

4 Fossil Record of Miocene Hominoids

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Abstract

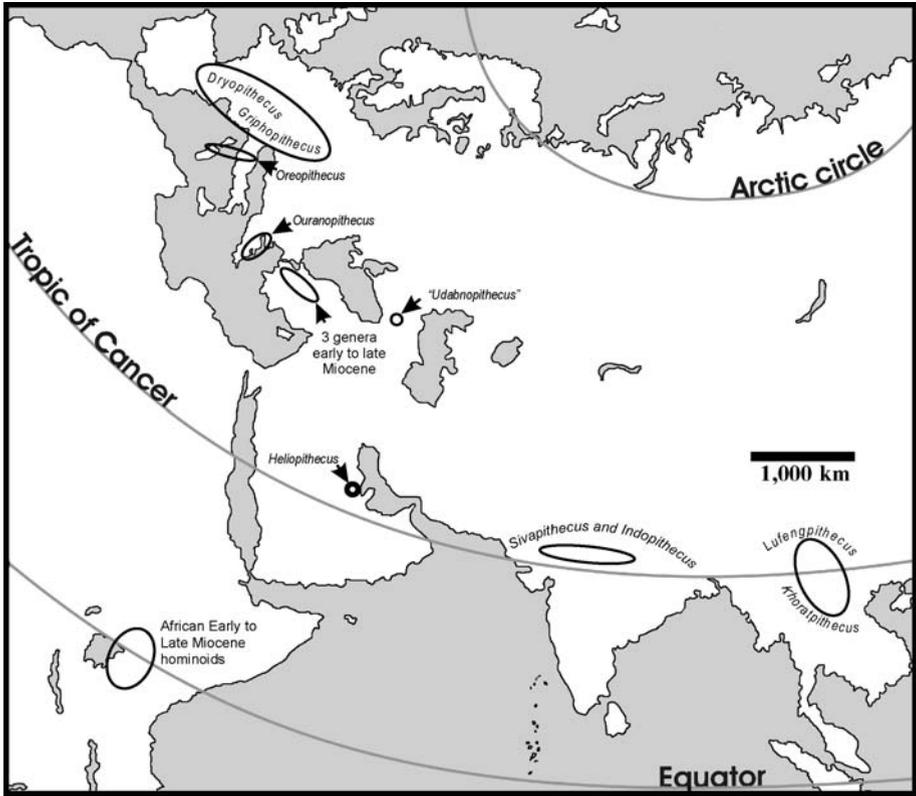
Hominoids, or taxa identified as hominoids, are known from much of Africa, Asia, and Europe since the Late Oligocene. The earliest taxa, from Africa, resemble extant hominoids but share with them mainly primitive characters. Middle and Late Miocene taxa are clearly hominoids, and by the end of the Middle Miocene most can be attributed to either the pongine (*Pongo*) or hominine (African ape and human) clade. Interestingly, there is no fossil record of the hylobatid clade (gibbons and siamangs). Miocene hominoids experienced a series of dispersals between Africa, Europe, and Asia that mirror those experienced by many other contemporaneous land mammals. These intercontinental movements were made possible by the appearance of land bridges, changes in regional and global climatic conditions, and evolutionary innovations. Most of the attributes that define the hominids evolved in the expansive subtropical zone that was much of Eurasia. Hominines and pongines diverge from each other in Eurasia, and the final Miocene dispersal brings the hominine clade to Africa and the pongine clade to Southeast Asia. Having moved south with the retreating subtropics, hominines and pongines finally diverge *in situ* into their individual extant lineages.

4.1 Introduction

Nonhuman fossil hominoids represent a highly diverse and successful radiation of catarrhine primates known from many localities ranging geographically from Namibia in the South, Germany in the North, Spain in the West, and Thailand in the East, and temporally from Oligocene deposits in Kenya to the Pleistocene of China (🔗 [Figure 4.1](#)). More than 40 genera of nonhuman hominoids are known (🔗 [Table 4.1](#)), probably a small percentage of the total number that have existed. Given the focus of these volumes on ape and especially human evolution, this survey of the fossil record of Miocene hominoids will concentrate on taxa that most or all researchers agree are hominoid and in particular on taxa that are most informative on the pattern and biogeography of modern hominoid origins.

■ Figure 4.1

Map showing the location of the Miocene taxa discussed in this chapter



4.1.1 What is a hominoid?

Most of the fossil taxa attributed to the Hominoidea or the Hominidea (new rank, [Table 4.2](#)) in this chapter are known to share derived characters with living hominoids. Because the two living families of the Hominoidea, Hylobatiidae and Hominidae, share characters that are either absent or ambiguous in their development in *Proconsul* and other Early Miocene taxa, a new rank is proposed here to express the monophyly of the Hominoidea and the monophyly of catarrhines more closely related to extant hominoids than to any other catarrhine. The magnafamily Hominidea (a rank proposed in a work on perissodactyl evolution [Schoch 1986]) unites Proconsuloidea with Hominoidea to the exclusion of other catarrhines. This differs from Harrison's use of the term proconsuloid that he sees as referring to the sister taxon to cercopithecoids and hominoids (Harrison 2002).

Table 4.1
Genera of fossil apes¹

Age	Ma	Genera	Important localities	Country	Material ²
Oligo.	25	<i>Kamoyapithecus</i> ³	Lothidok	Kenya	Cranioidental fragments
e M	21	New taxon	Meswa Bridge	Kenya	Cranioidental fragments
e M	?	<i>Morotopithecus</i>	Moroto	Uganda	Cranial, dental, postcrania
e M	?	<i>Kogolepithecus</i> ³	Moroto	Uganda	Dental
e M	19	<i>Ugandapithecus</i> ⁴	Napak/Songhor	K/U	Cranial, dental, postcrania
e M	19	<i>Xenopithecus</i> ³	Koru	Kenya	Cranioidental fragments
e M	19	<i>Proconsul</i>	Songhor/Koru	Kenya	Cranial, dental, postcrania
e M	19	<i>Limnopithecus</i> ³	Koru/Songhor	Kenya	Cranioidental
e M	19	<i>Rangwapithecus</i> ³	Songhor	Kenya	Cranioidental
e M	19	<i>Micropithecus</i> ³	Napak/Koru	K/U	Cranioidental
e M	19	<i>Kalepithecus</i> ³	Songhor/Koru	Kenya	Cranioidental fragments
e M	17.5–19	<i>Dendropithecus</i> ³	Rusinga/Songhor/Napak/Koru	K/U	Cranial, dental, postcrania
e M	17.5	cf. <i>Proconsul</i> ^f	Rusinga/Mfangano	Kenya	(Cranial, dental, postcrania)+
e M	17.5	<i>Turkanapithecus</i>	Kalodirr	Kenya	Cranial, dental, postcrania
e M	17.5	<i>Afropithecus</i>	Kalodirr	Kenya	Cranial, dental, postcrania
e–m M	17.5–15	<i>Simiolus</i>	Kalodirr/Maboko	Kenya	Cranial, dental, postcrania
e–m M	17.5–15	<i>Nyanzapithecus</i>	Rusinga/Maboko	Kenya	Cranial, dental, postcrania
e M	17	<i>Heliopithecus</i>	Ad Dabtiyah	S. Arabia	Cranioidental fragments
e M	16.5	cf. <i>Griphopithecus</i>	Engelswies	Germany	Dental
e M	16	<i>Griphopithecus</i>	Paşalar/Çandır	Turkey	Cranial, (dental)+, postcrania
m M	15	<i>Equatorius</i>	Maboko/Kipsarimon	Kenya	(Cranial, dental, postcrania)+
m M	15	<i>Mabokopithecus</i>	Maboko	Kenya	Dental
m M	15	<i>Nacholapithecus</i>	Nachola	Kenya	Partial skeleton
m M	13	<i>Pierolapithecus</i>	El Hostelets de Pierola	Spain	Partial skeleton
m M	13	<i>Kenyanpithecus</i>	Fort Ternan	Kenya	Cranial, dental, postcrania
m M	13	<i>Otaviipithecus</i>	Otavi	Namibia	Cranioidental, vertebra
m–l M	12–7	<i>Sivapithecus</i>	Potwar Plateau	Pakistan	(Cranial, dental, postcrania)+
m–l M	12–10	<i>Dryopithecus</i>	Rudabánya/Can Llobateres	H/S	(Cranial, dental, postcrania)+

■ **Table 4.1** (continued)

Age	Ma	Genera	Important localities	Country	Material ²
m-IM	?13.5-7	<i>Khoratpithecus</i> ⁶	Ban Sa/Khorat	Thailand	Cranioidental fragments
IM	10	<i>Ankarapithecus</i>	Sinap	Turkey	Cranial, dental, postcrania
IM	9.5	<i>Samburupithecus</i>	Samburu	Kenya	Cranioidental fragments
IM	9.5	<i>Ouranopithecus</i>	Ravin de la Pluie	Greece	(Cranioidental)+, 2 phalanges
IM	9-8	<i>Graecopithecus</i>	Pygros	Greece	Mandible
IM	9-8	<i>Lufengpithecus</i>	Lufeng	China	(Cranial, dental)+, postcrania
IM	8-7	New taxon	Çorakyerler	Turkey	Mandible, maxilla
IM	7	<i>Oreopithecus</i>	Baccinello/Monte Bamboli	Italy	(Cranial, dental, postcrania)+
IM	7-6	<i>Sahelanthropus</i>	Toros-Menalla	Chad	Cranioidental
IM	6.5	<i>Gigantopithecus</i>	Potwar Plateau	Pakistan	Mandible
IM	6	<i>Orrorin</i>	Lukeino	Kenya	Cranioidental, postcrania
IM	5.8-5.2	<i>Ardipithecus</i> ⁷	Alayla (Middle Awash)	Ethiopia	Cranioidental, postcrania

Oligo. = Oligocene, e M = Early Miocene, e-m M = Early-Middle Miocene, m M = Middle Miocene, m-IM = Middle-Late Miocene, IM = Late Miocene, K/U = Kenya and Uganda, H/S = Hungary and Spain.

¹These 40 genera include taxa from the Oligocene and Early Miocene that share mainly primitive characters with the Hominoidea but that appear to be derived relative to Pliopithecoids and Propliopithecoids.

²Material briefly described by part representation. Dental = mainly isolated teeth; Dental, mandible, maxilla = known only from these parts; Cranioidental fragments = teeth and few cranial fragments; Cranioidental = larger samples of more informative cranial material; Cranial, dental, postcrania = good samples from each region; (+) = very good representation of parts in parentheses.

³Unclear attribution to Hominoidea.

⁴Large taxon possibly distinct from *Proconsul*.

⁵*Proconsul* from later Early Miocene localities in Kenya is likely to be distinct from earlier Miocene *Proconsul* type material.

⁶Middle Miocene samples attributed to this taxon are more fragmentary and may not be congeneric.

⁷*Ardipithecus kadabba*.

■ Table 4.2

A taxonomy of the Hominidea

Cercopithecoidea (Magnafamily, new rank)	
Hominidea (Magnafamily, new rank)	
Proconsuloidea	Crown hominoids of uncertain status
<i>Proconsul</i>	<i>Kenyapithecus</i>
cf. <i>Proconsul</i>	<i>Oreopithecus</i>
<i>Samburupithecus</i>	Family incertae sedis
<i>Micropithecus</i>	<i>Afropithecus</i>
Hominoidea	<i>Morotopithecus</i>
Hylobatidae	<i>Heliopithecus</i>
<i>Hylobates</i>	<i>Griphopithecus</i>
Hominidae	<i>Equatorius</i>
<i>Pierolapithecus</i>	<i>Nacholapithecus</i>
<i>Dryopithecus</i>	<i>Otavipithecus</i>
<i>Ouranopithecus</i>	Superfamily incertae sedis
<i>Graecopithecus</i>	<i>Rangwapithecus</i>
<i>Sivapithecus</i>	<i>Nyanzapithecus</i>
<i>Lufengpithecus</i>	<i>Mabokopithecus</i>
<i>Khoratpithecus</i>	<i>Turkanapithecus</i>
<i>Ankarapithecus</i>	Magnafamily incertae sedis
<i>Gigantopithecus</i>	<i>Kamoyapithecus</i>
<i>Sahelanthropus</i>	<i>Dendropithecus</i>
<i>Orrorin</i>	<i>Simiolus</i>
<i>Homo</i>	<i>Limnopithecus</i>
<i>Ardipithecus</i>	<i>Kalepithecus</i>
<i>Praeanthropus</i>	
<i>Australopithecus</i>	
<i>Paraustralopithecus</i>	
<i>Paranthropus</i>	
<i>Pongo</i>	
<i>Pan</i>	
<i>Gorilla</i>	

A few taxa are included in this review if they are too poorly known to preserve unambiguous hominoid synapomorphies but closely resemble other better-known fossil hominoids. In general, fossil and living hominoids retain a primitive catarrhine dental morphology. This makes it difficult to assign many fossil taxa to the Hominoidea since a large number are known only from teeth and small portions of jaws. Dentally, the most primitive Hominidea differ only subtly from extinct primitive catarrhines (propliopithecoids and pliopithecoids) (🔗 Figure 4.2, node 1). Propliopithecoids (*Propliopithecus*, *Aegyptopithecus*) are usually smaller and have much more strongly developed molar cingula, higher cusped premolars, and smaller incisors and canines (Begun et al. 1997; Rasmussen 2002). Pliopithecoids (*Pliopithecus*, *Anapithecus*) are also generally smaller and have molars with more strongly expressed cingula, more mesial protoconids,

and relatively small anterior teeth (Begun 2002). However, the differences between Late Miocene hominids and Late Miocene pliopithecoids are more marked than between Early Miocene Hominidea and pliopithecoids, making defining features less than clear-cut. Cranially Hominidea have a completely ossified tubular ectotympanic, which distinguishes them from both propiopithecoids and pliopithecoids but not from cercopithecoids. However, few Miocene Hominidea fossils preserve this region. Hylobatids, cranially the most primitive extant hominoid, share many features found in short-faced Old and New World monkeys, again making it difficult to tease out synapomorphies. Hominoids show a tendency to expand the length and superoinferior thickness or robusticity of the premaxilla, with increasing overlap with the palatine process of the maxilla over time, but once again this is not present in hylobatids or early well-preserved specimens of *Proconsul*, for example (Begun 1994a). Only one specimen of Early Miocene Hominidea is complete enough to say much about the brain, and there are no unambiguous synapomorphies linking it to hominoids. The brain of *Proconsul* is similar relative to body size to both hylobatids and papionins, the Old World monkeys with the largest brains, and the sulcal pattern, while debatable, lacks most if not all hominoid features (Falk 1983; Begun and Kordos 2004). Like hylobatids, most cercopithecoids, and most mammals other than hominids, a portion of the brain of *Proconsul* occupied a large subarcuate fossa. Cranial and dental evidence also suggests that *Proconsul* was moderately delayed in terms of life history, another similarity with extant hominoids (Kelley 1997, 2004).

Postcranially, *Proconsul* more clearly represents the ancestral hominoid morphotype, though this too is the subject of debate. *Proconsul* fossils exhibit hominoid attributes of the elbow, wrist, vertebral column, hip joint, and foot, though in all cases these are subtle and disputed (Beard et al. 1986; Rose 1983, 1988, 1992, 1994, 1997; Ward et al. 1991; Ward 1993, 1997; Begun et al. 1994; but see Harrison 2002, 1987). *Proconsul* has a suite of characters consistent with the hypothetical ancestral morphotype of the hominoids, and it should not be surprising that these are poorly developed at first, only to become more refined as hominoids evolve. In comparison to the hominoid outgroup (cercopithecoids), we can expect the earliest hominoids to show subtle indications of increased orthograde, positional behaviors with increased limb flexibility and enhanced grasping capabilities and no tail, generalized (primitive) dentition, encephalization at the high end of extant cercopithecoids of comparable body mass, and life history variables closer to extant hominoids than to extant cercopithecoids. *Proconsul* has all of these attributes.

If these are the features that define the Hominidea, which taxa among Miocene fossil catarrhines are not Hominidea? Even the earliest cercopithecoids

(victoriapithecids) are easily distinguished from hominoids (Benefit and McCrossin 2002). Pliopithecoids, often grouped with the “apes,” are even more distantly related. They are clearly stem catarrhines lacking synapomorphies of all crown catarrhines including *Proconsul* and *Victoriapithecus* (Begun 2002). The most informative among these synapomorphies are the tubular ectotympanic and the entepicondylar groove (often referred to as the absence of an entepicondylar foramen). In the following sections, I will summarize current knowledge of the Miocene Hominidea, focusing on well-known taxa that serve to illustrate important events in hominoid evolutionary history (► [Figure 4.2](#)).

4.2 Origins of Hominidea

It is likely that hominoids originated in Africa from an ancestor that, if known, would be grouped among the Pliopithecoidae. Pliopithecoids, currently known only from Eurasia, share with all catarrhines the same dental formula and possibly with crown catarrhines a reduction of the midface, subtle features of the molar dentition, and a partial ossification of the ectotympanic tube (Begun 2002). The presence of pliopithecoids in Africa is suggestive but remains to be demonstrated (Andrews 1978; Begun 2002). The oldest and most primitive catarrhine that can lay claim to hominoid status however is African (► [Table 4.1](#)). *Kamoyapithecus*, from the Oligocene of Kenya, differs from other Oligocene catarrhines (propliopithecoids) in being larger and having canines and premolars that more closely resemble Miocene hominoids than Oligo-Miocene non-hominoids (Leakey et al. 1995). Only craniodental material of *Kamoyapithecus* has been described, and it is so primitive as to make attribution to the Hominoidea difficult. Though it would fail to fall among the Hominoidea in a quantitative cladistic analysis due to its fragmentary preservation and primitive morphology, it makes in my view a good hominoid precursor.

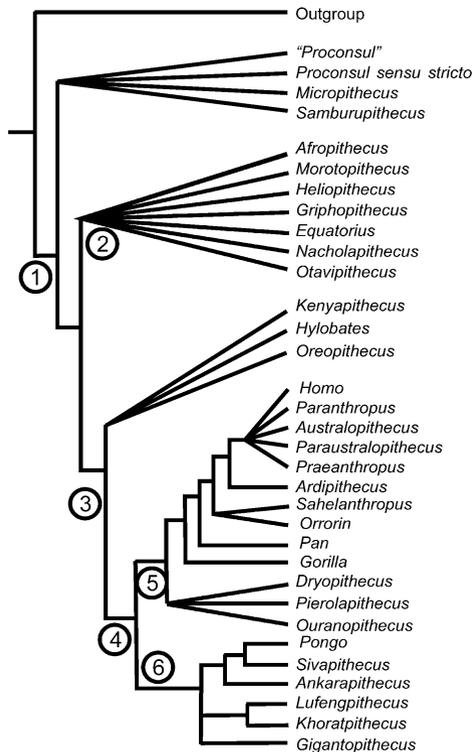
4.3 Proconsuloidea

4.3.1 *Proconsul*

The superfamily Proconsuloidea, as defined by Harrison (2002), includes many mainly Early Miocene taxa. As noted, in this chapter a number of taxa from this group are interpreted to represent primitive Hominidea or hominoids. A hypothetical ancestral morphotype for the Hominidea is given in ► [Figure 4.2](#) (node 1). Node 1 represents the bifurcation of *Proconsul* from hominoids with more

■ Figure 4.2

Cladogram depicting the relations among Miocene Hominidea discussed in this chapter. The cladogram is resolved only at the level of the family in many cases, except within the Hominae, where most clades are resolved. Numbered nodes refer to characters or suites of characters that serve to define clades. They are not intended as comprehensive lists of synapomorphies. Node 1: Reduced cingula, delayed life history (M1 emergence), incipient separation of the trochlea and capitulum, increased hip and wrist mobility, powerful grasping, no tail. Node 2: Thick enamel, increased premaxillary robusticity, further reduction in cingula, increase in P_4 talonid height, possible increases in forelimb dominated positional behaviors. Node 3: Further "hominoidization" of the elbow. The position of *Kenyapithecus* is extremely unclear. Without this taxon, node 3 features the numerous characters of the hominoid trunk and limbs related to suspensory positional behavior. Node 4: Hominae (see text). Node 5: Hominae (see text). Lack of resolution of the hominini reflects continuing debate on relations among Pliocene taxa that is beyond the scope of this chapter. *Pierolapithecus* may be a stem hominid or stem hominine, as depicted here. Node 6: Ponginae (see text). *Gigantopithecus* is probably a pongine but the relations to other pongines are unclear



apparent synapomorphies to living hominoids. *Proconsul* as described here is based mainly on the sample from Rusinga Island, Kenya along with other localities of the same age. These include the species *Proconsul heseloni* (Walker et al. 1993) and *Proconsul nyanzae* (Le Gros Clark and Leakey 1950). The type

specimen of *Proconsul africanus* (Hopwood 1933) is from Koru, which is 1-to 2-Myr older, as is the type of *Proconsul major* (Le Gros Clark and Leakey 1950) from Songhor (Drake et al. 1988). There is evidence that the younger species of *Proconsul* that are the basis of the description here belong to a different genus from the older type sample (see below). However, as this is not the appropriate venue to name a new genus, I will follow convention and refer to the Rusinga sample as *Proconsul*.

