reconstructed based on a mirror image of the better preserved left side; **B**, view from below of the interorbital space of IPS 18000 showing the extensive frontal sinus, outlined on the right side; **C**, lateral view of the frontal fragment showing the frontal’s joint surface of the frontozygomatic suture; **D**, view from superiorly and medially showing the zygomatic’s joint surface of the frontozygomatic suture. Scale bar: 1 cm.
apes and a large number of characters shared between dryopithecins and African apes (Begun et al. 1997; Begun 2001).

Turkey

In 2007 Güleç et al. published a new species of Ouranopithecus, O. turkae, from Çorakyerler, Turkey. The Çorakyerler fossil assemblage is correlated to MN 11, or between 8.7 and 7.4 Ma (Güleç et al. 2007). I had the opportunity to examine and prepare the type specimen, a very large male palate. As noted elsewhere (Begun et al. 2003; Güleç et al. 2007), the specimen resembles Ouranopithecus more closely than any other fossil ape. The specimen is considerably larger than the largest Ouranopithecus specimen, and in fact it fits comfortably on the mandible of Indopithecus giganteus Pilgrim, 1915 (often referred to as Gigantopithecus bilaspurensis Simons & Chopra, 1969). There are also important differences from Ouranopithecus, which justify in my view the recognition of a new genus.

The Çorakyerler maxilla (CO 205) is a large presumed male palate with LI1-M3, RC-M2, preserving portions of the right palatine process to the midline, a small fragment of the left palatine process, most of the left alveolar process, and much of the palatal surface of the right premaxilla. There is some distortion along both tooth rows, but a good estimate of dental arcade shape is possible (Fig. 4). The specimen preserves a portion of the right edge of the nasal aperture along the canine root. The left side preserves the base of the zygomatic process and the inferior extension of the canine fossa (Fig. 4). The canine and M3 are fully erupted and lightly worn.

The new genus from Turkey is distinguished from other hominoids including Ouranopithecus macedoniensis, by the following dentognathic characteristics: a short, vertical premaxilla and lower face: narrow palate relative to postcanine size: broad, higher zygomatic root: broad, diamond-shaped canine cross-section at the cervix: homomorphic P3 and P4: oval and symmetrical P3 with pre- and postparacrista of equal length: M3 larger than M2. In addition to the characters noted above, it is further distinguished from Ouranopithecus in the following characters: larger size, smaller relative canine size, lower crowned male canines, low crowned I1 with a highly complicated labial surface morphology, extreme upper incisor heteromorphy, incisors nearly aligned with the canines (modified from Güleç et al. [2007]).

The Çorakyerler sample shares characters with Ouranopithecus related to a heavily masticated diet, which is often associated with an adaptation to more open habitats than those of living great apes. Indeed, both genera occur in Eurasia at a time of considerable decline in forest cover, drier climates and increased seasonality (Bernor 1983; Bonis et al. 1994; Bernor et al. 1996; Solounias et al. 1999; Agustí et al. 2003; Begun & Nagoldwalla 2004; Begun 2005; Merceron et al. 2005a; Koufos et al. 2006; Agustí 2007; Strömberg et al. 2007). As noted earlier, many of these characters occur in Pliocene hominins, but also in other fossil hominids with large jaws and thickly enameled teeth. Because the Çorakyerler sample has derived characters shared with African apes and humans not found in Ouranopithecus, it is considered different at the genus level.