4.3.1.1 Postcranial morphology

Proconsul and other proconsuloids are defined by a large number of characters. *Proconsul* is a generalized arboreal quadruped but is neither monkey-like nor apelike (Rose 1983). The following summary is mainly from Rose (1997), Ward (1997), and Walker (1997). In addition to the characters noted that emphasized its hominoid affinities, *Proconsul* has limbs of nearly equal length, with scapula positioned laterally on the thorax and the ovoid and narrow glenoid positioned inferiorly, as in generalized quadrupeds. The thorax is transversely narrow and deep superoinferiorly, and the vertebral column is long and flexible, especially in the lumbar region. The innominate is long with a narrow ilium and an elongated ischium. The sacrum is narrow, and its distal end indicates that it articulated with a coccygeal and not a caudal vertebra, in other words *Proconsul* had a coccyx and not a tail (Ward et al. 1991).

In the details of limb morphology, *Proconsul* also combines aspects of monkey and ape morphology. *Proconsul* forelimbs lack the characteristic elongation of ape forelimbs. The humeral head is oriented posteriorly relative to the transverse plane and the humeral shaft is convex anteriorly, both of which are consistent with the position of the glenoid fossa and the shape of the thorax. The distal end of the humerus lacks the enlargement of the capitulum and trochlea and other details of the hominoid elbow, but it does have a narrow zona conoidea and a mild trochlear notch. The medial epicondyle is also more posteriorly oriented as in monkeys. The proximal ends of the radius and ulna are consistent with the morphology of the distal humerus. The radial head is small and ovoid, the ulnar trochlea is narrow and has a poorly developed keel, and the radial notch is positioned anteriorly. The ulna also has a large olecranon process. All of these features are consistent with generalized pronograde (above branch) quadrupedalism as opposed to antipronograde (suspensory or below branch) (see Ward Volume 2 Chapter 6).

Distally, the radial carpal surface is flat and articulates mainly with the scaphoid. The ulnar head is comparatively large with a long and prominent

styloid process that articulates directly with the pisiform and triquetrum, unlike living hominoids, which have greatly reduced ulnar styloids and no contact with the carpals. The carpals are small transversely. The scaphoid is separate from the os centrale and the midcarpal joint is narrow. The hamate hamulus is small, and the surface for the triquetrum is flat and mainly medially oriented (Beard et al. 1986). The metacarpal surfaces of the distal carpals are small and comparatively simple as are the corresponding surfaces on the metacarpal bases. The metacarpals are short and straight and their heads transversely narrow. The proximal ends of the proximal phalanges are slightly dorsally positioned as in palmigrade quadrupeds. All the phalanges are short and straight compared to apes, though secondary shaft features, in particular of the proximal phalanges, suggest powerful grasping (Begun et al. 1994).

The hindlimbs of *Proconsul* are also dominated by monkey-like characters. The long bones are long and slender. The femoral head is small compared to apes, but its articulation with the acetabulum indicates more mobility compared to most monkeys. The feet of *Proconsul* are monkey-like in their length to breadth ratio (they are narrow compared to great ape feet). *Proconsul* tarsals are elongated relative to breadth and the metatarsals long compared to the phalanges. Like those of the hands, the foot phalanges of *Proconsul* are straighter and less curved than in apes but with more strongly developed features related to grasping than in most monkeys. The hallucial phalanges are relatively robust, suggestive of a powerfully grasping big toe. Body mass estimates for the species of *Proconsul*, based mainly on postcranial evidence, range from about 10 to 50 kg (Ruff et al. 1989; Rafferty et al. 1995).

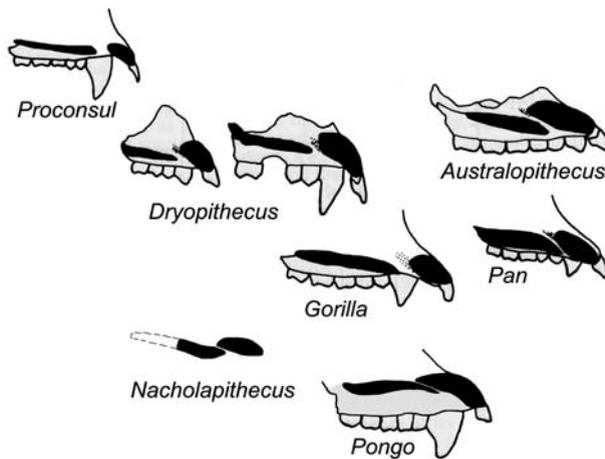
4.3.1.2 Craniodental morphology

As noted, *Proconsul* has a moderate amount of encephalization (comparable to hylobatids and papionins), a short face with a fenestrated palate (▶ [Figure 4.3](#)), a smoothly rounded and somewhat airorhynchous face (▶ [Figure 4.4](#)), and a generalized dentition. Morphologically, the dentition is consistent with a soft fruit diet, and microwear analysis suggests the same (Kay and Ungar 1997). The somewhat enlarged brain of *Proconsul* implies a degree of life history delay approaching the hominoid pattern (Kelley 1997, 2004).

One aspect of the cranium of *Proconsul* that has received some attention is the frontal sinus. Walker (1997) interprets the presence of a frontal sinus in *Proconsul* to indicate its hominid status, citing the presence of large frontal sinuses in some great apes. Other researchers have suggested that the frontal

■ Figure 4.3

Midsagittal cross section of a number of Hominidea palates showing some of the features described in the text. *Proconsul* has a small premaxilla and a fenestrated palate (large foramen and no overlap between the maxilla and premaxilla). *Nacholapithecus* has a longer premaxilla with some overlap. It is similar to *Afropithecus* and conceivably could be the primitive morphotype for the Hominidae. *Pongo* and *Sivapithecus* have a similar configuration but with further elongation and extensive overlap between the maxilla and premaxilla, producing a smooth subnasal floor. Hominines have robust premaxillae that are generally shorter and less overlapping than in *Sivapithecus* and *Pongo*. *Dryopithecus* is most similar to *Gorilla*, which may represent the primitive condition for hominines. *Pan* and *Australopithecus* have further elongation and overlap, but the configuration differs from *Pongo*. This morphology is suggested to be an important synapomorphy of the *Pan/Homo* clade (Begun 1992b). Modified from Begun (1994)

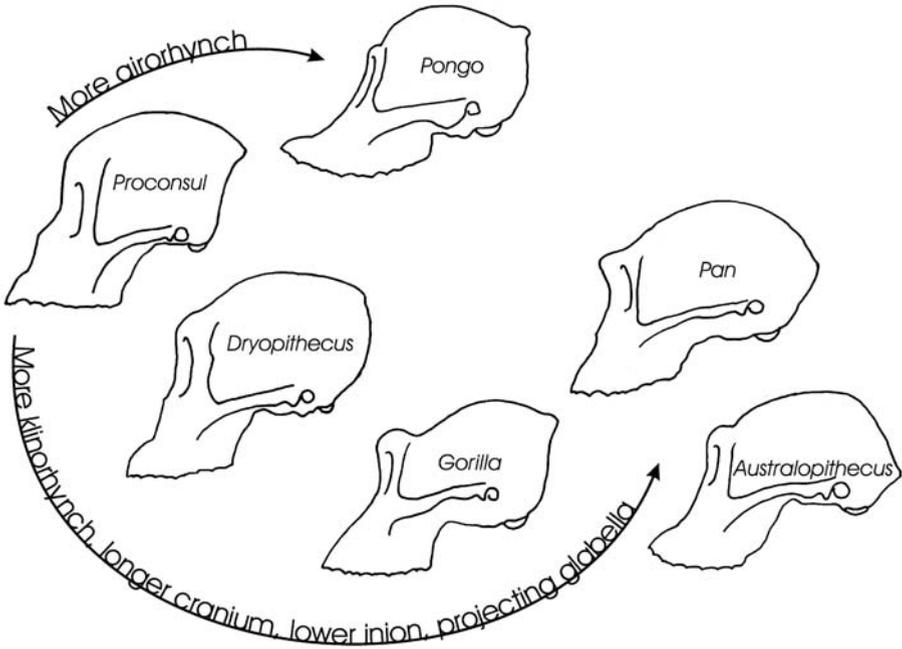


sinus is a primitive character, as it is found in *Aegyptopithecus* and many New World monkeys (Andrews 1992; Rossie et al. 2002). The confusion stems from the use of one term to describe several different characters. As Cave and Haines (1940) noted long ago, frontal sinuses in primates have various ontogenetic origins, and it is likely that they are not homologous across the primates. New World monkeys have frontal sinuses that are outgrowths from the sphenoid sinus, as is also the case for hylobatids. On the other hand, *Pongo*, which occasionally has a frontal sinus, derives it from the maxillary sinus. African apes and humans normally have large frontal sinuses derived from the ethmoidal sinuses. “Frontal sinuses” then are actually three different characters, frontosphenoidal sinuses, frontomaxillary sinuses, and frontoethmoidal sinuses.

While it is possible to establish the ontogenetic origin of a pneumatized frontal bone in living primates, it is more difficult in fossil primates. However, the placement and size of the frontal sinuses correlate very well with their ontogenetic

■ Figure 4.4

Lateral views of some Hominidea crania showing possible changes through time. A mildly airorhynch *Proconsul* may be a good ancestral morphotype for hominoid craniofacial hafting, as a similar degree of airorhynch is also found in hylobatids (Shea 1988). *Dryopithecus* shares with other hominines neurocranial elongation (though this also occurs in hylobatids), the development of supraorbital tori, klinorhynch and probably in association with the latter, a true frontoethmoidal sinus. Modified from Kordos and Begun (2001)



origin, offering a protocol for identifying the specific type of frontal sinus present in a fossil (Begun 1994a). Frontosphenoidal sinuses invade large portions of the frontal squama but not the supraorbital or interorbital regions. Frontomaxillary sinuses are infrequent in *Pongo*, but when they occur they are associated with narrow canals or invaginations connecting the maxillary sinuses to a small pneumatization of the frontal via the interorbital space. In African apes and humans, the frontoethmoidal sinuses arise from a spreading of the ethmoidal air cells in the vicinity of nasion, resulting in large pneumatizations from below nasion into the supraorbital portion of the frontal. The actual amount of frontal pneumatization is variable, while the presence of a large sinus around nasion is constant. Therefore, while we cannot observe the development of frontal pneumatization in fossil primates, and we do not have adequate ontogenetic series to directly reconstruct this growth, we can infer the type of frontal pneumatization from its position, extent, and connection to the source sinus. In *Proconsul*, as in hylobatids, New World monkeys, and *Aegyptopithecus*, the frontal pneumatization is

extensive and occupies the frontal squama, consistent with a frontosphenoidal sinus. Thus, the “frontal sinus” in *Proconsul* is a primitive character, as suggested by Andrews (1992), but for different reasons. The frontal pneumatization of *Dryopithecus*, on the other hand, conforms to the pattern seen exclusively in African apes and humans (see below).

In summary, *Proconsul* was an above branch mid- to large-sized catarrhine with a diet dominated by soft fruits and a somewhat slower life history than cercopithecoids. Encephalization may imply other similarities to hominoid behavioral or social ecology, or it may simply be a consequence of relatively large body mass and/or a slower life history (Kelley 2004; Russon and Begun 2004). The slightly enhanced range of motion in *Proconsul* limbs may imply some degree of orthograde, or it may be a consequence of lacking a tail or of large body mass in an arboreal milieu, or some combination of all three (Beard et al. 1986; Begun et al. 1994; Kelley 1997).

4.3.2 Other possible proconsuloids

A number of taxa are regarded by many researchers as having a probable close relationship to *Proconsul*. The three with the best evidence for affinities to the proconsuloids are *Proconsul sensu stricto*, *Micropithecus*, and *Samburupithecus*. As noted, the type species of the genus *Proconsul* is *P. africanus*. *P. africanus* and *P. major*, which are both older than *Proconsul* from Rusinga, are also more primitive and lack synapomorphies shared by *Proconsul* from Rusinga and other hominoids (see below). Other taxa listed in [Table 4.2](#) are either more likely to be hominoids given similarities to known hominoids (*Rangwapithecus*, *Nyanzapithecus*, *Mabokopithecus*) or they are so primitive or poorly known as to cast doubt on their magnafamily status.

4.3.2.1 *Proconsul sensu stricto*

The older species of *Proconsul sensu stricto* from Songhor and Koru (*P. africanus* and *P. major*) probably represent a different genus from *P. heseloni* and *P. nyanzae*, the samples on which the descriptions of *Proconsul* presented here are based. A new genus would replace *P. heseloni* and *P. nyanzae*, as *P. africanus* has priority. *Proconsul sensu stricto* from Songhor and Koru has elongated postcanine teeth, more strongly developed cingula, upper premolars with strong cusp heteromorphy and conical, individualized molar cusps, all of which suggest that the older species are in fact more primitive. The two older species differ from each other

only in size. Postcrania attributed to *Proconsul* from the older *Proconsul sensu stricto* localities are distinct from postcrania from the younger *Proconsul* localities such as Rusinga, in details that have been correlated to paleoecological differences (Andrews et al. 1997). While sufficiently similar to the better-known younger *Proconsul* sample to warrant placing both in the same superfamily, the more modern morphology of the younger *Proconsul* sample will almost certainly require taxonomic recognition.

Ugandapithecus, a recently named genus based on the sample of *P. major*, adds to the confusion (Senut et al. 2000). *P. africanus* is smaller than “*Ugandapithecus*” *major* but is morphologically closer to it in the attributes noted above. Thus, while *Ugandapithecus* is probably a junior subjective synonym of *Proconsul sensu stricto*, it turns out that *Proconsul* as traditionally defined probably does represent more than one genus. Senut et al. (2000) have suggested that large-bodied hominoids from Moroto, in Uganda, may also be attributed to *Ugandapithecus* (hence the name, though the type is from Kenya), that is, *P. major*, calling into question the interpretation that hominoid cranial and postcranial fossils from Moroto belong to one taxon (*Morotopithecus*). However, the evidence for more than one large hominoid genus at Moroto is not strong (see below).

4.3.2.2 *Micropithecus*

Micropithecus (Fleagle and Simons 1978) is a small catarrhine with comparatively broad incisors and long postcanine teeth with low cusps and rounded occlusal crests. The cingula are less strongly developed than most other Early Miocene catarrhines. Males and females exhibit marked size dimorphism. Comparisons to living catarrhines suggest a body mass of about 34.5 kg (Harrison 2002). While Harrison (2002) considers this taxon to be even more distantly related to the Hominoidea than are the Proconsuloidea, the subtly more modern features of the dentition suggest that it may belong to the Proconsuloidea. Fleagle and Simons (1978) in fact attribute *Micropithecus* to the Hominoidea, although as noted the features shared with hominoids are very subtle. If *Micropithecus* is a proconsuloid, as suggested here, it would indicate that the proconsuloids were quite diverse in body mass, as is the case in all catarrhine superfamilies.

4.3.2.3 *Samburupithecus*

Samburupithecus is another possible proconsuloid, known only from a large maxillary fragment from the Late Miocene of the Samburu region of Kenya

(Ishida and Pickford 1997). Ishida and Pickford (1997) have suggested that *Samburupithecus* is an early member of the African ape and human clade. However, *Samburupithecus* retains many primitive characters of the Proconsuloidea. These include a low root of the zygomatic processes, a strongly inclined nasal aperture edge, the retention of molar cingula, and thick enamel with high dentine relief (Begun 2001). *Samburupithecus* is most likely to be a late surviving proconsuloid. Its unusual dental characters (e.g., large molars with individualized cusps separated by deep narrow fissures) are reminiscent of morphological “extremes” found in terminal lineages with long evolutionary histories. *Oreopithecus*, *Gigantopithecus*, *Paranthropus*, *Daubentonia*, and *Ekgmowechashala* all share with *Samburupithecus* exaggerated occlusal features compared to other members of their respective clades. The size and occlusal morphology of *Samburupithecus* that superficially resembles *Gorilla* (Ishida and Pickford 1997) may be related in part to the fact that both are ends of long phylogenetic branches. In a pattern analogous to long branch attraction in molecular systematics, there is a tendency for separate long isolated lineages to converge in certain aspects of their morphology (Begun 2001). For whatever the reason, in its details *Samburupithecus* is primitive and more likely to belong to the proconsuloids than the hominoids.

4.4 Early hominoids

4.4.1 *Afropithecus*

A number of late Early Miocene and Middle Miocene taxa share characters with extant Hominoids and are included here in the Hominoidea. *Afropithecus* (Leakey and Leakey 1986) is known from several localities in northern Kenya dated to 17–17.5 Ma (Leakey and Walker 1997). *Afropithecus* shares an increase in premaxillary robusticity and length with most extant hominoids (🔗 [Figure 4.3](#)). Like many Late Miocene and Pliocene hominids, *Afropithecus* has very thick occlusal enamel as well. On the other hand, *Afropithecus* cranial morphology, particularly the morphology of the midface, recalls that of *Aegyptopithecus*. Thus, as with *Proconsul*, *Afropithecus* has a mosaic of primitive and derived characters (Leakey et al. 1991; Leakey and Walker 1997). Leakey and Walker (1997) have suggested that the unusual primitive looking face of *Afropithecus* may be related to a specialized scerocarp seed predator adaptation. This is functionally consistent with the robust, prognathic premaxilla, large, relatively horizontal incisors, large but relatively low-crowned canines, expanded premolars, thick enamel, and powerful chewing muscles of *Afropithecus*. A similar set of features

is found in modern primate seed predators such as pitheciines. It may be that some of the primitive appearance of the *Afropithecus* face is homoplastic with *Aegyptopithecus*.

A large cranial specimen of *Afropithecus* reveals some information on neurocranial morphology. KNM-WK 16999 preserves a portion of the braincase immediately behind the orbits. Postorbital constriction is very marked as are the anterior temporal lines. These converge to form a pronounced and very anteriorly situated sagittal crest. The small portion of the anterior cranial fossa preserved indicates a cerebrum that was constricted rostrally, lacking the frontal lobe expansion typical of extant and fossil great apes.

Afropithecus is similar in size to *Proconsul nyanzae*, based on cranial, dental, and postcranial dimensions (Leakey and Walker 1997). *Afropithecus* postcrania are very similar to those of *Proconsul*, so much so that Rose (1993) found them essentially indistinguishable. The postcranial adaptation, in terms of body mass and positional behavior, is *Proconsul*-like, while the craniodental anatomy is markedly distinct.

Another early hominoid taxon, *Heliopithecus*, is contemporaneous with *Afropithecus* and morphologically very similar, though it is only known from a fragmentary hemimaxilla and a few isolated teeth (Andrews and Martin 1987). Both *Heliopithecus* and *Afropithecus* share characters that are found next in the fossil record in Eurasia, which suggests that *Heliopithecus* and *Afropithecus* taxa may have a closer relationship to late Early Miocene and Middle Miocene hominoids from Europe than do proconsuloids.