The Çorakyerler specimens are great apes, with affinities to European and African taxa and not with Ankarapithecus or South or Southeast Asian taxa (Begun et al. 2003; Begun 2005; Güleç et al. 2007). The sample shows its greatest similarities to gorillas, chimpanzees and Ouranopithecus, and is intermediate in age between Ouranopithecus and the earliest known African hominids (Brunet et al. 2002; Vignaud et al. 2002; Güleç et al. 2007; Lebatard et al. 2008). Previous interpretations of Ouranopithecus had suggested this genus as a good candidate for Pliocene hominid ancestry based on derived dentognathic features shared with later African Pliocene Australopithecus (see above). While the upper premolars of CO 205 and non-robust Australopithecus strongly resemble one another, A. anamensis Leakey, Feibel, McDougall & Walker, 1995 and A. afarensis Johanson, White & Coppens, 1978 have more primitive postcanine teeth (White 1977; Ward et al. 2001; Güleç et al. 2007). Furthermore, all late Miocene African hominids (Orrorin Coppens, Senut, Pickford, Gommery, Mein & Cheboi, 2001, Ardipithecus White, Asfaw & Suwa, 1994, and Sahelanthropus Brunet et
al., 2002) lack dentognathic specializations associated with heavily masticated diets (Haile-Selassie 2001; Senut et al. 2001; Brunet et al. 2002; Haile-Selassie et al. 2004; Güleç et al. 2007). Evidence from functional morphology and known relations among fossil and living hominids strongly suggests that Ouranopithecus and the Çorakyerler hominine evolved many or all of these dietary adaptations in parallel with later African hominids (Begun & Kordos 1997b; Begun 2007b). On the other hand, the features the Çorakyerler hominine shares with African apes and humans and not Ouranopithecus may indicate a closer relationship to this larger clade (Fig. 2B). A number of characters are shared with Gorilla, and occasionally found in other hominids, including narrow palates, reduced premolar occlusal outline and cusp heteromorphy, peg-shaped I2, short premaxilla and vertically implanted anterior teeth, and a thin maxillary palatine process. Some of these characters, such as the peg-shaped I2, are primitive for the African ape and human clade, as suggested on the basis of previous comparisons to Dryopithecus and Ouranopithecus (Begun 1994, 2001, 2002; Begun & Kordos 1997).

The presence of a fossil great ape in a relatively open habitat in the Turolian of Turkey will require a rethinking of ideas of Eurasian hominoid extinctions, previously attributed to environmental changes at this time (Bonis & Koufos 1999; Bonis et al. 1999; Solounias et al. 1999; Eronen & Rook 2004; Rook &
Begun D. R.

Begun D. R. (1994; Ungar 1996; Begun & Kordos 1997b; Kay & Ungar 1997; Smith et al. 2003). This has been widely interpreted as an adaptation to a soft fruit diet. However, there are some differences between thinly enameled dryopithecins and chimpanzees. The incisors of the fossil taxa tend to be narrow compared to chimpanzees, and relatively tall crowned. It has been suggested that this may be a response to the need to process foods with tough protective coverings (Begun & Kordos 1997). The narrow mesiodistal length of the teeth may have served to generate higher more focused occlusal forces, and the crown height may be a response to wear. Strongly developed lingual marginal ridges and labial pillars may also have served to resist labiolingual bending and torsion. This interpretation is supported by a recent analysis of incisor crown curvatures that also links thinly enameled dryopithecins to hard object feeders (Deane 2007). The combination of a soft fruit frugivore signal from molar occlusal morphology, microwear, shearing quotients and enamel thickness and a hard object feeding signal from the incisors is unique and may indicate that hard object processing was part of a fallback feeding strategy that allowed dryopithecins to exploit a wider range of more difficult to process foods in times of resource shortage. The mandibular corpora of these thinly enameled dryopithecins are also somewhat more robust than in chimpanzees, which is consistent with this interpretation.

BULGARIA

Spassov & Geraads (2008) describe a hominid P4 from a Turolian locality in the Chirpan district of southern Bulgaria. They estimate the age of this fossil assemblage at about 7 Ma, which makes it most likely somewhat younger that the Çorakyerler hominine. Spassov & Geraads (2008) indicate that the new Bulgarian specimen resembles Ouranopithecus. They do not speculate on the ecological context of the new hominin from Bulgaria, though the presence of the proboscidean Anancus Aymard, 1855 and the spiral horned antelope Protragelaphus Dames, 1883 suggests perhaps a relatively open woodland environment (Cerling et al. 1999; Merceron et al. 2005b; Spassov & Geraads 2008), which would be broadly consistent with the paleoecology of Ouranopithecus localities (Bonis et al. 1999; Merceron et al. 2007a).

ECOLOGICAL DIVERSITY IN EUROPEAN MIOCENE HOMININES

The large number of European Miocene hominine taxa bear witness to a broad range of dietary and positional behavior adaptations. In terms of diet there are two major patterns. The older dryopithecins, Dryopithecus, Hispanopithecus and Rudapithecus resemble living chimpanzees in molar occlusal morphology, enamel thickness, gross and microwear, and shearing quotients (Begun 1994; Ungar 1996; Begun & Kordos 1997b; Kay & Ungar 1997; Smith et al. 2003). This has been widely interpreted as an adaptation to a soft fruit diet. However, there are some differences between thinly enameled dryopithecins and chimpanzees. The incisors of the fossil taxa tend to be narrow compared to chimpanzees, and relatively tall crowned. It has been suggested that this may be a response to the need to process foods with tough protective coverings (Begun & Kordos 1997). The narrow mesiodistal length of the teeth may have served to generate higher more focused occlusal forces, and the crown height may be a response to wear. Strongly developed lingual marginal ridges and labial pillars may also have served to resist labiolingual bending and torsion. This interpretation is supported by a recent analysis of incisor crown curvatures that also links thinly enameled dryopithecins to hard object feeders (Deane 2007). The combination of a soft fruit frugivore signal from molar occlusal morphology, microwear, shearing quotients and enamel thickness and a hard object feeding signal from the incisors is unique and may indicate that hard object processing was part of a fallback feeding strategy that allowed dryopithecins to exploit a wider range of more difficult to process foods in times of resource shortage. The mandibular corpora of these thinly enameled dryopithecins are also somewhat more robust than in chimpanzees, which is consistent with this interpretation. Rudapithecus and Hispanopithecus localities are interpreted as closed forests but with a greater degree of seasonality than is typical for tropical or many subtropical forests today (Andrews et al. 1997; Agustí et al. 1999, 2003; Bernor et al. 2004; Rook et al. 2004; Agustí 2007; Merceron et al. 2007b). This suggests periods of resource shortage that would have made an effective fallback feeding strategy of paramount importance for survival. It is possible that the ability to exploit more embedded foods also represents a pre-adaptation that led eventually to a more extreme and committed hard object feeding strategy in Ouranopithecus.

As noted above, Ouranopithecus had a robust masticatory apparatus with all the classic indica-
tors of a hard object diet. These include hyperthick enamel, large postcanine teeth with low, rounded cusps, robust mandibles and powerfully developed attachment sites for the muscles of mastication (Bonis & Koufos 1993, 1994, 1997; Begun & Kordos 1997b; Begun 2007b). This is supported by dental microwear analyses as well (Ungar & Kay 1995; Ungar 1996; Merceron et al. 2005c). Ouranopithecus also appears to have some reduction in the size of the canines, at least in the maxilla, which leaves more room in the jaw for enlarged postcanine teeth. The anterior teeth are often very strongly worn, suggesting intensive anterior dental processing, which is often associated with embedded foods. The paleoecology of Ouranopithecus localities is widely regarded as more open than earlier dryopithecins (Bonis et al. 1999), and this is also consistent with a feeding strategy emphasizing embedded foods, with perhaps a greater percentage coming from terrestrial sources.

There is an interesting functional parallel between the dryopithecins and crown hominines (African apes and fossils and living humans). Both clades are very diverse and speciose when all fossil taxa are considered. And both clades run the spectrum from soft fruit frugivores (e.g., Rudapithecus, Pan) to extreme hard object feeders (Ouranopithecus, Paranthropus). This could be revealing of an emergent property of cranial biology in hominines. Hominine cranial form and possibly other adaptations such as brain size channel a radiation of taxa that tended to fill the same niches independently, first in Europe in the middle to late Miocene, and later in Africa in the late Miocene and Pliocene (Begun & Kordos 1997).