4.4.2 *Morotopithecus*

Morotopithecus is a fossil hominoid from Uganda dated to about 21 Ma by some and 17 Ma by others (Gebo et al. 1997; Pickford et al. 2003). It is best known from a large cranial specimen including most of the palate (Pilbeam 1969). For many years, this specimen was attributed to *Proconsul major*, but it is clear that it and other specimens from Moroto are sufficiently distinct to justify a new genus. *Morotopithecus* is similar in size to *Proconsul major* and larger than *Proconsul nyanzae* and *Afropithecus*. It lacks the distinctive subnasal morphology of *Afropithecus* and has a *Proconsul*-like premaxilla that is short, gracile, and does not overlap the palatine process of the maxilla, resulting in a large incisive fenestration (🔗 [Figure 4.3](#)). *Morotopithecus* has a broad palate, large anterior teeth, especially the canines, which are tusklike, a piriform aperture broadest about mid way up, and an interorbital space that appears to be relatively narrow, though it is damaged. However, the most important distinction of *Morotopithecus* is the

morphology of the postcrania, which are said to be modern hominoid-like. Newly described specimens of *Morotopithecus* include the shoulder joint, hip joint, and details of the vertebral column. Walker and Rose (1968) described the vertebrae as hominoid-like, which has been confirmed by more recent discoveries and analyses. The glenoid fossa of *Morotopithecus* suggests a more mobile shoulder joint as does the morphology of the hip joint. However, it is the hominoid-like position of the transverse processes of the vertebrae that represents the strongest evidence for the hominid affinities of *Morotopithecus*. The roots of the transverse processes of the lumbar vertebrae of *Morotopithecus* are positioned posteriorly, as in extant great apes, suggesting a stiff lower back and an axial skeleton like that of extant hominoids.

4.4.3 Eurasian hominoid origins

As noted, *Heliopithecus* and *Afropithecus* have more robust jaws and teeth than Early Miocene proconsuloids, and this may represent a key adaptation that permitted the expansion of hominoids into Eurasia at about 17 Ma, when during a marine low stand a diversity of terrestrial mammals moved between Africa and Eurasia (Made 1999; Begun 2001; Begun et al. 2003). Toward the end of the Early Miocene, the movement of the southern landmasses northward, combined with a number of other developments (the Alpine and Himalayan orogenies, the earliest appearance the polar ice caps, and the Asian Monsoons), leads to a sequence of connections and barriers to terrestrial faunal exchange (Rögl 1999a, b; Adams et al. 1999; MacLeod 1999; Hoorn et al. 2000; Zhisheng et al. 2001; Guo et al. 2002; Liu and Yin 2002; Wilson et al. 2002). This period of global turbulence affected sea levels between continents cyclically such that for the remainder of the Miocene there would be periodic connections (low stands) and disconnections (high stands) between the continents. At about 17 Ma, a low stand that had permitted the exchange of terrestrial faunas between Eurasia and Africa (the Proboscidean datum) was coming to an end but not before hominoids possibly resembling *Afropithecus* and *Heliopithecus* dispersed from Africa into Eurasia (Heizmann and Begun 2001; Begun 2002, 2004; Begun et al. 2003).

At the end of the Early Miocene, about 16.5 Ma, hominoids of more modern dental aspect first appear in Eurasia. The oldest Eurasian hominoid is cf. *Griphopithecus*, known from a molar fragment from Germany. *Griphopithecus* (Abel 1902) is known mainly from large samples from Turkey of roughly the same age, while the type material is known from a probably later (14–15 Ma) locality, Děvinská Nová Ves, in Slovakia (Heizmann 1992; Andrews et al. 1996; Heizmann and Begun 2001; Begun et al. 2003). cf. *Griphopithecus* from Engelsweis in

Germany is a tooth fragment that has the more modern features of being thickly enameled with low dentine penetrance (tall dentine horns did not project into the thick enamel cap as in *Proconsul* and probably *Afropithecus*). *cf.* is the designation for a taxon that is similar enough to another taxon for there to be a strong likelihood that they are the same, but with some formally acknowledged uncertainty. *Griphopithecus* is better known from over 1,000 specimens, mostly isolated teeth, from 2 localities in Turkey (Çandır and Paşalar). One species, *Griphopithecus alpani* (Tekkaya 1974) is known from both localities, while a second somewhat more derived taxon is also found at Pasalar (Alpagut et al. 1990; Martin and Andrews 1993; Kelley and Alpagut 1999; Ward et al. 1999; Kelley et al. 2000; Kelley 2002; Güleç and Begun 2003).

Griphopithecus alpani has robust mandibles with strongly reinforced symphyses, broad, flat molars with thick enamel, and reduced cingulum development compared to *Proconsul*. It retains primitive tooth proportions (small M1 relative to M2), anterior tooth morphology, and postcanine occlusal outline shape. A few fragments of the maxilla from Pasalar indicate a primitive morphology for the anterior palate (Martin and Andrews 1993). The morphology of *Griphopithecus* molars as well as their microwear indicates a diet allowing the exploitation of hard or tough fruits, though it is not clear if this means simply that they could exploit these resources when needed (a keystone resource) or if they were a favored source of food. Two postcranial specimens, a humeral shaft and most of an ulna, from the younger site of Klein Hadersdorf, Austria, are also similar to *Proconsul* and indicate that *Griphopithecus* was a large bodied above branch arboreal quadruped similar in size and positional behavior to *Proconsul nyanzae* (Begun 1992a).

4.4.4 East African Middle Miocene thick-enameled hominoids

Shortly after the appearance of *Griphopithecus* in Western Eurasia, dispersals between Eurasia and Africa were interrupted by the Langhian transgression (Rögl 1999a). Following the Langhian, at about 15 Ma, dispersals resumed in a number of mammal lineages, probably also including hominoids (Begun et al. 2003a, b). Hominoids closely similar to *Griphopithecus* in dental morphology appear in Kenya at this time. *Equatorius* is known from 15-Ma localities in the Tugen Hills and at Maboko, both in Kenya. This taxon, previously attributed to *Kenyapithecus*, is very similar to *Griphopithecus* but has a distinctive incisor morphology and reduced cingula, probably warranting a distinct genus status (Ward et al. 1999; Kelley et al. 2000; Ward and Duren 2002; *contra* Begun 2000,

2002; Benefit and McCrossin 2000). *Equatorius* is also known from a good sample of postcrania, including most of the bones of the forelimb, vertebral column, hindlimb long bones, and a few pedal elements (Ward and Duren 2002). Like *Griphopithecus*, which is much less well known postcranially, *Equatorius* is similar to *Proconsul nyanzae* in postcranial size and morphology.

Nacholapithecus (Ishida et al. 1999) is known from deposits of the same age in the Samburu Basin of Kenya (Nakatsukasa et al. 1998). Like *Equatorius*, *Nacholapithecus* is known from a relatively complete skeleton, more complete in fact than the best specimen of *Equatorius*. From this exceptional skeleton, we know that *Equatorius* is similar to other Middle Miocene hominoids in most aspects of the jaws and teeth but unique in aspects of limb morphology. Kunitatsu et al. (2004) provide evidence that the anterior portion of the palate of *Nacholapithecus* is hominid-like in its length and degree of overlap with the palatine process of the maxilla (🔗 [Figure 4.3](#)). This morphology is the principal evidence for the hominoid status of this species. However in its details, the anterior palate of *Nacholapithecus* is unlike that of hominids (see below).

The postcranial skeleton of *Nacholapithecus* is similar to other Middle Miocene hominoids in having the general signature of a generalized, palmigrade, arboreal quadruped, but differs from *Equatorius*, also known from fore and hindlimb, in the enlarged size and robusticity of its forelimb. While not like extant nonhuman hominoids in forelimb length relative to the hindlimb, *Nacholapithecus* forelimbs are large and powerful, indicating a form of positional behavior emphasizing powerful forelimb grasping (Ishida et al. 2004).

Kenyapithecus (Leakey 1962) is the most derived of the Middle Miocene African hominoids and may be the earliest hominid (🔗 [Table 4.2](#)). *Kenyapithecus* is known only from a small sample from Fort Ternan in Kenya, though a second species may be present in Turkey (see below). Like other Middle Miocene hominoids, *Kenyapithecus* has large flat molars with broad cusps and thick enamel. The maxilla of *Kenyapithecus*, however, is derived in having a high root of the zygomatic, a probable hominid synapomorphy. While McCrossin and Benefit (1997) believe that *Equatorius* and *Kenyapithecus* represent a single species, most researchers have concluded that two genera are present and that *Kenyapithecus* is derived relative to *Equatorius* (Harrison 1992; Ward et al. 1999), and that is the view adopted here. As noted, it has been suggested that *Kenyapithecus* is also present at Pasalar. If so, and if *Kenyapithecus* is indeed an early hominid, this would date the origin of the hominid family to at least 16 Ma. However, there is a roughly 3 Ma gap between possible *Kenyapithecus* at Paşalar and the type material from Fort Ternan.

One last Middle Miocene hominoid deserves mention here. *Otavipithecus* is the only Miocene hominoid known from southern Africa, from the 13-Ma site of

Berg Aukas in Namibia (Conroy et al. 1992). Several specimens have been described, including the type mandible, a frontal fragment, and a few postcrania (Conroy et al. 1992; Pickford et al. 1997; Senut and Gommery 1997). It has been suggested that *Otaviopithecus* has affinities to hominids (Conroy et al. 1992; Ward and Duren 2002), but it preserves primitive proconsuloid characters such as a small M_1 compared to M_2 , a long M_3 , parallel tooth rows, a small space for the mandibular incisors, low P_4 talonid, and tall, centralized molar cusps (Begun 1994b). Singleton (2000) carried out the most comprehensive analysis of *Otaviopithecus* and concluded that it may be related to *Afropithecus*, which is broadly consistent with the placement of the taxon in [▶ Figure 4.2](#).

4.4.5 Summary of Middle Miocene hominoid evolution

The radiation of Middle Miocene hominoids in Africa was short lived. Having apparently dispersed from Eurasia by about 15 Ma, they are extinct by 12.5–13 Ma. Aside from a few fragmentary specimens that most likely represent the end of the *Proconsul* lineage (Hill and Ward 1988), hominoids would not appear again in Africa until the latest Miocene when they are represented by the earliest known hominins. Given the rarity of hominoid localities in the early Middle Miocene, the biogeographic hypothesis of the dispersal of Middle Miocene hominoids presented here is debatable. It is certainly possible, for example, that Early Miocene *Griphopithecus*-like fossils will be found in Africa that will show that *Equatorius*, *Nacholapithecus*, and *Kenyapithecus* all evolved *in situ* in Africa and that apparently earlier fossils from Eurasia are either misdated or are early offshoots of this clade with no direct relationship to later hominids (Ward and Duren 2002). However, the evidence as it currently stands supports the scenario presented here to be tested by new discoveries.

4.5 Early hominids

While *Kenyapithecus* shares a synapomorphy with the Hominidae (position of the zygomatic root), the first clear-cut hominids are known from Eurasia and share numerous cranial, dental, and postcranial synapomorphies with living hominids. The extant Hominidae is divided into two subfamilies, Ponginae and Homininae, and both are represented by roughly contemporaneous fossil taxa. The earliest hominines are represented by *Pierolapithecus*, *Dryopithecus*, and *Ouranopithecus*, all with affinities to fossil hominins and extant hominines, and the earliest pongines are represented by *Ankarapithecus*, *Sivapithecus*, and relatives. Miocene

hominines are known from western Eurasia, while Miocene pongines are known from South and East Asia, reflecting the basic biogeographic division of the two hominid subfamilies today.

4.5.1 Fossil pongines

The oldest sample of fossils widely interpreted as pongine is *Sivapithecus* from the middle Chinji formation of Siwaliks of Pakistan (Raza et al. 1983; Rose 1984, 1989; Kappelman et al. 1991; Barry et al. 2002). Specimens referred *Sivapithecus indicus* that are known to come from the middle Chinji formation share characters with later *Sivapithecus* and other hominids including reduced or absent molar cingula, relatively large M1, reduced premolar cusp heteromorphy, long, buccolingually compressed canines, broad based nasal aperture, elongated and robust premaxilla partly overlapping the maxilla and, as in *Kenyapithecus*, a high position to the zygomatic root. They share specifically with later *Sivapithecus* fewer clear-cut characters, such as probably strongly heteromorphic upper incisors (known only from the roots), and broad, flat cusped molars with thick enamel, though these characters are also found in most other Middle and many Late Miocene hominoids. One specimen of Chinji *Sivapithecus*, GSP 16075, represents a portion of the palate with the connection between the maxilla and premaxilla partially preserved. The maxillary–premaxillary relationship is highly diagnostic of *Sivapithecus* and the pongine clade, and the morphology of the Chinji specimen has been interpreted to share characters of this complex (Raza et al. 1983; Ward 1997; Kelley 2002). However, while the specimen does have a relatively elongated, horizontal, and robust premaxilla, the area of the incisive fossa and foramen are not preserved. In the absence of this region, it is difficult to distinguish Chinji *Sivapithecus* from later *Sivapithecus*, including later *Sivapithecus indicus*, to which it is assigned, versus another pongine, *Ankarapithecus*. Resolution of this uncertainty may help to clarify the biogeography of pongine origins (see below).

4.5.2 *Sivapithecus*

4.5.2.1 *Sivapithecus* craniodental evidence

Most of the *Sivapithecus* samples, including the best-known specimens with the clearest evidence of pongine affinities, are from younger localities of the Siwaliks of India and Pakistan, dated between 10.5 and 7.5 Ma (Barry et al. 2002). In the

following section, I discuss *Sivapithecus* in some detail because it is in many ways critical to understanding Late Miocene hominoid evolution. Three species are generally recognized in this sample, the best known of which is *Sivapithecus sivalensis* (Lydekker 1879), from localities ranging in age from 9.5 to 8.5 Ma. (Kelley 2002). In addition to the characters outlined above, *Sivapithecus sivalensis* is known from a suite of cranial characters strongly indicative of pongine affinities (Pilbeam 1982). These include unfused tympanic and articular portions of the temporal bone, a posterosuperiorly directed zygomatic arch with deep temporal and zygomatic processes, vertically oriented frontal squama, supraorbital costae or rims, a narrow interorbital space, elongated nasal bones, tall, narrow orbits, wide, anteriorly oriented zygoma, narrow, pear-shaped nasal aperture, externally rotated canines, long, horizontally oriented nasoalveolar clivus that is curved along its length but flat transversely and a subnasal region with the posterior pole of the premaxilla merging into the anterior edge of the maxillary palating process to form a flat, nearly continuous subnasal floor (🔗 [Figure 4.3](#)) and a strongly concave facial profile from glabella to the base of the nasal aperture. *Sivapithecus* is also likely to have been airorhynchous (having a dorsally deflected face), as in *Pongo* (🔗 [Figure 4.4](#)). All of these and other characters are described in more detail in Ward and Pilbeam (1983), Ward and Kimbel (1983), Ward and Brown (1986), Brown and Ward (1988), Ward (1997). *Sivapithecus sivalensis* is not identical to *Pongo* in cranial morphology however, even if the similarities are striking and detailed. *Sivapithecus sivalensis* is more robust than similarly size (female) *Pongo* in features related to the masticatory apparatus, including aspects of the zygomatic and temporal bones, maxillary robusticity, and molar morphology. The molars in particular are easily distinguished from those of *Pongo* in having thicker enamel and in lacking the complex pattern of crenulations seen in unworn *Pongo* molars. However, overall the number of derived characters shared with *Pongo* is quite high (Ward 1997; Kelley 2002).

Sivapithecus indicus (Pilgrim 1910) is the oldest species, and if the middle Chinji fossils are included, it would range from 12.5 to 10.5 Ma (Kelley 2002). It is the smallest species, at least in terms of dental size, and appears to have a slightly shorter nasoalveolar clivus or premaxilla compared to *Sivapithecus sivalensis* (see above). *Sivapithecus parvada* (Kelley 1988) is considerably larger than the other species and is known from the Nagri formation locality Y311, about 10 Ma. *Sivapithecus parvada* males are about the dental size of female gorillas. The upper central incisors are especially long mesiodistally, the M_3 is larger than the M_2 , the premolars are relatively large, and the symphysis of the mandible is very deep (Kelley 2002).

4.5.2.2 *Sivapithecus* postcrania

Sivapithecus postcrania have been described in many publications (Pilbeam et al. 1980, 1990; Rose 1984, 1986, 1989; Spoor et al. 1991; Richmond and Whalen 2001; Madar et al. 2002). They combine a mixture of characters, some suggesting more palmigrade postures and others suggestive of more suspensory positional behavior. This has been interpreted by some to indicate that *Sivapithecus* is more primitive than any living hominoid, all of which, even humans, share numerous characters of the shoulder and forelimbs related to suspensory behavior or an ancestry of suspensory behavior (Pilbeam 1996, 1997; Pilbeam and Young 2001, 2004). This view, also shared by McCrossin and Benefit (1997), has dramatic implications for the interpretation of the hominoid fossil record. All Late Miocene hominoids, including *Sivapithecus*, share many characters of the cranium and dentition with living hominoids. If *Sivapithecus* is more primitive than extant hominoids, given its apparently primitive postcrania, then all the apparently derived hominid features of *Sivapithecus* would have evolved in parallel in *Sivapithecus*, and as these authors suggest, by extension in all Late Miocene hominoids (*Oreopithecus*, *Dryopithecus*, *Ouranopithecus*, and *Lufengpithecus*, etc.). These parallelisms include not only craniodental morphology but also details of life history and as it turns out, many postcranial characters as well. In fact, the apparently primitive characters of *Sivapithecus* postcrania are small in number compared to the large number of clearly derived hominid characters from throughout the skeleton and known biology of all Late Miocene hominids. Rather than rejecting the hominid status of *Sivapithecus* and other Late Miocene hominids because not all of their postcranial morphology is strictly hominid or even extant hominoid-like, it is much more likely that these few characters reflect mosaic evolution of the hominid skeleton, uniquely derived features of the anatomy of *Sivapithecus*, as well as some parallelism in extant hominoids (Begun 1993; Begun et al. 1997; see below).

Sivapithecus postcrania, though they have been the subject of more discussions related to phylogeny, are actually less well known than *Proconsul*, *Equatorius*, or *Nacholapithecus*. The following is summarized mainly from Rose (1997), Richmond and Whalen (2001), and Madar et al. (2002). Much more information is available from all the references cited earlier. Two species of *Sivapithecus* are known from the humerus, which is unlike that of modern hominoids in the curvature of the shaft and the development of the deltopectoral plane. The bicipital groove is also broad and flat and suggests a posteriorly oriented humeral head, as in the Early and Middle Miocene Hominidea described earlier. However, the humerus has such an unusual morphology that the orientation of the head,

which is already somewhat difficult to predict from bicipital groove position (Larson 1996), cannot be reconstructed with great confidence. Nevertheless, the morphology of the proximal humerus in *Sivapithecus* is suggestive of some form of pronograde quadrupedalism as seen, for example, in extant cercopithecoids. If the humeral head were oriented more posteriorly, it would also be consistent with a scapula that is placed on the side of a compressed rib cage, as in typical mammalian quadrupeds, and unlike extant hominoids (Rose 1989; Ward 1997). No direct evidence is available for the thorax or any part of the axial skeleton of *Sivapithecus*, however, so this will also have to await further discoveries. The deltopectoral plane and the curvature of the shaft of the humeri in *Sivapithecus* are quite strongly developed compared to most cercopithecoids and indicate in my view a unique form of positional behavior that is neither extant hominoid nor extant cercopithecoid-like (Madar, et al. 2002). The distal end of the humerus is in the main hominoid-like, including a well-developed trochlea separated from the capitulum by a deep, well-defined groove (the zona conoidea), though in a few details of the posterior surface there are similarities to *Proconsul* and *Kenyapithecus* (Rose 1997). Overall, however, the functional morphology of the elbow of *Sivapithecus* is most like the hominoid elbow in its ability to resist movements other than flexion and extension at the elbow joint, a hallmark of the Hominoidea (Rose 1988).

The *Sivapithecus* forearm is poorly known, especially the proximal portions of the ulna and radius, which would help to more fully understand the *Sivapithecus* elbow. A juvenile radial shaft is known that is described as *Proconsul*-like, though as a juvenile it is not clear to what extent any hominoid-like characters, such as curvature and the nature of the ligamentous/muscular insertions, would be expressed. On the other hand, the few carpal bones that are known show a mixture of hominoid and non-hominoid features. The capitate of *Sivapithecus* has a somewhat expanded and rounded head, as in great apes, but overall is transversely narrow and elongated proximodistally compared to great apes. The joint surface for the third metacarpal is irregular as in great apes. The hamate is similar in length/breadth proportions and has a less strongly projecting hamulus than do great ape hamates (Spoor et al. 1991). The joint on the hamate for the triquetrum is oriented as in gorillas and also most other nonhominoid anthropoids, and its shape suggests a stabilizing function at the wrist, which differs fundamentally from the typical mobility of the ulnar side of the wrist in extant hominoids. The proximal end of a first metacarpal is similar in morphology to hominids and Early Miocene Hominidea in being saddle shaped, a configuration considered to represent a good compromise between mobility and stability in a wide variety of positions. The manual phalanges are long and curved, with strongly developed ridges for the flexor muscles and their sheaths.

One complete phalanx has a relatively deep and somewhat dorsally positioned articular surface for the metacarpal head, which is more typical of palmigrade quadrupeds. However, it is not completely clear if this is from a hand or a foot, and if the latter is the case, a similar morphology exists in some hominoids as well.

The hindlimb of *Sivapithecus* is less well known but generally more similar to extant hominoids than the forelimb. The femur is known from proximal and distal ends but not from the same individual (Rose 1986; Madar et al. 2002). The hip joint as represented by the femoral head and neck was mobile in many directions, though it has a well-developed fovea capitis, unlike *Pongo*, which is highly distinctive (but not unique) in lacking a ligamentum teres of the femur and thus its attachment site to the femur, the fovea capitis. The distal end of the femur preserves evidence of a knee joint that is consistent with this interpretation, implying a knee joint loaded in positions away from the sagittal plane. The knee also has a number of features allowing for rotation of the leg and foot to adjust the lower extremity to a variety of positions close to and further away from the center of mass (Madar et al. 2002). In all of these features, the femur is more like that of hominoids than other anthropoids.

Other hindlimb elements include several tarsal bones, phalanges, and a well-preserved hallucial skeleton (Conroy and Rose 1983; Rose 1984, 1986, 1994). The tarsals are perhaps more like those of great apes than any other part of the post-cranium of *Sivapithecus* (Rose 1984; Madar et al. 2002), indicating the presence of a broad foot, able to assume many positions but stable in all of them, and supportive of body mass loading from many directions. The hallux or big toe is strikingly robust, much more so than in *Pongo*, and indicates a strongly developed grasping capability in the foot. The phalanges are also by and large hominoid-like, with well-developed features related to powerful flexion of the toes, a critical function in antipronograde activities (climbing as well as suspension).

4.5.2.3 *Sivapithecus* phylogeny and paleobiology

Overall, the morphology of *Sivapithecus* strongly supports a close phylogenetic relationship to *Pongo* but an adaptation that differed from *Pongo* in important aspects. Microwear suggests that *Sivapithecus* had a diet that was similar to that of chimpanzees while gnathic morphology suggests more of a hard object diet (Teaford and Walker 1984; Kay and Ungar 1997). Perhaps this reflects a capacity to exploit fallback or “keystone” resources in times of scarcity. Most hominoids are known to practice this strategy (Tutin and Fernandez 1993; Tutin et al. 1997). The case of gorillas may be most relevant to the question of the diet of *Sivapithecus*.

Most gorillas have diets similar to chimpanzees but are able to exploit terrestrial herbaceous vegetation (THV) in lean seasons when soft fruit is less available or in contexts in which they are sympatric with chimpanzees (Tutin and Fernandez 1993; Tutin et al. 1997). The microwear results may reflect the preferred and most common components of the diet, while the morphology of the jaws and teeth may reflect a critical adaptation to a keystone resource on which survival would depend during stressful periods.

Postcranial evidence clearly indicates that *Sivapithecus* was not orang-like in its positional behavior. In fact, it was unique; there are probably no living analogues. *Sivapithecus* combines clear indications of pronograde forelimb postures and a palmigrade hand position with more antipronograde activities such as vertical climbing and clambering implied by elbow joint stability over a wide range of flexion/extension, powerful grasping hands and feet, an especially powerful hallux, and hindlimbs capable of wider ranges of joint excursions than in extant pronograde quadrupeds (Madar et al. 2002). It is difficult to imagine exactly what the positional behavior of *Sivapithecus* might have been like.

One constant in the postcranial functional morphology of *Sivapithecus* is arboreality. Perhaps *Sivapithecus* used its powerful limbs in climbing and bridging or clambering activities, spreading the limbs across multiple supports to access smaller branches. In a sense it is orang-like without the suspension. While *Sivapithecus* managed to distribute its considerable body mass across the tops of several branches, orangs do the same but from below. The advantage to suspension is added stability on horizontal supports in large animals, which otherwise need to generate very high levels of torque to stay atop a branch (Grand 1972, 1978; Cartmill 1985). Orang males are larger than *Sivapithecus* and may be beyond the threshold where pronograde limb postures are possible in the trees. The fact that the proximal half of the humerus of *Sivapithecus*, while similar to that of a pronograde quadruped, is exceptionally robust, with extremely well-developed shoulder muscle attachments, may be an indication of a unique approach to this problem.

Sivapithecus does share numerous postcranial features, especially of the elbow and hindlimb, with extant hominoids and *Dryopithecus*. It is therefore possible that the more monkey-like morphology of the proximal humerus and portions of the hands and feet are actually homoplasies with cercopithecoids caused by the adoption of more pronograde postures in a hominoid that evolved from a more suspensory ancestor (Begun et al. 1997). This requires many fewer homoplasies than the alternative hypothesis that all extant hominoid characters in all Late Miocene hominoids are homoplasies (Pilbeam 1996, 1997; McCrossin and Benefit 1997; Pilbeam and Young 2001, 2004). There is some evidence from the functional morphology of *Sivapithecus* to support the hypothesis that its

form of pronograde arboreal quadrupedalism is actually superimposed on a suspensory hominoid groundplan.

The problem of angular momentum causing instability in a large mammal standing on top of a branch is alleviated in part by spreading the limbs apart on a wide support or across several supports, which *Sivapithecus* seems to have been capable of doing (Madar et al. 2002). It can also be all alleviated by placing the center of mass closer to the support, which is suggested for *Griphopithecus* (Begun 1992a), and may have also occurred in *Sivapithecus*, as a consequence of its habitually more laterally placed limbs (Madar et al. 2002). The positioning of the limbs more laterally in hominoids is part of the suite of characters related to trunk morphology and scapular position. It is not facilitated by monkey-like trunks and scapular positions, which promote more parasagittal limb movements. Finally, an important response to angular momentum is to increase the torque generated by the limbs on the support, to prevent excessive excursions from a balanced position, especially when a single support of only modest size is used, again suggested to be an aspect of the positional behavior of *Sivapithecus* (Madar et al. 2002). Higher torque results from more powerful gripping, also characteristic of *Sivapithecus* (Madar et al. 2002), and may have been boosted by especially powerfully developed shoulder joint adduction and medial rotation, particularly if the shoulder is in a relatively abducted position to begin with, as in hominoids.

The morphology of the proximal half of the humerus in *Sivapithecus* is consistent with very powerful adduction and medial rotation by deltoideus and pectoralis major. These muscles left extremely prominent scars on the humerus of *Sivapithecus*. If the arm of *Sivapithecus* were positioned as in extant hominoids, laterally on a posteriorly positioned scapula, the adduction and medial rotation capacities of deltoideus and pectoralis would be increased by increasing the relative mass of the clavicular portion of deltoideus, which is unknown in *Sivapithecus*. However, in addition to the need for powerful muscles, which existed in *Sivapithecus*, these functions would also be enhanced by other attributes known in *Sivapithecus*. The extension of the muscles along the shaft distally and the possible decreased humeral neck torsion would increase the moment arm for these muscles in adduction and reposition the insertions of these muscles medially, possibly to make more of the deltoideus available for adduction and medial rotation. The strong mediolateral curvature of the shaft may result from high mediolateral bending stresses that would result from very powerful shoulder adduction on a fixed limb. The proximal shaft is also very broad mediolaterally, suggestive of strong mediolaterally directed stresses. While speculative, it is certainly conceivable that the upper part of the forelimb of *Sivapithecus* was less monkey-like than generally perceived and may not imply that much of the trunk

was of the primitive anthropoid type. A small number of autapomorphies of the shoulder of *Sivapithecus* may have allowed this taxon to practice a relatively efficient form of arboreal pronograde quadrupedalism while maintaining the capacity for many of the antipronograde activities of hominoids, though probably not frequent upper limb below branch suspension. This hypothesis is functionally consistent with the morphology of the *Sivapithecus* postcranium in general and is certainly more parsimonious than the hypothesis that would interpret all Late Miocene hominoid characters as homoplasies.

4.5.3 *Ankarapithecus*

Aside from some material from Nepal attributed to *Sivapithecus* (Munthe et al. 1983), *Sivapithecus* is known only from India and Pakistan. Specimens from central Anatolia, Turkey, once attributed to *Sivapithecus* (Andrews and Tekkaya 1980) are now assigned to *Ankarapithecus*, following the original conclusions of Ozansoy (1957, 1965). *Ankarapithecus meteai* is known from a male palate and mandible from two different individuals and a female partial skull (mandible and face) from a third locality, all close to each other in location and geologic time (Kappelman et al. 2003a). Begun and Güleç (1995, 1998) resurrected the nomen *Ankarapithecus* based mainly on the morphology of the premaxilla and the relationship between this bone and the maxilla but concluded that *Ankarapithecus* is nonetheless in the pongine clade. Alpagut et al. (1996) and Kappelman et al. (2003) described newer and much more complete fossils of *Ankarapithecus* and concluded that it is a stem hominid (sharing a common ancestor with both pongines and hominines). The new fossils discovered and described by these authors include the region around the orbits, which lacks some of the characters of *Sivapithecus*. The interorbital region is intermediate in breadth between *Pongo*, with the narrowest interorbitals, and African apes and the orbits themselves are broad rather than tall and narrow. Alpagut et al. (1996) and Kappelman et al. (2003) also interpret the supraorbital region as a supraorbital torus, characteristic of African apes and humans and some European Late Miocene taxa, and they interpret a frontal sinus in the cranium of *Ankarapithecus* as a frontoethmoidal sinus. These authors see the mixture of hominine and pongine characters as an indication that *Ankarapithecus* precedes their divergence.

4.5.3.1 Craniodental evidence

The frontal sinuses in *Ankarapithecus* appear to be confined to the frontal squama and do not invade the frontal supraorbital region from a broad expansion of the

ethmoidal sinuses. They are positioned and developed as in extant taxa with frontal pneumatizations derived either from the sphenoidal or maxillary sinuses and are unlike those derived from the ethmoid (see above discussion). The frontal pneumatization in *Ankarapithecus* is unlikely to be a frontoethmoid sinus and thus is not a synapomorphy of the hominines. The supraorbital region, while robust, is morphologically similar to the robust supraorbital costae of large orangs or *Cebus* and also unlike the bar-like supraorbital tori of African apes. Thus, the supraorbital region of the *Ankarapithecus* cranium is more pongine than hominine-like and, like the maxilla, probably represents the primitive morphology for the pongines (see below).

In *Ankarapithecus* the premaxilla, the portion of the palate with the alveoli for the incisors and the mesial half of the canines, is unlike that of *Sivapithecus* and more like that of African apes. The premaxilla is long, but it does not overlap the palatine process of the maxilla to fill the incisive fossa to the degree seen in *Sivapithecus*. Instead, the subnasal fossa is stepped (there is a drop between the base of the nasal aperture and the floor of the nasal cavity) into an incisive fossa that is most like that of some chimpanzees, a relatively large depression opening into a canal (the incisive canal that runs between the premaxilla and maxilla to exit on the palatal side via the incisive foramen). *Dryopithecus* has a similar configuration of the subnasal fossa, incisive canal and incisive foramen, though the fossa is larger and the canal is shorter in length and larger in caliber, as in some gorillas (Begun 1994a) (▶ [Figure 4.3](#)). The premaxilla of *Ankarapithecus* is curved or convex anteroposteriorly as in *Sivapithecus*, African apes, and *Dryopithecus* but it is also convex transversely, as in African apes and *Dryopithecus* unlike *Sivapithecus*, which has a transversely flatter premaxilla. In all of these features, *Ankarapithecus* expresses a condition intermediate between pongines and hominines, which I consider primitive for the pongines (Begun and Güleç 1998). Alpagut et al. (1996) and Kappelman et al. (2003b) have suggested that these characters indicate that *Ankarapithecus* precedes the divergence of pongines and hominines. Other features of the morphology of *Ankarapithecus* resemble pongines more clearly, including canine implantation, zygoma size and orientation, orbital margin morphology, nasal length, and dental morphology. Overall, *Ankarapithecus* most closely resembles *Sivapithecus* and *Pongo* but retains a more primitive palatal morphology that suggests it is at the base of the pongine clade.

4.5.3.2 Postcranial evidence

Some postcrania of *Ankarapithecus* are known, including a well-preserved radius and two phalanges (Kappelman et al. 2003). A femur tentatively identified as

primate is more likely in my opinion to be from a carnivore. The radius shares characters with extant great apes including features of the radial head and comparatively long radial neck (Kappelman et al. 2003). Other hominoid-like features described or figured in Kappelman et al. (2003) but not identified as hominoid-like by these authors include a proximodistally compressed and more circular radial head, a deep radial fovea, flat as opposed to concave shaft surface along the anterior surface, a more distal origin of the interosseus crest, and a smooth distal dorsal surface. The specimen actually strikes me as quite hominoid-like with a few features more normally associated with large nonhominoid anthropoids, a pattern more or less in keeping with other Late Miocene hominoids. The phalanges are said to be relatively straight and thus non-hominoid-like, but only distal portions are preserved. They too strike me as more hominoid-like than Kappelman et al. (2003) suggest, given its distal shaft robusticity, dorso-palmar compression, and distopalmarly projected condyles. The curvature and ridges for the flexor musculature are said to be poorly developed compared to hominoids, but this may be related to many factors (preservation, age, digit attribution).

Overall, *Ankarapithecus* is characterized by many features found in other pongines and is probably the most basal known member of that clade. Like *Sivapithecus*, it was much more massive in the development of its masticatory apparatus than *Pongo*, and its postcranium, though very poorly known, suggests arboreality and at least some features of hominoid-like antipronograde positional behaviors, but probably lacking the degree of suspension seen in *Dryopithecus*, *Oreopithecus*, and extant hominoids (but see Kappelman et al. 2003).

4.5.4 Other probable fossil pongines

4.5.4.1 *Gigantopithecus*

Extremely large fossil hominoids, larger than any extant primate, have been known from Asia since the early part of the twentieth century. *Gigantopithecus blacki* (Koenigswald 1935) is a Pleistocene taxon known from numerous isolated teeth and a few mandibles. It is recent enough to be outside the purview of this review and has been described many times elsewhere. *Gigantopithecus giganteus* (Pilgrim 1915) is a Late Miocene possible member of this genus known from a lower molar and mandible from the Late Miocene of the Siwaliks that are mainly distinguished from *Sivapithecus* by size. They are larger than any *Sivapithecus* and the only known mandible is distinctive in having reduced anterior tooth crown heights and molarized or enlarged premolars. *G. blacki*, on the other hand, is

larger still and has highly complicated postcanine occlusal morphology and relatively even larger mandibles and smaller anterior teeth. Because *G. giganteus* and *G. blacki* share characters of the lower jaws and teeth that appear commonly during the course of hominoid evolution (in fact, in many other mammal lineages as well), the relationship between the two is uncertain. Jaws and teeth in general, and mandibles in particular, are magnets for homoplasy in primate evolution (Begun 1994b), and this may be another example. However, the most parsimonious hypothesis is that *G. giganteus* is a primitive member of the *Gigantopithecus* clade and that the strong similarity to *Sivapithecus* in the molars, apart from size, suggests that it is the sister clade to that taxon. If a better ancestor for *Gigantopithecus blacki* turns up, the nomen *Indopithecus* is available for *G. giganteus* (► [Table 4.1](#)).

4.5.4.2 *Lufengpithecus*

Thousands of fossils, mostly isolated teeth, are known from a number of localities in Yunnan province, southern China. These are attributed to the genus *Lufengpithecus* (Wu 1987), widely believed to be a pongine. Kelley tentatively recognizes three species of *Lufengpithecus*, distinguished mainly by size and geography (each is known from a single site). *Lufengpithecus* shares a few cranial characters with other pongines including a small, pear-shaped nasal fossa, aspects of the implantation of the canine roots in the maxilla, a deep canine fossa, supraorbital costae, and anteriorly oriented zygoma (Schwartz 1997 and personal observations). However, while it lacks many of the detailed similarities of the face between *Sivapithecus* and *Pongo*, its teeth are much more like those of *Pongo* than *Sivapithecus* in details of occlusal morphology, including the unusual presence of highly complex wrinkling or crenulations (Kelley 2002). The face of *Lufengpithecus* is unlike those of *Sivapithecus* and *Pongo* in having broad orbits, a broad interorbital space, a comparatively short premaxilla, high crowned incisors and canines, compressed and very tall crowned male lower canines. Though very damaged, my impression is that the nasal floor is unlike the smooth floor of *Sivapithecus* and *Pongo* but possibly more similar to the morphology in *Ankarapithecus*.

L. lufengensis (Xu et al. 1978) from a site near Shihuiba, in Lufeng county, is the best-known species of the genus and is also known from a number of postcranial remains including fragments of a scapula, clavicle, radius, first metatarsal, and two phalanges. None have been published in detail, but all of these specimens show clear indications of modern hominid morphology associated with suspensory positional behaviors (personal observations). This is especially true of the phalanges, which are strongly curved and bear the markings of

powerful flexor tendons. The metatarsal is similar to that of *Sivapithecus* in its relative robusticity.

Until the fossils attributed to *Lufengpithecus* are published in detail, it will be impossible to be confident in assessing their taxonomic and phylogenetic relations. At this point, it seems likely that *Lufengpithecus* is a pongine and probably a sister taxon to the *Pongo*–*Sivapithecus*–*Ankarapithecus* clade. However, the generally more *Pongo*-like morphology of the molar occlusal surfaces and the more clearly hominoid-like morphology of the postcrania are enigmatic and suggest caution in interpreting evolutionary relationships.

4.5.4.3 *Khoratpithecus*

Two samples of East Asian Miocene hominoids have recently come to light. Chaimanee et al. (2003) describe a Middle Miocene sample of hominoids from Thailand they originally attributed to a species of *Lufengpithecus*. The age of the locality is not completely certain, and it is possible that the fauna could be correlated with a more recent magnetostratigraphic interval, but for now the sample is considered to date to the late Middle Miocene or early Late Miocene. However, on the basis of more recently discovered Late Miocene hominoid fossils from Thailand, Chaimanee et al. (2004) described a new genus, *Khoratpithecus*, and revised their previous taxonomic conclusions to include the Middle Miocene taxon in the newly named genus as well. The fossils, a sample of isolated teeth and a well-preserved mandible, are very similar to *Lufengpithecus* but show a number of differences in the anterior dentition and lower jaw (Chaimanee et al. 2004). Chaimanee et al. (2004) interpret *Khoratpithecus* to be more closely related to *Pongo* than is any other pongine, mainly based on the shared derived character of a missing anterior digastric muscle. More fossils are needed to test this hypothesis more fully. The greater significance of these discoveries is the location, in Thailand, and the possibly early age, Middle Miocene.