Diversity in positional behavior in dryopithecins is less well documented, mainly because postcrania are not described for Ouranopithecus. Hispanopithecus and Rudapithecus are both interpreted as highly arboreal (Begun 1988, 1992b, c, 1994, 2007b; Moyà-Solà & Köhler 1996; Begun & Kordos 1997; Almécija et al. 2007). Interpretations differ however on the precise nature of the arboreal locomotion in the two genera. Hispanopithecus is thought by some to have been a strong climber with well-developed characters related to orthogrady and suspension while retaining features indicative of palmigrady (Almécija et al. 2007). Like Rudapithecus, Hispanopithecus has long, strongly curved phalanges with strongly developed fibrous flexor sheath ridges, all of which is associated in living primates with a specialized adaptation to suspensory positional behavior (Susman 1979; Begun 1993; Richmond & Whalen 2001; Deane & Begun 2008). However, the metacarpal heads in Hispanopithecus are strongly constricted dorsally, with deep collateral ligament pits expanded dorsally. The proximal articular surfaces of the proximal phalanges are said to be oriented more dorsally than in modern hominoids. These characters and the presence of short metacarpals are interpreted to indicate that the hand postures of Hispanopithecus included frequent hyperextension at the metacarpo-phalangeal joint, which is a feature of palmigrade primates (Almécija et al. 2007). However, palmigrade monkeys do not have metacarpal heads as dorsally constricted as Hispanopithecus. Hominoids, in contrast, lack these joint characteristics and, given the great development of their flexor musculature, they have limited mobility in extension (Tuttle 1969). The metacarpal heads also lack the typical palmar grooves, or fluting, of the joint surface proximally that are found in most palmigrade monkeys that are related to the presence of sesamoid bones (Lewis 1977; Almécija et al. 2007). While the proximal articular surfaces of the proximal phalanges have some dorsal expansion, they are large, deep and rounded, and extend palmarly between the two large palmar tubercles, again unlike the condition in palmigrade monkeys in which they tend to be broad, shallow and in a more dorsal position. The proximal end of the proximal phalanges are clearly tilted palmarly and do not really face dorsally to any significant extent. The shortness of the metacarpals relative to the phalanges is also not clear cut. Comparisons are limited to the fourth digital ray, in which the metacarpal is in two pieces. Although the authors indicate that the length can be easily reconstructed, the result is a fourth metacarpal that is significantly shorter than the second metacarpal, much more so than in extant anthropoids, except hylobatids, which otherwise have very slender metacarpals. It is also very unusual to see a large second metacarpal and small second proximal phalanx compared
to the fourth digital ray. In hylobatids the fourth ray proximal phalanx is shorter and smaller in articular dimensions than the second. If the fourth metacarpal were really as short as is indicated in Almécija et al. (2007), one would expect a similar pattern with the proximal phalanges.

While the metacarpal robusticity and phalangeal relative size are uncertain in *Hispanopithecus*, the morphology of the metacarpal heads and the proximal articular surfaces of the proximal phalanges, which are neither monkey-like nor ape-like, may suggest a unique feature of the positional repertoire of *Hispanopithecus*. Frequent palmigrady would suggest the need to stabilize the metacarpo-phalangeal joint in hyperextension, which should lead to dorsal expansion of the distal metacarpal articular surface and collateral ligament pits that are more palmarly displaced. The opposite is the case in *Hispanopithecus*. Large dorsal collateral ligament pits would cause the collateral ligaments to become taut and bring the joint into maximum close packed position in a relatively wide range of flexion, as expected in a suspensory animal. The joint would be relatively loose in extension. Instead of palmigrady, the unusual morphology of the metacarpo-phalangeal joint may simply reflect the need to stabilize the joint in a wide range of flexed postures.