4.5.5 Fossil hominines

At about the same time that hominids appear in Asia, they make their first appearance in Europe. As is the case with the earliest pongines, the earliest hominines lack a number of synapomorphies of living hominines (African apes and humans) and are less distinct from related non-hominines than are more recently evolved hominines. This has led naturally to differences of opinion

regarding the systematics of this group. There are three main interpretations of the evolutionary relations among the taxa included here in the Homininae. As noted, some researchers conclude that no known Eurasian Late Miocene taxon has a specific relationship to extant hominoids (Pilbeam 1996, 1997; McCrossin and Benefit 1997; Pilbeam and Young 2001, 2004). Most researchers, however, accept the hominid status of these fossil taxa but are divided as to their interrelationships. Some researchers (Andrews 1992) have concluded that European Late Miocene hominids are best viewed as stem hominids, preceding the divergence of hominines and pongines. Others interpret most or all Eurasian hominines to be members of the pongine clade (Moyà-Solà et al. 1995). Finally, some researchers interpret most or all European hominids to be hominines, although there is disagreement among them as to the precise pattern of relations (Bonis and Koufos 1997; Begun and Kordos 1997). As my interpretation falls with the last group, this will be reflected in this chapter. I will however attempt to outline the major arguments from each perspective.

4.5.6 *Pierolapithecus*

The oldest known genus of hominine is the recently described partial skeleton of *Pierolapithecus* (Moyà-Solà et al. 2004). The specimen, from northern Spain, is dated to about 13 Ma based on biostratigraphic evidence (Moyà-Solà et al. 2004). The specimen includes most of a face which, though badly distorted, preserves nearly all the teeth and many informative facial characters. It also includes a partial postcranial skeleton, the most informative parts of which are some lumbar vertebrae, ribs, and a number of hand and foot bones. Moyà-Solà et al. (2004) interpret *Pierolapithecus* to be a basal or stem hominid. They cite the lumbar vertebrae, which preserve evidence of a hominoid-like vertebral column and by extension rib cage. This is indicated by the position of the lumbar transverse processes, placed more posteriorly in hominoids to stiffen the lower back (Ward 1993). However, the morphology of the lumbar vertebrae in *Pierolapithecus* is more hylobatid-like, extant hominids having even more posteriorly positioned transverse processes. Other aspects of the postcranium that clearly support the hominoid status of *Pierolapithecus* include ribs indicative of a broad, anteroposteriorly compressed rib cage, robust clavicle, and a wrist morphology indicating no direct contact between the carpus at the triquetrum and the ulna (Moyà-Solà et al. 2004). These features are shared with all extant hominoids, though hylobatids are somewhat intermediate in carpal/ulnar contact between non-hominoid anthropoids with direct contact and hominoids with a large intervening articular meniscus (Lewis 1989).

The carpals in general are hominid-like in their overall morphology, including relative size, robusticity, and general pattern of the orientation of the joint surfaces. The lunate, triquetrum, and hamate in particular closely resemble small chimpanzees, but it is not clear if these are derived characters for hominines or hominids. Moyà-Solà et al. (2004) describe the phalanges of *Pierolapithecus* as being relatively shorter, less curved, and with metacarpal joint surfaces facing more dorsally than in *Dryopithecus*, a clearly suspensory hominine, which they interpret to mean that *Pierolapithecus* had a palmigrade hand posture. At the same time, the attributes of the thorax and hand suggest antipronograde limb positions, which is somewhat contradictory. They resolve this dilemma with the suggestion that *Pierolapithecus* was a powerful vertical climber but not suspensory. This is similar to the suggestion made earlier regarding *Sivapithecus*, though the morphology of the phalanges does not in fact rule out suspension. The phalanges are curved compared to most arboreal primates and have strongly developed flexor muscle attachments, even if these are not so strongly expressed as in *Dryopithecus* (Begun and Ward 2005).

Moyà-Solà et al. (2004) interpret various craniodental attributes of *Pierolapithecus* to reflect its stem hominid status as well. The face is prognathic with an enlarged premaxilla. The zygomatic root is high, the nasal aperture broad, and the postcanine teeth have a typical hominid morphology (elongated, relatively large M¹, absence of cingula, reduced premolar cusp heteromorphy, buccolingually large incisors, compressed canines). The premaxilla is expanded compared to early and exclusively Middle Miocene hominoids and appears to have an overlap posteriorly with the maxilla as in hominids. However, according to these authors, it lacks the distinctive attributes of either the hominine or pongine clade.

Some of the distinctive attributes of *Pierolapithecus* may be related to distortion. The glabella is unlikely to have been as posterior as it appears, the midface is clearly badly damaged and was not as prognathic as in *Afropithecus*, as the authors suggest, and the premaxilla is obviously displaced relative to the palatine process of the maxilla (Begun and Ward 2005). In my view, the face much more closely resembled *Dryopithecus*, though it is still distinct enough to justify a separate genus.

All in all, *Pierolapithecus* closely resembles *Dryopithecus*, known from contemporaneous and younger localities in Spain and elsewhere in Europe. In fact, it may be that *Pierolapithecus catalaunicus* is synonymous with Middle Miocene *Dryopithecus fontani* (see below). Both are from the same time period and nearby localities, but the mandibles and humeral shaft of *D. fontaini* cannot be directly compared to the sample of *Pierolapithecus*. If future discoveries of fossils of both samples reveal that they are synonymous, *Dryopithecus* would have priority over

Pierolapithecus. Younger samples currently attributed to *Dryopithecus*, which are distinguishable from *Pierolapithecus*, would require another nomen, several of which are available. Once again, it is premature to revise the taxonomy of *Dryopithecus* in the absence of more data from the Middle Miocene samples.

While aspects of the postcrania may be more primitive, and aspects of the face unique, justifying a separate genus from Late Miocene *Dryopithecus*, there is evidence to suggest that *Pierolapithecus* is a stem hominine and not as Moyà-Solà et al. (2004) conclude a stem hominid (Begun and Ward 2005). Details of dental morphology are strikingly similar to *Dryopithecus*. Despite the unusually small M^3 and elongated upper canine, most of the teeth could easily be mistaken for those of *Dryopithecus* and show features distinctive for that genus including relatively tall crowned and mesiodistally narrow upper incisors, compressed canines, premolars with prominent cusps separated by a broad deep basin and molars with marginalized or peripheralized, relatively sharp cusps. The contact between the premaxilla and the maxilla appears to also have been very similar to *Dryopithecus* in being stepped with only a modest degree of overlap between the two. The supraorbital region, though described by Moyà-Solà et al. (2004) as having thin supraorbital arches, actually closely resembles *Dryopithecus* specimens from Spain and Hungary, with subtle tori emerging from a more prominent glabella. In my view, *Pierolapithecus* is close to the common ancestor of the Hominidae but already shares a common ancestor with the Hominae (Begun and Ward 2005). Its postcranial morphology, however, is probably very close to that of the hominid ancestral morphotype (🔗 [Figure 4.2](#)).

4.5.7 *Dryopithecus*

The first fossil hominoid genus ever described was *Dryopithecus*, based on fossils from St. Gaudens in France, attributed to *D. fontani* (Lartet 1856). Today *Dryopithecus* is known from at least four species ranging in time from the late Middle Miocene, about 12–13 Ma, to the Late Miocene, about 9 Ma, and ranging geographically from Spain in the west to Georgia in the east (a mandible from Gansu province in China with badly damaged teeth attributed to *Dryopithecus wuduensis* [Xu and Delson 1988] is not distinguishable in my view from a large cercopithecoid). The following account is mainly from Begun (2002). The oldest species of *Dryopithecus*, *D. fontani*, is known from Middle Miocene deposits in France and Austria and is roughly contemporaneous with *Pierolapithecus*, and *Sivapithecus*. *D. crusafonti* is known from two localities in Spain from the early part of the Late Miocene. *D. laietanus* and *D. brancoi* are the latest occurring species of *Dryopithecus* and are known respectively from sites in Spain for the former and

Germany and Hungary for the latter. Two younger Miocene teeth from Udabno, in Georgia, are often attributed to *D. brancoi* but may be another species.

4.5.7.1 *Dryopithecus fontani*

D. fontani is known from three male mandibles and a humerus, all from the same locality in France, and a female mandible from Austria. Two isolated upper teeth from La Grive in France usually attributed to *D. fontani* may belong to *Pierolapithecus*. They are the only specimens currently attributed to *D. fontani* that can be directly compared to *Pierolapithecus* (Begun et al. 2006). The mandibles and their dentitions are typically hominid in being comparatively robust with well-developed symphyseal tori, large incisors, compressed canines, elongated post-canine teeth with peripheralized cusps and lacking cingula, P₄ with trigonids and talonids of nearly equal height, and molars of nearly equal size, especially M1 and M2. The teeth of all *Dryopithecus* are thinly enameled with dentine horns penetrating well into the enamel caps. *D. fontani* is distinguished from other species of *Dryopithecus* in having a mandible that shallows (becomes lower compared to breadth) distally, a high frequency of buccal notches on the lower molars, and comparatively robust lower canines.

D. fontani is also known from a humeral shaft from the type locality that has been described as chimpanzee-like (Pilbeam and Simons 1971; Begun 1992a). It is the only nearly complete humerus of the genus. It is comparatively long and slender with poorly developed muscle insertion scars and a slight mediolateral and anteroposterior curvature. Neither the proximal nor the distal epiphyses are preserved, but the diaphysis preserved close to each epiphysis is hominoid-like. Proximally, it is rounded in cross section with a bicipital groove position suggesting some degree of humeral torsion (but see Rose 1997; Larson 1998). Distally, it is mediolaterally broad and anteroposteriorly quite flat, with a large, broad, relatively shallow olecranon fossa (Begun 1992a).

4.5.7.2 Spanish *Dryopithecus*

D. crusafonti (Begun 1992c) is known from a sample of isolated teeth and a palatal fragment from one site and a well-preserved mandible from a second, both in northern Spain. *D. crusafonti* is dentally similar to *D. fontani* but has distinctive upper central incisors, a more robust mandible lacking the distal shallowing, upper molars of nearly the same size and a number of subtle features of dental morphology.

D. laietanus (Villalta and Crusafont 1944) is known from several slightly younger sites in Spain. Dentally, it is smaller but similar to other species of *Dryopithecus* and lacks the unique dental characters of *D. crusafonti*. It is the best-known species of the genus because of the recent discovery of a partial skeleton (Moyà-Solà et al. 1996). Like *D. crusafonti*, *D. laietanus* has tall, relatively narrow upper central incisors, though not to the degree seen in *D. crusafonti*. The mandible is relatively robust. A partial cranium of *D. laietanus* displays numerous hominid cranial characters (broad nasal aperture base, high zygomatic roots, shallow subarcuate fossa, and probable enlarged premaxilla with maxillary overlap, although the specimen is damaged in that area). A few hominine characters are found on this specimen as well (supraorbital tori connected to glabella, frontoethmoidal sinus, inclined frontal squama and thin enamel).

The most significant specimen of *D. laietanus* is a partial skeleton that may or may not be associated with the face (Moyà-Solà et al. believe they are, but the cranium was found widely separated from the postcranial specimens and appears a bit too large for the face). Nevertheless, this is an exceptional and important specimen. The most significant features of the postcranial skeleton of *D. laietanus* are the numerous and unambiguous indications of both well-developed suspensory positional behavior and clear hominid synapomorphies. These include elongated forelimb, large hands with powerful, curved, elongated digits, comparatively short and robust hindlimb, and a hominid-like lumbar region. Other attributes interpreted to be present in this partial skeleton, such as an elongated clavicle and limb proportions approaching those of *Pongo*, are based on fragmentary evidence and are less reliable. The specimen has some unusual features for a hominid such as short metacarpals, but overall it is quite modern. The humerus, though fragmentary, is like that of *D. fontani* and unlike that of *Sivapithecus*.

4.5.7.3 *Dryopithecus brancoi*

In the second half of the nineteenth century, shortly after the initial discovery and description of *Dryopithecus fontani*, additional fossil hominoid teeth began to turn up in Germany. These were eventually assembled to define the new species, *D. brancoi* (Schlosser 1901), though not before considerable taxonomic shuffling (see Begun 2002 for more historical details). *D. brancoi* is based on an isolated M₃ which, while not the ideal type specimen, can be effectively distinguished from the other species. To help in species identification, the species diagnosis was revised by Begun and Kordos (1993) based on the excellent sample from Rudabánya, Hungary, and this is the definition used here.

D. brancoi is known the type locality in Germany (Salmendingen) and from Rudabánya and is dated between 9 and 10 Ma. The younger date is based on the type locality, which is poorly dated, such that the older age may be more accurate. Six other localities in Germany, Austria, and Georgia may also contain *D. brancoi*, but as the specimens are all isolated teeth it is difficult to be certain. *D. brancoi* shares all the hominid characters already described for other Late Miocene hominids, but the cranium is better preserved in this taxon than in any other, and provides additional details (► [Table 4.3](#)).

■ **Table 4.3**

Great ape and African ape craniodental character states of *Dryopithecus*

Great ape character states	African ape character states
Labiolingually thick incisors	Biconvex premaxilla
Compressed canines	Stepped subnasal fossa
Elongated premolars and molars	Patent incisive canals
M1 = M2	Broad, flat nasal aperture base
No molar cingula	Shallow canine fossa
Reduced premolar cusp heteromorphy	Supraorbital torus
High root of the zygomatic	Inflated glabella
Elongated midface	Frontal sinus above and below nasion
Broad nasal aperture below the orbits	Projecting entoglenoid process
Reduced midfacial prognathism	Fused articular and tympanic temporal
Elongated, robust premaxilla	Broad temporal fossa
Premaxilla–palatine overlap	Deep glenoid fossa
Shallow subarcuate fossa	Elongated neurocranium
Enlarged semicircular canals	Moderate alveolar prognathism
Large brain	Klinorhynch
High cranial base (Begun 2004)	

D. brancoi shares with other *Dryopithecus* all the details of canine and postcanine tooth morphology outlined above. It shares relatively narrow and labiolingually thick upper central incisors with other *Dryopithecus*, though not to the degree seen in *D. crusafonti*. In addition to the hominid characters of *Dryopithecus* previously noted (► [Table 4.3](#)), *D. brancoi* preserves a few details of the face and many details of the neuro and basicrania, with further evidence of its hominid status. The zygoma are high, prominent, and oriented anterolaterally, as in hominines, and the number and position of the zygomaticofacial foramina is variable (this character has been proposed as one that could establish the pongine affinities of *Dryopithecus*, but the configuration in *D. brancoi* is hominine-like [Kordos and Begun 2001]) The neurocranium is large with a reconstructed cranial capacity in the range of extant chimpanzees (*D. brancoi* is the only Late Miocene hominid for which cranial capacity reconstruction is possible from

direct measurements of the brain case [in two individuals]) (Kordos and Begun 1998, 2001; Begun and Kordos 2004).

Among the hominine characters preserved in the cranial sample of *D. brancoi* are a relatively low and elongated neurocranium, with the inion displaced inferiorly (▶ [Table 4.3](#)). The interorbital and supraorbital regions have sinuses that are largest above and Glabella is prominent and continuous with small supraorbital tori separated from the frontal squama by a mild supratoral sulcus (Begun 1994a). The temporal bone, in addition to preserving evidence of a shallow subarcuate fossa (a hominid character), suggests fusion of the articular and tympanic portions and preserves details of the temporomandibular joint found only in hominines (Kordos and Begun 1997). A recently discovered and described cranium is the first to include a well-preserved neurocranial and facial skeleton in connection and shows clearly that the cranium of *Dryopithecus* was klinorhynch (having a ventrally deflected face), which it shares with African apes among the hominoids (Kordos and Begun 2001) (▶ [Figure 4.4](#)).

The nasoalveolar clivus or premaxilla is hominine like in its orientation, size, surface anatomy, and relations (▶ [Figure 4.3](#)). It is biconvex, long compared to Early Miocene Hominidea and hylobatids (proportionally equal in length to *Gorilla*), with a posterior pole that is elevated relative to the nasal floor, giving a stepped morphology to the subnasal fossa (Begun 1994a; ▶ [Figure 4.3](#)). The resulting incisive fossa of the subnasal floor is deep and well defined, the incisive canal is short and large in caliber, and the incisive foramen on the palatal side is comparatively large. This suite of characters is found in *Gorilla* as well and suggests that this is the ancestral morphology for hominines. *Pan* and *Australopithecus* share the synapomorphic condition of a more elongated but still biconvex premaxilla, which along with their spatulate upper central incisors and neurocranial morphology is among the most important morphological synapomorphies of the chimpanzee–human clade (Begun 1992c).

D. brancoi is well represented by postcrania, including a distal humerus that is hominid-like in all details related to trochlear and capitular morphology, even more so than *Sivapithecus* in having broad and shallow fossae for the processes of the radius and ulnae (see above). The ulna is robust with a strongly developed trochlear keel and a radial facet orientation that indicates forearm bones positioned for enhanced antipronograde postures (Begun 1992a). The scaphoid is *Pongo*-like in morphology and was not fused to the os centrale, as it is in African apes and humans (Begun et al. 2003). The capitate is large with a complex metacarpal articular surface, as in African apes, but the head is comparatively narrow and the bone overall is elongated compared to African apes, again more like the condition in *Pongo* and *Sivapithecus*. The phalanges are long, strongly curved, and marked by sharp ridges for the flexor musculature, indicative of

suspensory positional behavior (Begun 1993). Recently discovered femora of a very small individual of *D. brancoi* are short, with a large head, long neck, and extremely robust shaft, consistent with the hominoid pattern, and again especially similar to *Pongo*. The foot is also apelike in its broad, flat talar body and mobile but large entocuneiform and hallux.

4.5.7.4 Paleobiology of *Dryopithecus*

All four species of *Dryopithecus* display dental morphological characters that are very similar to extant *Pan* and suggest a soft fruit diet (Begun 1994a). Microwear analyses support this assessment (Kay and Ungar 1997). The gnathic morphology of *Dryopithecus* is gracile compared to many other Late Miocene hominids (less robust mandibles, thinner occlusal enamel, smaller attachment sites for the muscles of mastication), which is both consistent with a soft fruit diet and more similar to extant African apes, *Pan* in particular. Postcranially, *Dryopithecus* is unambiguously suspensory, but it does lack a few synapomorphies, particularly of the extremities that characterize all extant hominids. These have to do mainly with the robusticity of the bones of the carpus and tarsus, which may be attributable to a “red queen hypothesis” phenomenon, as in the case of the progressive development of shearing quotients during the course of hominoid evolution (Kay and Ungar 1997). In the fossil record of many mammals, there is evidence of a shift toward a certain adaptation (folivory, frugivory, suspension, climbing, bipedalism, etc.) that becomes increasingly refined in individual lineages descended from the common ancestor initially expressing the behavior. In order to remain competitive, the descendants must, in essence, run to stay in the same place, as increasingly efficient versions of the same adaptation appear independently (van Valen 1973). *Dryopithecus* was an arboreal, suspensory, soft fruit frugivore with a dentition similar to *Pan*, living in subtropical forests but probably capable of exploiting a variety of resources, possibly including meat (Kordos and Begun 2002).

4.5.8 *Ouranopithecus*

A large hominid sharing characters of *Dryopithecus* and *Sivapithecus* was first described from northern Greece and attributed to the genus *Dryopithecus* (to which *Sivapithecus* was also attributed at the time) (Bonis et al. 1975). Soon it became clear that the sample from Greece was distinct from both *Sivapithecus* and *Dryopithecus*, and the new nomen *Ouranopithecus* was proposed (Bonis and Melentis 1977).

Ouranopithecus is a large hominid, the approximate size of a large male chimpanzee or female gorilla, whose morphology is similar to that of *Dryopithecus* but with a much more robust masticatory adaptation (Begun and Kordos 1997). *Ouranopithecus* has a palate that is similar to *Dryopithecus* in the degree and pattern of overlap of the maxilla and premaxilla (Bonis and Melentis 1987; Begun and Kordos 1997). The morphology of the nasoalveolar clivus is also similar to *Dryopithecus* and extant hominines. The nasal aperture is broad at its base, the interorbital space is broad and the orbits are rectangular. The zygomatic roots arise relatively low and anteriorly on the maxilla, which is interpreted as a homoplasy with Early Miocene taxa, as a similar condition is also found in robust australopithecines that share with *Ouranopithecus* a very robust masticatory apparatus (Begun and Kordos 1997). The glabella is projecting, and like *Dryopithecus* it is continuous with subtle tori above each orbit. The frontal squama is concave above glabella, but this is somewhat exaggerated by damage. Dentally, *Ouranopithecus* is similar to *Dryopithecus* and other hominids in tooth proportions and overall dental morphology. It differs from *Dryopithecus* in having hyperthick occlusal enamel, molars with broad cusps and flat basins, mesiodistally longer incisors and relatively low crowned male upper canines. The mandibles are also more robust than in *Dryopithecus* and have strongly reinforced symphyses. The female mandibles tend to be more robust (or shallower) than the male mandibles. One mandible preserves the condylar process, which is large and strongly convex anteroposteriorly. *Ouranopithecus* is also known from two unpublished phalanges.

In many publications, summarized in Bonis and Koufos (1997), it has been argued that *Ouranopithecus* is a hominin (specifically related to humans), mainly on the basis of canine reduction and masticatory robusticity. However, these features occur repeatedly during hominoid evolution. *Ouranopithecus* is most parsimoniously interpreted as a terminal member of the *Dryopithecus* clade, with a number of craniodental specializations related to an increase in masticatory robusticity (Begun and Kordos 1997; Begun 2001, 2002). The large jaws and teeth and hyperthick enamel, as well as microwear studies, suggest an ability to exploit hard and/or tough fruits, nuts, and other dietary resources (Kay 1981; Ungar 1996; Bonis and Koufos 1997; Kay and Ungar 1997)

4.5.8.1 *Graecopithecus*

Another taxon, *Graecopithecus* (Koenigswald 1972), is also known from Greece but from a much younger locality over 200 km from the *Ouranopithecus* localities. It is similar to *Ouranopithecus*, and some have suggested that the two

samples belong to the same genus, which would be called *Graecopithecus*, since this nomen has priority (Martin and Andrews 1984). In my view the generic distinction is warranted. *Graecopithecus*, known only from a poorly preserved mandible with a fragmentary M_1 , a very worn M_2 and root fragments, is similar to *Ouranopithecus* in apparently having thick occlusal enamel. However, it is the overall size of female *Ouranopithecus* but has an M_2 bigger than some male *Ouranopithecus*, and the M_2 is actually broader than the mandibular corpus at the level of the M_2 . The symphysis is more vertical and the M_1 is relatively small (Begun 2002). *Graecopithecus* is morphologically distinguishable from *Ouranopithecus*, much younger in age, and geographically distant from *Ouranopithecus* localities.

4.5.9 *Oreopithecus*

The other European Miocene hominoid discovered and described during the nineteenth century is the highly unusual *Oreopithecus* (Gervais 1872). Over the years *Oreopithecus* has been called a pig, prosimian, monkey, and ape, the last being the attribution most researchers agree on today (Harrison and Rook 1997; Begun 2002). *Oreopithecus* is younger than other Late Miocene European hominoids and is known from about 6 to 7 Ma localities in Italy. At the time, most of the Italian peninsula was separated from the rest of Europe by the sea, as is today the Italian island of Sardinia, where one *Oreopithecus* locality is found. In the Late Miocene, all *Oreopithecus* localities were insular, and the faunas associated with them are unique and difficult to compare to continental European faunas (Harrison and Rook 1997). *Oreopithecus* is a product of its insular environment as well and is characterized by many unique adaptations that make it difficult to understand its relations to other hominoids.

In its craniodental morphology, *Oreopithecus* is similar to *Dryopithecus* and African apes in having apparently thin enamel, but otherwise the morphology of the teeth is quite unique. Like other hominids, *Oreopithecus* has compressed canines, reduced premolar cusp heteromorphy, and reduced or absent molar cingula. However, the incisors are small and low crowned, the P_4 has a primitive looking low talonid compared to the trigonid, the postcanine dentition has tall, isolated cusps, and the lower molars have a unique occlusal morphology with a centroconid connected to the four principal cusps by a well-developed system of crests. The upper molars are also strongly “cristodont,” which makes them appear similar to the lower molars, superficially resembling the condition of upper and lower molar bilophodonty in Old World monkeys.

The mandible is strongly built with some specimens being quite robust transversely and others deeper. The ramus is expansive to accommodate large temporalis and masseter muscles, which is also evidenced by the prominent temporal crests and pronounced postorbital constriction. The face is badly damaged but appears to have had a short and relatively gracile premaxilla, which is consistent with the small incisors. The brain case is also badly damaged but was clearly small, housing a much smaller brain than great apes of comparable body mass (Harrison 1989; Begun and Kordos 2004). Like *Sivapithecus* and non-hominids, the articular and temporal portions of the temporal bone are not fused but like hominids the subarcuate fossae are small. The ectocranial crests are very strongly marked while the frontal is comparatively smooth, without tori, and the postorbital constriction is marked.

The most impressive aspect of *Oreopithecus* is its postcranium. A remarkably complete but crushed skeleton along with many other isolated postcranial elements is known from *Oreopithecus*. The axial skeleton (rib cage and trunk) is hominoid-like in its short lower back and broad thorax, and the pelvis is also comparatively short and broad, as in hominids. The forelimbs are very elongated compared to the hindlimbs, the glenoid fossa of the scapula is deep, and the elbow has all the typical hominoid features described previously including a very short olecranon process, which is not known for other Late Miocene hominids. The femur is short and robust with a large head, and the knee joint indicates mobility in several planes. The hand is long but narrow, and the foot is comparatively short, though in both the hand and foot the digits are long and curved. The carpals and tarsals are primitive hominoid-like in being transversely gracile compared to their length.

Oreopithecus combines primitive and derived hominoid characters that ironically make it extremely difficult to place phylogenetically, despite its relatively complete preservation. Harrison and Rook (1997) consider *Oreopithecus* to be a stem hominid closely related to *Dryopithecus*. Moyà-Solà et al. (1997, 1999) interpret both *Dryopithecus* and *Oreopithecus* to be stem pongines, and they have also concluded that *Oreopithecus* was an arboreal biped with a well-developed precision grip. However, these conclusions are based in part on an erroneous reconstruction of the hand of *Oreopithecus* (Susman 2004 and personal observations) and a very unlikely reconstruction of the foot (Köhler and Moyà-Solà 1997 and personal observations). Rook et al. (1999) interpret CT scans of the innominate of *Oreopithecus* to imply a remodeling of bone consistent with bipedalism, but alternative interpretations are in my view more likely (Wunderlich et al. 1999). Overall, the overwhelming signal from the postcranium of *Oreopithecus* is of a suspensory arboreal adaptation. The long, curved phalanges are

unambiguous indicators of suspension and incompatible with either bipedalism or a precision grip.

Though some have interpreted aspects of the cranial morphology of *Oreopithecus* to have resulted from neoteny leading to a superficially primitive morphology (Moyà-Solà et al. 1997; Alba et al. 2001), it is very difficult to identify heterochrony in fossil taxa (Rice 1997), and the much more straight forward interpretation is that *Oreopithecus* does in fact retain a number of primitive characters not found in other Late Miocene or extant hominids (Harrison 1986; Harrison and Rook 1997; Begun 2002). These include a short, gracile premaxilla, large incisive foramen, low position of the zygomatic root, small brain, a number of features of the basicranium and several postcranial characters (gracile phalanges, transversely small carpals, short, relatively gracile tarsal, etc.). It is very unlikely that a single growth process resulting from selection for bipedalism and an omnivorous diet, as suggested by Alba et al. (2001), would have produced such a diversity of consistently primitive characters throughout the skeleton.

The extraordinary morphology of the cranium and dentition of *Oreopithecus* are probably related to a specialized folivorous adaptation. *Oreopithecus* molars have the highest shearing quotients of any hominoid, which is consistent with a high-fiber diet (Kay and Ungar 1997). The exceptionally developed chewing muscles of *Oreopithecus*, its robust mandibles, and even the small size of its brain are all consistent with a folivorous diet requiring high-bite forces but relatively little planning or “extractive foraging” (Begun and Kordos 2004).

4.6 Late Miocene hominid extinctions and dispersals

Hominids first appear and quickly radiate in the Middle Miocene of Eurasia, but between about 10 and 9 Ma they begin to disappear. The view presented here is that the hominids from western Eurasia are hominines, and those in the east are pongines (Begun 2004). Descendants of each subfamily eventually disperse south of the Tropic of Cancer as other taxa become extinct in Eurasia (Begun et al. 1997; Begun 2001, 2004). This view has been supported by genetic evidence (Stewart and Disotell 1998) and criticized based on differing interpretations of the fossil record. For example, it has been noted that Africa is a more likely place for the origin of the Hominidae and the Homininae, but because it is poorly sampled, especially in the Late Miocene, the fossils that would support this interpretation remain to be discovered. In fact, many Late Miocene localities are known from Africa, a number with paleoecological indications of forested settings (Begun 2001, 2004), yet no hominids have ever been identified in Africa dating between

Kenyapithecus and *Sahelanthropus*. A few specimens from this time period are known, such as *Samburupithecus*, but as noted this taxon retains many primitive dental and maxillary characters (Begun 2001). Isolated teeth from Ngorora have been described as having affinities primarily with the Proconsuloidea or Middle Miocene East African hominoids (e.g., *Equatorius*) (Hill and Ward 1988; Begun 2001; Hill et al. 2002). Pickford and Senut (2005) have recently described teeth from Ngorora and Lukeino have been described as chimpanzee and gorilla-like, but in my view the older teeth cannot be distinguished from others with affinities to the Proconsuloidea, and the younger teeth are probably from *Orrorin*, known from the same locality (Lukeino). An African origin of these clades also fails to explain the pattern in Eurasia that includes hominids with African great ape morphology in the west and Asian great ape morphology in the east (Begun 2004).

Hominids appear to have moved south from Eurasia in response to global climate changes that produced more seasonal conditions in Eurasia toward the end of the Miocene (Quade, et al. 1989; Leakey et al. 1996; Cerling et al. 1997; Begun 2001, 2004). Much evidence exists for climate change throughout much of Eurasia in the Late Miocene, which led to the development of more seasonal conditions. This culminates in the Messinian Salinity Crisis that led to the desiccation of the Mediterranean basin at the end of the Miocene (Hsü et al. 1973; Clauzon et al. 1996; Krijgsman et al. 1999). Other consequences include the development of Asian Monsoons, desertification in North Africa, the early phases of Neogene polar ice cap expansion and the expansion of North American grasslands (Garcés et al. 1997; Hoorn et al. 2000; Zhisheng et al. 2001; Griffin 2002; Guo et al. 2002; Janis et al. 2002; Liu and Yin 2002; Wilson et al. 2002). In both Europe and Asia, subtropical forests retreat and are increasingly replaced by more open country grasslands and steppes (Bernor et al. 1979; Bernor 1983; Fortelius et al. 1996; Cerling et al. 1997; Bonis et al. 1999; Magyar et al. 1999; Solounias et al. 1999; Fortelius and Hokkanen 2001). In some places, forests persisted and elsewhere more severe changes occurred, creating a number of refugia, some of which continued to host hominids well into the period of climatic deterioration. This is the case for the *Oreopithecus* localities of Tuscany and Sardinia (Harrison and Rook 1997). Other well-known localities, such as Dorn-Dürkheim in Germany, retain a strongly forested character, though they lack hominoids (Franzen 1997; Franzen and Storch 1999).

There is a gradient of extinctions of forest forms from West to East corresponding to the gradient of appearance of more open country faunas from east to west (Bernor et al. 1979; Fortelius et al. 1996; Begun 2001, 2004). Between about 12 and 10 Ma *Dryopithecus* disappears from localities in Europe, becoming

very rare by 9.5 Ma in Spain and Germany. This wave of extinctions ends coincident with an important faunal event in Western Europe known as the mid-vallesian crisis, when a major turnover of terrestrial faunas leads to the widespread extinction of local taxa generally attributed to the development of more open conditions (Moyà-Solà and Agustí 1990; Fortelius et al. 1996). The youngest specimens possibly attributable to *Dryopithecus* are the most easterly, currently assigned to *Udabnopythecus* from the 8- to 8.5-Ma locality of Udabno in Georgia (Gabunia et al. 2001).

In the eastern Mediterranean, hominids persist to the end of this time. *Ouranopithecus* in Greece is mainly known from the end of the hominid presence in Europe, and may be a terminal taxon of the *Dryopithecus* clade (Begun and Kordos 1997). In Anatolia at the eastern edge of the faunal province that includes Greece and the eastern Mediterranean (the Greco-Iranian province [Bonis et al. 1999]), a very large hominid resembling *Ouranopithecus* may be as young as 7–8 Ma in age (Sevim et al. 2001). At this time, forest taxa are increasingly replaced by more open country forms. This is true of virtually all mammalian orders. Among the primates, hominoids decline and cercopithecoids are on the increase (Andrews et al. 1996). Grazing ungulates and grassland or dry ecology adapted micromammals also become more common (Fortelius et al. 1996; Agustí et al. 1999; Bonis et al. 1999; Solounias et al. 1999).

The dispersal of Late Miocene faunas between Eurasia and Africa is complex and includes both open and more forest adapted taxa. Among the more open country taxa, horses disperse from North America to the Old World, and modern bovids and giraffids appear to have dispersed from Europe to Africa (Dawson 1999; Made 1999; Solounias et al. 1999; Agustí et al. 2001). Among the more close setting mammals, hippos move from Africa to Europe, and pigs of varying ecological preferences move from Asia to Europe and Africa (Fortelius et al. 1996; Made 1999). Small carnivores (mustelids, felids, and viverrids), larger carnivores (ursids, hyaenids) porcupines, rabbits, and chalicotheres, most of which also prefer more closed settings, also disperse from Eurasia to Africa (Leakey et al. 1996; Ginsburg 1999; Heissig 1999; Made 1999; Winkler 2002).

Many of these dispersals involved forest or wetter ecology taxa (hippos, some suids, primates, carnivores, rodents, and chalicotheres), which is consistent with the evidence of climate change at that time. Taxa disperse south into Africa as conditions continue to deteriorate leading to the Messinian crisis, among them probably the ancestors of the African apes and humans. This scenario has hominid ancestors leave Africa in the Early Miocene and return as hominines in the Late Miocene, but this is precisely what seems to have occurred in several mammalian lineages, including those represented by Late Miocene African species of *Orycteropus* (aardvark), several small carnivores, the hippo *Hexaprotodon*,

and possibly the proboscideans *Anancus*, *Deinotherium*, and *Choerolophodon* (Leakey et al. 1996; Ginsburg 1999; Heissig 1999; Made 1999; Boisserie et al. 2003; Werdelin 2003; Begun and Nargolwalla 2004).

4.7 Summary and conclusions

The Miocene epoch witnesses several adaptive radiations of hominoids and hominoid-like primates. It was indeed the golden age of the Hominoidea. Many catarrhines appear in East Africa in the Early Miocene, some of which are surely related to living hominoids. A few of the basic attributes of the Hominoidea appear at this time, including the absence of a tail, somewhat extended life history, and a hylobatid level of encephalization, and hints of powerful hand and foot grips and a propensity for more vertical climbing. Among the diversity of Early Miocene Hominidea, a group emerged that may have had an adaptation to a diet dependent on more embedded resources, leading to a dispersal into Eurasia. Once there, hominoids flourish and expand, splitting into eastern and western clades that lead to extant hominids, and an early southern clade that becomes extinct. Early in the Late Miocene, the hominid radiation in Eurasia began to dwindle, with the earliest extinctions occurring in the west, and progressing eastward. Hominids and many other mammals experienced extinction events at this time, and many clades of Eurasian mammals also dispersed south, probably as a result of major global climatic events. Western Eurasian hominids dispersed into Africa leading the evolution of the African apes and humans, and eastern hominids dispersed into Southeast Asia, leading to the appearance of the *Pongo* clade. Shortly after their return to Africa, hominines diverged into their respective clades, probably relatively quickly. Gorillas remain the most conservative in many respects, though they achieve some of the largest body masses in any primate and specialize in their ability to exploit high-fiber keystone resources. Chimpanzees and humans diverged possibly within a million years of the emergence of the gorilla clade, the chimp clade remaining relatively conservative and the human clade experiencing much more rapid and dramatic evolutionary changes. Human ancestors retain the imprint of their Eurasia and African ape ancestors, and were very probably similar to extant African apes, particularly chimpanzees. That is, the fossil record of hominoid evolution suggests that humans evolved from a knuckle-walking, forest-dwelling soft fruit frugivore/omnivore. The details of the evolutionary events leading to the origin of the individual lineages of the Homininae remain to be worked out, a process hampered in part by a poor fossil record that, for example, includes almost no fossil relative of gorillas or chimpanzees (but see McBrearty and Jablonski 2005).