The other especially informative aspects of the postcrania of *Hispanopithecus* are the femur and lumbar vertebrae. The best preserved vertebrae show the typical great ape character of a dorsally displaced transverse process, which has been related to the presence of a short, stiff lower back (Moyà-Solà & Köhler 1996; Ward 2007). The well-preserved femur has features of the hip joint related to suspension and high hip mobility (Köhler et al. 2002). In sum, the postcranial skeleton of *Hispanopithecus* preserves much evidence of a highly arboreal, climbing, suspensory hominoid. Possible retention of relatively frequent palmigrady has been suggested but the evidence in my view is inconclusive.

*Rudapithecus* from Rudabánya is known from a number of phalanges, hand and foot bones, the distal end of the humerus, proximal ends of a radius and ulna, two partial femora and a partial pelvis. The phalanges, humeral, radial and ulnar specimens are very similar to extant great apes with a clear strong suspensory signal (Morbeck 1983; Begun 1988, 1992c, 1993, 1994; Begun & Kordos 1997; Deane & Begun 2008). Preliminary analysis of the femora, pelvis and hand bones is consistent with this interpretation. In most cases the great ape that *Rudapithecus* most closely approaches is *Pongo*. *Dryopithecus* (including *Pierolapithecus*) is represented by an exquisite skeleton including well-preserved ribs, vertebrae and hand bones (Moyà-Solà et al. 2004). The ribs point to a broad, shallow hominoid-like thorax and the carpals are great ape like in the absence of contact between the triquetrum and ulna. The vertebrae are intermediate in the position of the transverse processes and the phalanges are shorter and less curved than in *Hispanopithecus* (Moyà-Solà et al. 2004). Moyà-Solà et al. (2004) interpret this mixture of characters to reflect a unique combination of behaviors, including powerful climbing and orthograde and palmigrade hand posture, but not suspension. Begun & Ward (2005) suggest that the vertebral and phalangeal characters of *Dryopithecus catalunicus* do not preclude suspension, and the strongly developed secondary shaft characters of the phalanges are most consistent with suspension, despite the somewhat reduced length compared to *Hispanopithecus*. It is noteworthy that many Old and New World monkeys practice suspensory positional behaviors, though perhaps not as adeptly as hominoids, and in some cases with the aid of a prehensile tail, despite lacking the hominoid-like characters of *Dryopithecus*. Either way, *Dryopithecus* is the oldest hominid with well-preserved and unambiguous evidence of a great ape body plan (Moyà-Solà et al. 2004).

AFRICAN LATE MIOCENE HOMININES AND THE PALEOBIOGEOGRAPHY OF HOMININE ORIGINS

As noted earlier, there is agreement among many researchers that the dryopithecins are hominines, even if there is some disagreement on their precise relationships to crown hominines. There are, however, hominines in the African late Miocene, and some suggest that these evolved not from European hominines but *in situ* in Africa. The European taxa
are either dismissed as non-hominine or considered to have dispersed into Europe in the middle Miocene from an unknown middle Miocene African ancestor (Rook & Bernor 2004; Pickford & Senut 2005; Kunimatsu et al. 2007; Suwa et al. 2007). The evidence of the hominine affinities of the dryopithecins is actually quite strong, both from the analysis of Ouranopithecus and the Dryopithecus-Hispanopithecus-Rudapithecus group (see above and the numerous references cited). The real question is not whether European late Miocene hominins are hominines, but, do the European hominines represent one or more side branches of hominine evolution, having dispersed into Europe one or more times from unknown ancestors, or is the much larger record of Miocene hominines in Europe the true source of later hominines that dispersed into Africa in the late Miocene? There is strong evidence for the latter hypothesis in data from the morphology, geochronology and paleobiogeography of European hominines and other land mammals (Begun 2001, 2005, 2007a; Begun & Nargolwalla 2004; Nargolwalla 2009). The morphological evidence is reviewed above. Hominines occur in Europe more than 2 million years before they appear in Africa. They are more widespread and diverse than African hominines. Many land mammals are known to have expanded their ranges between Africa and Europe in the late Miocene, during the temporal interval between the first appearance of Vallesian European hominines and the first appearance of African hominines, including many taxa with preferences for forests (Fortelius et al. 1996; Leakey et al. 1996; Dawson 1999; Ginsburg 1999; Heissig 1999; Made 1999; Solounias et al. 1999; Agustí et al. 2001; Winkler 2002; Lehmann et al. 2006; Agustí 2007; Likius et al. 2007; Nargolwalla 2009). These dispersals or range expansions are widely believed to be related to changing climatic conditions in Europe, including increases in seasonality and a decline in forest cover (Bernor et al. 1979; Bernor 1983; Quade et al. 1989; Fortelius et al. 1996; Leakey et al. 1996; Agustí et al. 1999, 2001, 2003; Bonis & Koufos 1999; Cerling 1999; Cerling et al. 1999; Magyar et al. 1999; Solounias et al. 1999; Fortelius & Hokkanen 2001; Koufos 2003; Eronen & Rook 2004; Fortelius et al. 2006; Agustí 2007). The claim that the ecology of the most likely dispersal route between Europe and Africa, the eastern Mediterranean, was already too inhospitable for apes (Rook & Bernor 2004), is misleading for several reasons. Firstly, the drying that is typical of the broadly defined “Pikermian biome” begins to show an impact on environments after 10 Ma, and it was not until 8-9 Ma that the effects become pronounced (Solounias et al. 1999; Agustí et al. 2003; Eronen & Rook 2004; Fortelius et al. 2006; Agustí 2007). There is no paleoecological evidence to suggest that the eastern Mediterranean was inhospitable to forest living primates before 10 Ma. Secondly, many recent analyses question the overall “savanna-like” quality of the eastern Mediterranean in the late Miocene, and several stress the persistence of forest even after 10 Ma, despite the overall drying trend. Akgün et al. (2007) identify mixed mesophytic and swamp forest assemblages in western Anatolia in the late Miocene. Bruch et al. (2006) found evidence for a warm and humid climate overall in the Pannonian basin and well into the Balkans in many fossil plant localities until 9 Ma, with no indication of a Mediterranean climate. Pickford et al. (2006) identify a humid climate in the southern Mediterranean between 10-11 Ma. Fortelius et al. (2006) produced palaeoprecipitation maps for the late Miocene, through to about 9.5 Ma, which show very little regional differentiation between central Europe and the eastern Mediterranean. Ivanov et al. (2002) and Griffin (2002) describe fluctuating cycles of warm/humid and cooler/drier conditions in the northern Balkans in the late Miocene. Finally, the ape that dispersed from Europe to Africa is undiscovered at present, and therefore we have no knowledge of its ecological preferences, but if it was like many living primates it was probably capable of surviving in a diversity of environments. Thus, there is no reason a priori to believe that hominines could not have taken part in the general dispersal of land mammals between Europe and Africa during the late Miocene, and in fact Darwin speculated 150 years ago that this may well have taken place.

There is a good chance that African hominines evolved from a European ancestor. What is the nature of this ancestor and the dynamics of early hominine evolution in Africa? While the broad picture...
microCT analysis revealing several characters of the
enamodentine junction (EDJ) that support this alloca-tion. Pickford et al. (2009) recently described
as hominoid a very poorly preserved mandibular
specimen from Niger with an estimated age of
5-11 Ma. This specimen, along with other isolated
teeth from Kenya in the same temporal range
(Pickford & Senut 2005), are too poorly preserved
to be assigned to any known hominoid clade with
any confidence.