References

- Abel O (1902) Zwie neue Menschenaffen aus den Leithakalkbildungen des wiener Bekkens. S Ber Akad Wiss Wien Math Nat 1: 1171–1202
- Adams CG, Bayliss DD, Whittaker JE (1999) The terminal Tethyan event: A critical review of the conflicting age determinations for the disconnection of the Mediterranean from the Indian Ocean. In: Whybrow PY, Hill A (eds) Vertebrate faunas of Arabia. Yale University Press, New Haven, pp 477–484
- Agustí J, Cabrera L, Garcés M, Llenas M (1999) Mammal turnover and global climate change in the late Miocene terrestrial record of the Vallès Penedès basin (NE Spain). In: Agustí J, Rook L, Andrews P (eds) Hominoid evolution and climate change in Europe. Volume 1: The evolution of Neogene terrestrial ecosystems in Europe. Cambridge University Press, Cambridge, pp 397–412
- Agustí J, Cabrera L, Garcés M (2001) Chronology and zoogeography of the Miocene hominoid record in Europe. In: Bonis L de, Koufos GD, Andrews P (eds) Hominoid evolution and environmental change in the Neogene of Europe. Volume 2. Phylogeny of the Neogene hominoid primates of Eurasia. Cambridge University Press, Cambridge, pp 2–18
- Alba DM, Moyà-Solà S, Köhler M, Rook L (2001) Heterochrony and the cranial anatomy of *Oreopithecus*: Some cladistic fallacies and the significance of developmental constraints in phylogenetic analysis. In: Bonis L de, Koufos GD, Andrews P (eds) Hominoid evolution and environmental change in the Neogene of Europe. Cambridge University Press, Cambridge, pp 284–315
- Alpagut B, Andrews P, Martin L (1990) New Miocene hominoid specimens from the middle Miocene site at Pasalar. J Hum Evol 19: 397–422
- Alpagut B, Andrews P, Fortelius M, Kappelman K, Temizsoy I, Lindsay W (1996) A new specimen of *Ankarapithecus metei* from the Sinap formation of central Anatolia. Nature 382: 349–351
- Andrews P (1978) A revision of the Miocene Hominoidea from East Africa. Bull Brit Mus Nat Hist (Geol) 30: 85–224
- Andrews P (1992) Evolution and environment in the Hominoidea. Nature 360: 641–646
- Andrews P, Martin LB (1987) The phyletic position of the Ad Dabtiyah hominoid. Bull Brit Mus Nat Hist 41: 383–393
- Andrews P, Tekkaya I (1980) A revision of the Turkish Miocene hominoid *Sivapithecus metei*. Paleontology 23: 85–95
- Andrews P, Harrison T, Delson E, Bernor RL, Martin L (1996) Distribution and biochronology of European and Southwest Asian Miocene Catarrhines. In: Bernor RL, Fahlbusch V, Mittmann H-W (eds) The evolution of western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp 168–295
- Andrews P, Begun DR, Zylstra M (1997) Interrelationships between functional morphology and paleoenvironments in Miocene hominoids. In: Begun DR, Ward CV, Rose MD (eds) Function, phylogeny, and fossils: Miocene hominoid evolution and adaptations. Plenum Press, New York, pp 29–58
- Barry JC, Morgan ME, Flynn LJ, Pilbeam D, Behrensmeyer AK, Raza SM, Khan IA, Badgley C, Hicks J, Kelley J (2002) Faunal and environmental change in the Late Miocene Siwaliks of Northern Pakistan. Paleobiol Mem 28: 1–72
- Beard KC, Teaford MF, Walker A (1986) New wrist bones of *Proconsul africanus* and *Proconsul nyanzae* from Rusinga Island, Kenya. Folia Primatol (Basel) 47: 97–118
- Begun DR (1992a) Phyletic diversity and locomotion in primitive European hominids. Am J Phys Anthropol 87: 311–340
- Begun DR (1992b) Miocene fossil hominids and the chimp-human clade. Science 257: 1929–1933
- Begun DR, Ward CV, Deane AS, Kivell TL, Nargolwalla MC, Taylor ND (2006) Stem hominine or hominid? The phylogeny and functional anatomy of *Pierolapithecus*: Am. J. Phys. Anthropol S42, p. 63
- Begun DR (1992c) *Dryopithecus crusafonti* sp. nov., a new Miocene hominid species from

- Can Ponsic (Northeastern Spain). *Am J Phys Anthropol* 87: 291–310
- Begun DR (1993) New catarrhine phalanges from Rudabánya (Northeastern Hungary) and the problem of parallelism and convergence in hominoid postcranial morphology. *J Hum Evol* 24: 373–402
- Begun DR (1994a) Relations among the great apes and humans: New interpretations based on the fossil great ape *Dryopithecus*. *Yrbk Phys Anthropol* 37: 11–63
- Begun DR (1994b) The significance of *Otaviipithecus namibiensis* to interpretations of hominoid evolution. *J Hum Evol* 27: 385–394
- Begun DR (2000) Middle Miocene hominoid origins. *Science* 287: 2375a
- Begun DR (2001) African and Eurasian Miocene hominoids and the origins of the Homi- nidae. In: Bonis L de, Koufos GD, Andrews P (eds) *Hominoid evolution and environmental change in the Neogene of Europe. Volume 2. Phylogeny of the Neogene Hominoid Primates of Eurasia*. Cambridge University Press, Cambridge, pp 231–253
- Begun DR (2002) European Hominoids. In: Hartwig W (ed) *The primate fossil record*. Cambridge University Press, Cambridge, pp 339–368
- Begun DR (2004) *Sivapithecus* is east and *Dryopithecus* is west, and never the twain shall meet. *Anthropol Sci ON LINE ISSN: 1348–8570*
- Begun DR, Güleç E (1995) Restoration and reinterpretation of the facial specimen attributed to *Sivapithecus meteai* from Sinap Tepe (Yassiören), Central Anatolia, Turkey. *Am J Phys Anthropol Suppl* 20: 63–64
- Begun DR, Güleç E (1998) Restoration of the type and palate of *Ankarapithecus meteai*: Taxonomic, phylogenetic, and functional implications. *Am J Phys Anthropol* 105: 279–314
- Begun DR, Kordos L (1993) Revision of *Dryopithecus brancosi* SCHLOSSER, 1901 based on the fossil hominoid material from Rudabánya. *J Hum Evol* 25: 271–285
- Begun DR, Kordos L (1997) Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene and living hominids. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid evolution and adaptations*. Plenum Publishing Co., New York, pp 291–316
- Begun DR, Kordos L (2004) Cranial evidence of the evolution of intelligence in fossil apes. In: Russon AE, Begun DR (eds) *The evolution of thought: Evolutionary origins of great ape intelligence*. Cambridge University Press, Cambridge, pp 260–279
- Begun DR, Nargolwalla MC (2004) Late Miocene hominid biogeography: Some recent perspectives. *Evol Anthropol* 13: 234–238
- Begun DR, Ward CV (2005) Comment on “*Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain.” *Science* 308: 203c
- Begun DR, Teaford MF, Walker A (1994) Comparative and functional anatomy of *Proconsul* phalanges from the Kaswanga primate site, Rusinga Island, Kenya. *J Hum Evol* 26: 89–165
- Begun DR, Ward CV, Rose MD (1997) Events in hominoid evolution. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid origins and adaptations*. Plenum Press, New York, pp 389–415
- Begun DR, Geraads D, Güleç E (2003a) The Çandır hominoid locality: Implications for the timing and pattern of hominoid dispersal events. *Cour Forschung Inst Senckenberg* 240: 251–265
- Begun DR, Güleç E, Geraads D (2003b) Dispersal patterns of Eurasian hominoids: Implications from Turkey. *Deinsea* 10: 23–39
- Begun DR, Kivell T, Kordos L (2003c) New Miocene primate postcranial fossils from Rudabánya, Hungary. *Am J Phys Anthropol* 120(S36): 63–64
- Begun DR (2005) *Sivapithecus* is east and *Dryopithecus* is west, and never the twain shall meet: *Anthropol Sci*, vol 113, p 53–64
- Benefit B, McCrossin ML (2000) Middle Miocene hominoid origins. *Science* 287: 2375a
- Benefit BR, McCrossin ML (2002) The Victoriapithecidae, Cercopithecoidea. In: Hartwig W (ed) *The primate fossil record*. Cambridge University Press, Cambridge, pp 241–253
- Bernor RL (1983) Geochronology and zoogeographic relationships of Miocene Hominoidea.

- In: Corruccini RS, Ciochon RL (eds) *New interpretations of ape and human ancestry*. Academic Press, New York, pp 21–64
- Bernor RL, Andrews PJ, Solounias N, Van Couvering JAH (1979) The evolution of “Pon-tian” mammal faunas: Some zoogeographic, paleoecologic and chronostratigraphic considerations. *Ann Géol Pays Hellèn*: 81–89
- Boisserie J-R, Brunet M, Andossa L, Vignaud P (2003) Hippopotamids from the Djurab Pliocene faunas, Chad, Central Africa. *J Afr Earth Sci* 36: 15–27
- Bonis L de, Koufos G (1997) The phylogenetic and functional implications of *Ouranopithecus macedoniensis*. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid origins and adaptations*. Plenum Press, New York, pp 317–326
- Bonis L de, Melentis J (1977) Un nouveau genre de primate Hominaide dans le Vallésien de Macédoine. *CR Acad Sci D*: 1393–1396
- Bonis L de, Melentis J (1987) Intérêt de l’anatomie naso-maxillaire pour la phylogénie de Hominidea. *CR Acad Sci Paris* 304: 767–769
- Bonis L de, Bouvrain G, Melentis J (1975) Nouveaux restes de primates hominoïdes dans le Vallésien de Macédoine (Grèce). *CR Acad Sci D Paris* 182: 379–382
- Bonis L de, Bouvrain G, Koufos G (1999) Palaeoenvironments of late Miocene primate localities in Macedonia, Greece. In: Agusti J, Rook L, Andrews P (eds) *The evolution of neogene terrestrial ecosystems in Europe*. Cambridge University Press, Cambridge, pp 413–435
- Brown B, Ward S (1988) Basicranial and facial topography in *Pongo* and *Sivapithecus*. In: Schwartz JH (ed) *Ourang-utan Biology*. Oxford University Press, New York, pp 247–260
- Cartmill M (1985) Climbing. In: Hildebrand M, Bramble D, Leim KE, Wake DB (eds) *Functional vertebrate morphology*. Belknap Press, Cambridge, pp 73–88
- Cave AJE, Haines RW (1940) The paranasal sinuses of the anthropoid apes. *J Anat* 74: 493–523
- Cerling T, Harris JR, MacFadden BJ, Leakey MG, Quade J, Eisenmann V, Ehleringer JR (1997) Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389: 153–158
- Chaimanee Y, Jolly D, Benammi M, Tafforeau P, Duzer D, Moussa I, Jaeger J-J (2003) A middle Miocene hominoid from Thailand and orangutan origins. *Nature* 422: 61–65
- Chaimanee Y, Suteethorn V, Pratueng J, Vidthayanon C, Marandat B, Jaeger J-J (2004) A new orang-utan relative from the Late Miocene of Thailand. *Nature* 427: 439–441
- Clauzon G, Suc J-P, Gautier F, Berger A, Loutre M-F (1996) Alternate interpretation of the Messinian salinity crisis: Controversy resolved? *Geology* 24: 363–366
- Conroy GC, Rose MD (1983) The evolution of the Primate foot from the earliest Primates to the Miocene Hominoids. *Foot and Ankle* 3: 342–364
- Conroy GC, Pickford M, Senut B, Couvering VJ (1992) *Otavipithecus namibiensis*, first Mio-cene hominid from southern Africa. *Nature* 356: 144–148
- Dawson MR (1999) Bering down: Miocene dispersals of land mammals between North America and Europe. In: Rössner G, Heissig K (eds) *The miocene land mammals of Europe*. Dr. Friedrich Pfeil, München, pp 473–483
- Drake RE, Van Couvering JA, Pickford MH, Curtis GH, Harris JA (1988) New chronology for the Early Miocene mammalian faunas of Kisingiri, Western Kenya. *J Geol Soc Lond* 145: 479–491
- Falk D (1983) A reconsideration of the endo-cast of *Proconsul africanus*: Implications for primate brain evolution. In: Ciochon RL, Corruccini RS (eds) *New interpretations of ape and human ancestry*. Plenum Press, New York, pp 239–248
- Fleagle JG, Simons EL (1978) *Micropithecus clarki*, a small ape from the Miocene of Uganda. *Am J Phys Anthropol* 49: 427–440
- Fortelius M, Hokkanen A (2001) The trophic context of hominoid occurrence in the later Miocene of western Eurasia: A primate-free view. In: Bonis L de, Koufos GD, Andrews P (eds) *Hominoid evolution and climatic change in Europe. Vol 2: Phylogeny of the Neogene hominoid primates of Eurasia*.

- Cambridge University Press, Cambridge, pp 19–47
- Fortelius M, Werdelin L, Andrews P, Bernor RL, Gentry A, Humphrey L, Mittmann H-W, Viratana S (1996) Provinciality, diversity, turnover, and paleoecology in land mammal faunas of the later miocene of Western Eurasia. In: Bernor RL, Fahlbusch V, Mittmann H-W (eds) The evolution of Western Eurasian Neogene mammal faunas. Columbia University Press, New York, pp 415–448
- Franzen JL (1997) Die Säugetiere aus dem Turonium von Dorn-Dürkheim 1 (Rheinhausen, Deutschland). Steininger F, Frankfurt/M
- Franzen JL, Storch G (1999) Late Miocene mammals from Central Europe. In: Agustí J, Rook L, Andrews P (eds) Hominoid evolution and climate change in Europe. Vol 1: The evolution of neogene terrestrial ecosystems in Europe. Cambridge University Press, Cambridge, pp 165–190
- Gabunia L, Gabashvili E, Vekua A, Lordkipanidze D (2001) The late Miocene hominoid from Georgia. In: Bonis L de, Koufos G, Andrews P (eds) Hominoid evolution and environmental change in the neogene of Europe. Vol 2: Phylogeny of the neogene hominoid primates of Eurasia. Cambridge University Press, Cambridge, pp 316–325
- Garcés M, Cabrera L, Agustí J, Parés JM (1997) Old World first appearance datum of “*Hipparion*” horses: Late Miocene large-mammal dispersal and global events. *Geology* 25: 19–22
- Gebo DL, MacLatchy L, Kityo R, Deino A, Kingston J, Pilbeam D (1997) A Hominoid genus from the Early Miocene of Uganda. *Science* 276: 401–404
- Gervais P (1872) Sur un singe fossile, d'espèce non encore décrite, qui a été découvert au Monte-Bamboli (Italie). *CR Acad Sci Paris LXXIV*: 1217–1223
- Ginsburg L (1999) Order Carnivora. In: Rössner GE, Heissig K (eds) The miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp 109–148
- Grand TI (1972) A mechanical interpretation of terminal branch feeding. *J Mammal* 53: 198–201
- Grand TI (1978) Adaptations of tissue and limb segments to facilitate moving and feeding in arboreal folivores. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington DC, pp 231–241
- Griffin DL (2002) Aridity and humidity: Two aspects of the late Miocene climate of North Africa and the Mediterranean. *Palaeogeogr Palaeoclimatol Palaeoecol* 182: 65–91
- Güleç E, Begun DR (2003) Functional morphology and affinities of the hominoid mandible from Çandır. *Cour Forschung Inst Senckenberg* 240: 89–112
- Guo ZT, Ruddiman WF, Hao QZ, Wu HB, Qiao YS, Zhu RX, Peng SZ, Wei JJ, Yuan BY, Liu TS (2002) Onset of Asian desertification by 22 Myr ago inferred from loess deposits in China. *Nature* 416: 159–163
- Harrison T (1986) A reassessment of the phylogenetic relationship of *Oreopithecus bambolii*. *Gervais. J Hum Evol* 15: 541–583
- Harrison T (1987) The phylogenetic relationships of the early catarrhine primates: A review of the current evidence. *J Hum Evol* 16: 41–80
- Harrison T (1989) New estimates of cranial capacity, body size, and encephalization in *Oreopithecus Bambolii*. *Am J Hum Evol* 78: 237
- Harrison T (1992) A reassessment of the taxonomic and phylogenetic affinities of the fossil catarrhines from Fort Ternan, Kenya. *Primates* 33: 501–522
- Harrison T (2002) Late Oligocene to middle Miocene catarrhines from Afro-Arabia. In: Hartwig W (ed) The primate fossil record. Cambridge University Press, Cambridge, pp 311–338
- Harrison T, Rook L (1997) Enigmatic anthropoid or misunderstood ape: The phylogenetic status of *Oreopithecus bambolii* reconsidered. In: Begun DR, Ward CV, Rose MD (eds) Function, phylogeny and fossils: Miocene hominoid origins and adaptations. Plenum Press, New York, pp 327–362
- Heissig K (1999) Family Rhinocerotidae. In: Rössner GE, Heissig K (eds) The miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp 175–188
- Heizmann E (1992) Das tertiär in südwestdeutschland. *Stuttgarter Beiträge zur Naturkunde Serie C* 33: 1–90

- Heizmann E, Begun DR (2001) The oldest European hominoid. *J Hum Evol* 41: 465–481
- Hill A, Ward S (1988) Origin of the Hominidae: The record of African large hominoid evolution between 14 my and 4 my. *Yrbk Phys Anthropol* 32: 48–83
- Hoorn C, Ohja T, Quade J (2000) Palynological evidence for vegetation development and climatic change in the Sub-Himalayan Zone (Neogene, Central Nepal). *Palaeogeogr Palaeoclimatol Palaeoecol* 163: 133–161
- Hopwood AT (1933) Miocene Primates from Kenya. *Zool J Linnean Soc* 38: 437–464
- Hsü KJ, Cita MB, Ryan WBF (1973) The origin of the Mediterranean evaporites. *Initial Rep Deep Sea Drill Proj* 13: 1203–1231
- Ishida H, Pickford M (1997) A new late Miocene hominoid from Kenya: *Samburupithecus koptalami* gen. et sp. nov. *CR Acad Sci Ser D* 325: 823–829
- Ishida H, Kunimatsu Y, Nakatsukasa M, Nakano Y (1999) New hominoid genus from the middle Miocene of Nachola, Kenya. *Anthropol Sci* 107: 189–191
- Ishida H, Kunimatsu Y, Takano T, Nakano Y, Nakatsukasa M (2004) *Nacholapithecus* skeleton from the middle Miocene of Kenya. *J Hum Evol* 46: 1–35
- Janis CM, Damuth J, Theodor JM (2002) The origins and evolution of the North American grassland biome: The story from the hoofed mammals. *Palaeogeogr Palaeoclimatol Palaeoecol* 177: 183–198
- Kappelman J, Kelley J, Pilbeam D, Sheikh KA, Ward S, Anwar M, Barry JC, Brown B, Hake P, Johnson NM, Raza SM, Shah SMI (1991) The earliest occurrence of *Sivapithecus* from the middle Miocene Chinji Formation of Pakistan. *J Hum Evol* 21: 61–73
- Kappelman J, Richmond BG, Seiffert ER, Maga AM, Ryan TM (2003) Hominoidea (Primates). In: Fortelius M, Kappelman J, Sen S, Bernor R (eds) *Geology and paleontology of the Miocene sinap formation, Turkey*. Columbia University Press, New York, pp 90–124
- Kay RF (1981) The nut-cracker - a theory of the adaptations of the Ramapithecinae. *Am J Phys Anthropol* 55: 141–1151
- Kay RF, Ungar PS (1997) Dental evidence for diet in some Miocene catarrhines with comments on the effects of phylogeny on the interpretation of adaptation. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid evolution and adaptations*. Plenum Publishing Co., New York, pp 131–151
- Kelley J (1997) Paleobiological and phylogenetic significance of life history in miocene hominoids. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid evolution and adaptations*. Plenum Publishing Co., New York, pp 173–208
- Kelley J (1988) A new large species of *Sivapithecus* from the Siwaliks of Pakistan: *J Hum Evol*, vol 17, p 305–325
- Kelley J (2002) The hominoid radiation in Asia. In: Hartwig W (ed) *The primate fossil record*. Cambridge University Press, Cambridge, pp 369–384
- Kelley J (2004) Life history and cognitive evolution in the apes. In: Russon AE, Begun DR (eds) *The evolution of thought: Evolutionary origins of great ape intelligence*. Cambridge University Press, Cambridge, pp 280–297
- Kelley J, Alpagut B (1999) Canine sexing and species number in the Pasalar large hominid sample. *J Hum Evol* 36: 335–341
- Kelley J, Ward S, Brown B, Hill A, Downs W (2000) Middle Miocene hominoid origins. *Science* 287: 2375a
- Koenigswald GHR von (1935) Eine fossile Säugetierfauna mit *Simia* aus Südchina. *Proc Konink Neder Akad Wetenschappen* 38: 872–879
- Koenigswald GHR von (1972) Ein Unterkiefer eines fossilen Hominoiden aus dem Unterpliozän Griechenlands. *Proc Kon Nederl Akad Wet B* 75: 385–394.
- Köhler M, Moyà-Solà S (1997) Ape like or hominid-like? The positional behavior of *Oreopithecus bambolii* reconsidered. *Proc Natl Acad Sci USA* 94: 11747–11750
- Kordos L, Begun DR (1997) A new reconstruction of RUD 77, a partial cranium of *Dryopithecus branconi* from Rudábanya, Hungary.: *Am J Phys Anthropol*, vol 103, p 277–294
- Kordos L, Begun DR (1998) Encephalization and endocranial morphology in *Dryopithecus branconi*: Implications for brain evolution in