Chororapithecus
Suwa, Kono, Katoh, Asfaw &
Beyene, 2007, represented by a handful of isolated
teeth from 10-10.5 Ma deposits in Ethiopia, is
said to possibly be an early member of the Gorilla
clade (Suwa et al. 2007). The overall morphology
of the molars resembles many thickly enameled
late Miocene hominid molars, but the EDJ, while
mostly flat like most hominids with thick enamel,
has a subtle cresting pattern that Suwa
et al. (2007) interpret to be homologous to a much better devel-
oped crest on gorilla molars. Again, the connection
to Gorilla is possible, though much more data are
needed to make a strong case for this relationship.

Chororapithecus
is at least 2 Ma younger than
Dryopithecus, and does not therefore directly challenge the
hypothesis that hominines first appear in Europe.
However, it does present an interesting potential
scenario for the evolution of thinly enameled teeth
from a thickly enameled ancestor. Rook & Bernor
(2004) consider it unlikely that Ouranopithecus
could be ancestral to Aridpithecus, the latter hav-
ing thin molar enamel, although morphologically
the teeth are broadly similar to one another and
to australopithecines generally. The transformation
from a Chororapithecus dental morphology to that
of the extant gorilla is much more dramatic, and is
a cautionary tale about what it is wise to consider
likely or unlikely a priori in evolutionary history.

CONCLUSIONS

This review stresses the phyletic unity and eco-
logical diversity of European middle and late Miocene
hominines, and explicitly recognizes the pioneeri-ng efforts of Louis de Bonis in providing strong
evidence for decades to support the Afro-European
Miocene hominine connection. Diversity in European Miocene hominines parallels that of Pliocene to recent hominines, with a range of ecological preferences from suspensory, highly arboreal soft fruit frugivores living in closed forests, to hard object feeders, possibly much more terrestrial, living in more open settings.

The conclusion that hominines originate and experience their initial adaptive radiation in Europe is significant in setting the ecological and temporal context for the evolution of our subfamily. Hominines and pongines are likely to have evolved from early middle Miocene thickly enameled taxa, such as *Griphopithecus* from Europe and Western Asia or a close relative from later localities in Africa (*Nacholapithecus* Ishida, Kunimatsu, Nakatsukasa & Nakano, 1999, *Equatorius* Ward, Brown, Hill, Kelley & Downs, 1999, *Kenyapithecus* Leakey, 1962). While it may seem unnecessarily complicated to suggest that multiple dispersals and/or range extensions occurred between Africa and Eurasia during the evolution of the hominins before the hominines disperse from Europe to Africa a final time in the late Miocene (Begun 2002, 2005, 2007a; Andrews & Kelley 2007), this is the scenario proposed for several taxa including aardvarks, several carnivores, antelopes, hippos and probably at least one lineage of proboscidean (Leakey et al. 1996; Ginsburg 1999; Heißig 1999a, b; Made 1999; Boisserie et al. 2003; Werdelin 2003; Begun & Nargolwalla 2004; Lehmann et al. 2006; Likius et al. 2007; Koufos & Bonis 2008).

The major changes experienced by both the hominines and the pongines in Eurasia include diversification of positional behavior and the development of the extant hominin suspensory body plan, specialization of dietary adaptations, increases in overall body and brain size, and an overall slowing of life history (Begun & Kordos 2004; Kelley 2004; Russon & Begun 2004). The one aspect of hominid biology that unites all of these characteristics is behavioral flexibility and the ability to cope with diverse and changing ecological conditions (Potts 2004; Russon & Begun 2004). These adaptations first appear in Eurasia in response to Eurasian ecological conditions, and they are likely to have permitted hominins to survive and adapt to changing conditions in the late Miocene, and disperse into Southeast Asia and Africa. Specifically, the adaptations that developed in European hominines persist in extant hominines, and set the stage for the development of further changes in positional behavior, diet and eventually brain size that characterize the evolutionary history of the hominins.

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