- early hominids. *Am J Phys Anthropol Suppl* 26: 141–142
- Kordos L, Begun DR (2001) A new cranium of *Dryopithecus* from Rudabánya, Hungary. *J Hum Evol* 41: 689–700
- Kordos L, Begun DR (2002) Rudabánya: A late miocene subtropical swamp deposit with evidence of the origin of the african apes and humans. *Evol Anthropol* 11: 45–57
- Krijgsman W, Hilgen FJ, Raffi I, Sierro FJ, Wilson DS (1999) Chronology, causes and progression of the Messinian salinity crisis. *Nature* 400: 652–655
- Kunimatsu Y, Ishida H, Nakatsukasa M, Nakano Y, Sawada Y (2004) Maxillae and associated gnathodontal specimens of *Nacholapithecus kerioi*, a large-bodied hominoid from Nachola, northern Kenya. *J Hum Evol* 46: 365–400
- Larson SG (1996) Estimating humeral head torsion on incomplete fossil anthropoid humeri. *J Hum Evol* 31: 239–257
- Larson SG (1998) Parallel evolution in the hominoid trunk and forelimb. *Evol Anthropol* 6: 87–99
- Lartet E (1856) Note sur un grand singe fossile qui se rattache au groupe des singes supérieurs. *CR Acad Sci* 43: 219–223
- Le Gros Clark WE, Leakey LSB (1950) Diagnoses of East African Miocene Hominoidea. *Quart J Geol Soc Lond* 105: 260–263
- Leakey LSB (1962) A new Lower Pliocene fossil primate from Kenya. *Ann Mag Nat Hist* 13: 689–696
- Leakey M, Walker A (1997) *Afropithecus*: Function and phylogeny. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid evolution and adaptations*. Plenum Publishing Co., New York, pp 225–239
- Leakey MG, Leakey REF, Richtsmeier JT, Simons EL, Walker AC (1991) Similarities in *Aegyptopithecus* and *Afropithecus* facial morphology. *Folia Primatol* 56: 65–85
- Leakey MG, Ungar PS, Walker A (1995) A new genus of large primate from the late Oligocene of Lothidok, Turkana District, Kenya. *J Hum Evol* 28: 519–531
- Leakey MG, Feibel CS, Bernor RL, Harris JM, Cerling TE, Stewart KM, Storrs GW, Walker A, Werdelin L, Winkler AJ (1996) Lothagam: A record of faunal change in the Late Miocene of East Africa. *J Vert Paleontol* 16: 556–570
- Leakey REF, Leakey MG (1986) A new Miocene hominoid from Kenya. *Nature* 324: 143–148
- Lewis OJ (1989) *Functional morphology of the evolving hand and foot*. Clarendon Press, Oxford
- Liu X, Yin Z-Y (2002) Sensitivity of East Asian monsoon climate to the uplift of the Tibetan Plateau. *Palaeogeogr Palaeoclimatol Palaeoecol* 183: 223–245
- Lydekker R (1879) Further notices of Siwalik Mammalia. *Rec Geol Surv India* XII: 33–52
- MacLeod N (1999) Oligocene and Miocene palaeoceanography—a review. In: Whybrow PY, Hill A (eds) *Vertebrate faunas of Arabia*. Yale University Press, New Haven, pp 501–507
- Madar SI, Rose MD, Kelley J, MacLachy L, Pilbeam D (2002) New *Sivapithecus* postcranial specimens from the Siwaliks of Pakistan. *J Hum Evol* 42: 705–752
- Made J van der (1999) Intercontinental relationship Europe-Africa and the Indian subcontinent. In: Rössner GE, Heissig K (eds) *The miocene land mammals of Europe*. Dr. Friedrich Pfeil, München, pp 457–472
- Magyar I, Geary DH, Müller P (1999) Paleogeographic evolution of the late Miocene Late Pannon in Central Europe. *Palaeogeogr Palaeoclimatol Palaeoecol* 147: 151–167
- Martin L, Andrews P (1984) The phyletic position of *Graecopithecus freyberi* KOENIGSWALD. *Cour Forsch Inst Senckenberg* 69: 25–40
- Martin LB, Andrews P (1993) Species recognition in middle Miocene hominoids. In: Kimbel WH, Martin LB (eds) *Species, species concepts, and primate evolution*. Plenum Press, New York, pp 393–427
- McBrearty S, Jablonski NG (2005) First fossil chimpanzee. *Nature* 437: 105–108
- McCrossin ML, Benefit BR (1997) On the relationships and adaptations of *Kenyapithecus*, a large-bodied hominoid from the middle Miocene of eastern Africa. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and*

- fossils: Miocene hominoid origins and adaptations. Plenum Press, New York, p 241–267
- McCrossin ML (1997) New postcranial remains of *Kenyapithecus* and their implications for understanding the origins or hominoid terrestriality. *Am J Phys Anthropol Suppl* 24: 164
- Moyà-Solà S, Agustí J (1990) Bioevents and mammal successions in the Spanish Miocene. In: Lindsay EH, Fahlbusch V, Mein P (eds) *European neogene mammal chronology*. Plenum Press, New York, pp 357–373
- Moyà-Solà M, Köhler M (1995) New partial cranium of *Dryopithecus* Lartet, 1863 (Hominoidea, Primates) from the upper Miocene of Can Llobateres, Barcelona, Spain. *J Hum Evol* 29: 101–139
- Moyà-Solà S, Köhler M (1996) A *Dryopithecus* skeleton and the origins of great-ape locomotion. *Nature* 379: 156–159
- Moyà-Solà S, Köhler M (1997) The phylogenetic relationships of *Oreopithecus bambolii* Gervais, 1872. *CR Acad Sci Paris* 324: 141–148
- Moyà-Solà S, Köhler M, Rook L (1999) Evidence of hominid-like precision grip capability in the hand of the Miocene ape *Oreopithecus*. *Proc Natl Acad Sci USA* 96: 313–317
- Moyà-Solà S, Köhler M, Alba DM, Casanovas-Vilar I, Galindo J (2004) *Pierolapithecus catalaunicus*, a new middle Miocene great ape from Spain. *Science* 306: 1339–1344
- Munthe J, Dongol B, Hutchison JH, Kean WF, Munthe K, West RM (1983) New fossil discoveries from the Miocene of Nepal include a hominoid. *Nature* 303: 331–333
- Nakatsukasa M, Yamanaka A, Kunimatsu Y, Shimizu D, Ishida H (1998) A newly discovered *Kenyapithecus* skeleton and its implications for the evolution of positional behavior in Miocene East African hominoids. *J Hum Evol* 34: 659–664
- Ozansoy F (1957) Faunes de Mammifères du Tertiaire de Turquie et leurs revisions stratigraphiques. *Bull Min Res Explor Inst Turkey* 49: 29–48
- Ozansoy F (1965) Étude des Gisements continentaux et des mammifères du Cenozoïque de Turquie. *Mem Soc Geol France* ns 44: 1–92
- Pickford M, Senut B (2005) Hominoid teeth with chimpanzee- and gorilla-like features from the Miocene of Kenya: Implications for the chronology of ape-human divergence and biogeography of Miocene hominoids. *Anthropol Sci* 113: 95–102
- Pickford M, Moyà-Solà S, Köhler M (1997) Phylogenetic implications of the first African middle Miocene hominoid frontal bone from Otavi, Namibia. *CR Acad Sci Paris Sciences de la terre et des planètes* 325: 459–466
- Pickford M, Senut B, Gommery D, Musiime E (2003) New catarrhine fossils from Moroto II, early middle Miocene (ca. 17.5 Ma) Uganda. *CR Palevol* 2: 649–662
- Pilbeam DR (1969) Tertiary Pongidae of east Africa: Evolutionary relationships and taxonomy. *Bull Peabody Mus Nat Hist* 31: 1–185
- Pilbeam DR (1982) New hominoid skull material from the Miocene of Pakistan. *Nature* 295: 232–234
- Pilbeam DR (1996) Genetic and morphological records of the Hominoidea and hominid origins: A synthesis. *Mol Phylogeny Evol* 5: 155–168
- Pilbeam DR (1997) Research on Miocene hominoids and hominid origins: The last three decades. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid evolution and adaptations*. Plenum Publishing Co., New York, pp 13–28
- Pilbeam DR, Simons EL (1971) Humerus of *Dryopithecus* from Saint Gaudens, France. *Nature* 229: 406–407
- Pilbeam DR, Young NM (2001) *Sivapithecus* and hominoid evolution: Some brief comments. In: Bonis, L de Koufos GD, Andrews P (eds) *Hominoid evolution and environmental change in the neogene of Europe*. Cambridge University Press, Cambridge, pp 349–364
- Pilbeam DR, Young N (2004) Hominoid evolution: Synthesizing disparate data. *CR Palevol* 3: 305–321
- Pilbeam DR, Rose MD, Badgley C, Lipschultz B (1980) Miocene hominoids from Pakistan. *Postilla* 181: 1–94

- Pilbeam DR, Rose MD, Barry JC, Shah SMI (1990) New *Sivapithecus* humeri from Pakistan and the relationship of *Sivapithecus* and *Pongo*. *Nature* 384: 237–239
- Pilgrim G (1910) Notices of new mammalian genera and species from the Tertiaries of India. *Rec Geol Surv India* 40: 63–71
- Pilgrim G (1915) New Siwalik primates and their bearing on the question of the evolution of man and the anthropoidea. *Rec Geol Surv India* 45: 1–74
- Quade J, Cerling TE, Bowman JR (1989) Development of Asian monsoon revealed by marked ecological shift during the latest Miocene. *Nature* 342: 163–166
- Rafferty KL, Walker A, Ruff CB, Rose MD, Andrews PJ (1995) Postcranial estimates of body weight in *Proconsul*, with a note on a distal tibia of *P. major* from Napak, Uganda. *Am J Phys Anthropol* 97: 391–402
- Rasmussen DT (2002) Early catarrhines of the African Eocene and Oligocene. In: Hartwig W (ed) *The primate fossil record*. Cambridge University Press, Cambridge, pp 203–220
- Raza SM, Barry JC, Pilbeam D, Rose MD, Shah SMI, Ward S (1983) New hominoid primates from the middle Miocene Chinji Formation, Potwar Plateau, Pakistan. *Nature* 306: 52–54
- Rice SH (1997) The analysis of ontogenetic trajectories: When a change in size or shape is not heterochrony. *Proc Natl Acad Sci* 94: 907–912
- Richmond BG, Whalen M (2001) Forelimb function, bone curvature and phylogeny of *Sivapithecus*. In: Bonis L de, Koufos GD, Andrews P (eds) *Hominoid evolution and environmental change in the Neogene of Europe*. Cambridge University Press, Cambridge, pp 326–348
- Rögl F (1999a) Circum-Mediterranean Miocene paleogeography. In: Rössner G, Heissig K (eds) *The Miocene land mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp 39–48
- Rögl F (1999b) Oligocene and Miocene Palaeogeography and Stratigraphy of the circum-Mediterranean Region. In: Whybrow PY, Hill A (eds) *Vertebrate faunas of Arabia*. Yale University Press, New Haven, pp 485–500
- Rook L, Bondioli L, Köhler M, Moyà-Solà S, Macchiarelli R (1999) *Oreopithecus* was a bipedal ape after all: Evidence from the iliac cancellous architecture. *Proc Natl Acad Sci* 96: 8795–8799
- Rose MD (1983) Miocene hominoid postcranial morphology: Monkey-like, ape-like, neither, or both? In: Ciochon RL, Corruccini RS (eds) *New interpretations of ape and human ancestry*. Plenum Press, New York, pp 405–417
- Rose MD (1984) Hominoid postcranial specimens from the Middle Miocene Chinji Formation, Pakistan. *J Hum Evol* 13: 503–516
- Rose MD (1986) Further hominoid postcranial specimens from the Late Miocene Nagri formation of Pakistan. *J Hum Evol* 15: 333–367
- Rose MD (1988) Another look at the anthropoid elbow. *J Hum Evol* 17: 193–224
- Rose MD (1989) New postcranial specimens of catarrhines from the Middle Miocene Chinji Formation, Pakistan: Description and a discussion of proximal humeral functional morphology in anthropoids. *J Hum Evol* 18: 131–162
- Rose MD (1992) Kinematics of the trapezium-1st metacarpal joint in extant anthropoids and Miocene hominoids. *J Hum Evol* 22: 255–256
- Rose MD (1993) Functional anatomy of the elbow and forearm in primates. In: Gebo DL (ed) *Postcranial adaptation in nonhuman primates*. Northern Illinois University Press, DeKalb, pp 70–95
- Rose MD (1994) Quadrupedalism in some Miocene catarrhines. *J Hum Evol* 26: 387–411
- Rose MD (1997) Functional and phylogenetic features of the forelimb in Miocene hominoids. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid evolution and adaptations*. Plenum Publishing Co., New York, pp 79–100
- Rossie JB, Simons EL, Gauld SC, Rasmussen DT (2002) Paranasal sinus anatomy of *Aegyptopithecus* Implications for hominoid origins. *Proc Natl Acad Sci* 99: 8454–8456
- Ruff CB, Walker A, Teaford MF (1989) Body mass, sexual dimorphism and femoral proportions of *Proconsul* from Rusinga and

- Mfangano Islands, Kenya. *J Hum Evol* 18: 515–536
- Russon AE, Begun DR (2004) A composite of the common ancestor, and the evolution of its intelligence. In: Russon AE, Begun DR (eds) *The evolution of thought: Evolutionary origins of great ape intelligence*. Cambridge University Press, Cambridge, pp 353–368
- Schlosser M (1901) Die menschenähnlichen zähne aus dem Bohnerz der Schwäbischen. *Alb Zool Anz* 24: 261–271
- Schoch RM (1986) *Phylogeny reconstruction in paleontology*. Van Nostrand Reinhold, New York
- Schwartz JH (1997) *Lufengpithecus* and hominoid phylogeny: Problems in delineating and evaluating phylogenetically relevant characters. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny, and fossils: Miocene hominoid evolution and adaptations*. Plenum Press, New York, pp 363–388
- Senut B, Gommery D (1997) Postcranial skeleton of *Otavipithecus*, Hominoidea, from the middle Miocene of Namibia. *Ann Paleontol* 83: 267–284
- Senut B, Pickford M, Gommery D, Kunimatsu Y (2000) Un nouveau genre d'hominioïde du Miocène inférieur d'Afrique orientale: *Ugandapithecus major* (Le Gros Clark & Leakey, 1950). *CR Acad Sci Paris Sci Terre planètes* 331: 227–233
- Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y (2001) First hominid from the Miocene (Lukeino formation, Kenya). *CR Acad Sci Sci Terre Planètes* 332: 137–144
- Sevim A, Begun DR, Güleç E, Geraads D, Pehlevan Ç (2001) A new late Miocene hominid from Turkey: *Am J Phys Anthropol* (Supl. 32) p 134–135
- Shea BT (1988) Phylogeny and skull form in the hominoid primates. In: Schwartz J (ed) *Orang-Utan biology*. Oxford University Press, New York, pp 233–245
- Singleton M (2000) The phylogenetic affinities of *Otavipithecus namibiensis*. *J Hum Evol* 38: 537–573
- Solounias N, Plavcan JM, Quade J, Witmer L (1999) The paleoecology of the Pliocene Biome and the Savanna myth. In: Agusti J, Rook L, Andrews P (eds) *The evolution of neogene terrestrial ecosystems in Europe*. Cambridge University Press, Cambridge, pp 436–453
- Spoor CF, Sondaar PY, Hussain ST (1991) A hominoid hamate and first metacarpal from the later Miocene Nagri formation of Pakistan. *J Hum Evol* 21: 413–424
- Stewart C-B, Disotell TR (1998) Primate evolution: In and out of Africa. *Curr Biol* 8: 582–588
- Susman RL (2004) *Oreopithecus bambolii*: An unlikely case of hominidlike grip capability in a Miocene ape. *J Hum Evol* 46: 105–117
- Teaford MF, Walker AC (1984) Quantitative differences in the dental microwear between primates with different diets and a comment on the presumed diet of *Sivapithecus*. *Am J Phys Anthropol* 64: 191–200
- Tekkaya I (1974) A new species of Tortonian anthropoids (primates, mammalia) from Anatolia. *Bull Min Res Explor Inst Turkey* 83: 1–11
- Tutin CEG, Fernandez M (1993) Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lope Reserve, Gabon. *Am J Primatol* 30: 195–211
- Tutin CEG, Ham R, White LJT, Harrison MJS (1997) The primate community of the Lopé Reserve in Gabon: Diets, responses to fruit scarcity, and effects on biomass. *Am J Primatol* 42: 1–24
- Ungar PS (1996) Dental microwear of European Miocene catarrhines: Evidence for diets and tooth use. *J Hum Evol* 31: 335–366
- Valen L van (1973) A new evolutionary law. *Evol Theory* 1: 1–30
- Villalta JF, Crusafont M (1944) Dos nuevos antropomorfos del Mioceno español y su situación dentro de la moderna sistemática de los simios. *Notas Commun Inst Geol Min* 13: 91–139
- Walker A (1997) *Proconsul*: Function and phylogeny. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid evolution and adaptations*. Plenum Publishing Co., New York, pp 209–224

- Walker A, Teaford MF, Martin LB, Andrews P (1993) A new species of *Proconsul* from the early Miocene of Rusinga/Mfangao Island, Kenya. *J Hum Evol* 25: 43–56
- Walker AC, Rose M (1968) Some hominoid vertebrae from the Miocene of Uganda. *Nature* 217: 980–981
- Ward CV (1993) Torso morphology and locomotion in *Proconsul nyanzae*. *Am J Phys Anthropol* 92: 291–328
- Ward CV (1997) Functional anatomy and phyletic implications of the hominoid trunk and hindlimb. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominoid evolution and adaptations*. Plenum Publishing Co., New York, pp 101–130
- Ward CV, Walker AC, Teaford MF (1991) *Proconsul* did not have a tail. *J Hum Evol* 21: 215–220
- Ward S (1997) The taxonomy and phylogenetic relationships of *Sivapithecus* revisited. In: Begun DR, Ward CV, Rose MD (eds) *Function, phylogeny and fossils: Miocene hominid origins and adaptations*. Plenum Press, New York, pp 269–290
- Ward S, Brown B (1986) The facial skeleton of *Sivapithecus indicus*. In: Swindler DR, Erwin J (eds) *Comparative primate biology*. Alan R. Liss, New York, pp 413–452
- Ward S, Brown B, Hill A, Kelley J, Downs W (1999) *Equatorius*: A new hominoid genus from the middle Miocene of Kenya. *Science* 285: 1382–1386
- Ward SC, Duren DL (2002) Middle and late Miocene African hominoids. In: Hartwig W (ed) *The primate fossil record*. Cambridge University Press. Cambridge, pp 385–397
- Ward SC, Kimbel WH (1983) Subnasal alveolar morphology and the systemic position of *Sivapithecus*. *Am J Phys Anthropol* 61: 157–171
- Ward SC, Pilbeam DR (1983) Maxillofacial morphology of Miocene Hominoids from Africa and Indo-Pakistan. In: Corruccini RL, Ciochon RS (eds) *New interpretations of ape and human ancestry*. Plenum Press, New York, pp 211–238
- Werdelin L (2003) Mio-Pliocene carnivora from Lothagam, Kenya. In: Leakey MG, Harris JM (eds) *Lothagam: The dawn of humanity in Eastern Africa*. Columbia University Press, New York, pp 261–328
- Wilson G, Barron J, Ashworth A, Askin R, Carter J, Curren M, Dalhuisen D, Friedmann E, Fyodorov-Davidov D, Gilichinsky D, Harper M, Harwood D, Hiemstra J, Janeczek T, Licht K, Ostroumov V, Powell R, Rivkina E, Rose S, Stroeven A, Stroeven P, Meer van der J, Wizevich M (2002) The mount feather diamicton of the sirius group: An accumulation of indicators of Neogene antarctic lacial and climatic history. *Palaeogeogr Palaeoclimatol Palaeoecol* 182: 117–131
- Winkler AJ (2002) Neogene paleobiogeography and East African paleoenvironments: Contributions from the Tugen Hills rodents and lagomorphs. *J Hum Evol* 42: 237–256
- Wu R (1987) A revision of the classification of the Lufeng great apes. *Acta Anthropol Sin* 6: 81–86
- Wunderlich RE, Walker A, Jungers WL (1999) Rethinking the positional repertoire of *Oreopithecus*. *Am J Phys Anthropol* 108: 528
- Xu Q, Lu Q, Pan Y, Zhang X, Zheng L (1978) Fossil mandible of the Lufeng *Ramapithecus*. *Kexue Tongbao* 9: 544–556
- Xu X, Delson E (1988) A new species of *Dryopithecus* from Gansu, China. *Kexue Tongbao* 33: 449–453
- Zhisheng A, Kutzbach JE, Prell WL, Porter SC (2001) Evolution of Asian monsoons and phased uplift of the Himalaya-Tibetan plateau since late Miocene times. *Nature* 411: 62–66