# Distribution and Biochronology of European and Southwest Asian Miocene Catarrhines

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European later Neogene primate distribution is reviewed here. Three families of primates are discussed: cercopithecids by Delson, pliopithecids and oreopithecine hominids by Harrison, and other hominids mainly by Andrews and Martin. The chronologic and biogeographic framework for all these groups was initially developed here by Bernor, with subsequent input from the other authors. The final result is a truly collaborative effort in which each author comments on the others' sections. The classification we adopt is described for each group, with notes explaining the rationale behind the taxonomic decisions, but this work is not intended to be a systematic revision of the groups. Accompanying this section is a summary table with a complete listing of the primate-bearing localities in Europe and Southwestern Asia, and the species identifications for each (together with a brief synonymy where relevant), arranged by country and geographic region. Primate distribution patterns are then discussed in the final section and some provisional palaeogeographic conclusions reached.

## Systematics

### Pliopithecidae

The pliopithecids are a conservative group of catarrhines that had a small to medium body size and that were geographically broadly distributed throughout Eurasia during the Miocene. The family is first recorded during the latest early Miocene (late Orleanean), and it continues well into the late Miocene in both Western and Central Europe (until the late Vallesian) and China (until the latest Miocene). Circumstantial evidence lends support to the claim that the pliopithecids originated in Africa, probably some time during the Oligocene, but no direct antecedents have yet been identified outside Eurasia from the

Paleogere or the early part of the Miocene (Harrison 1987a; Bernor et al. 1988a; Harrison et al. 1991). The pliopithecids are taxonomically diverse, and the family includes at least eleven species, which range geographically from Western Europe to Southern China. Nine of these species are confined to Western and Central Europe, where they comprise at least half of the known catarrhine species from these two biogeographical provinces (tables 12.1 and 12.7).

From comparisons of their dental morphology, pliopithecids appear to have been adapted to a range of dietary behaviors, with taxa inferred to be specialized folivores (i.e., *Anapithecus* and *Laccopithecus*), and others that were apparently more eclectic feeders, capable of exploiting a combination of soft fruits and young leaves (i.e., *Pliopithecus*). Although our knowledge of pliopithecid oro-facial and postcranial anatomy is limited, it is likely, given inferred differences in dietary behavior, their estimated range of body sizes, and their reconstructed ecological associations, that their spectrum of adaptive diversity was broad.

Although abundant and broadly distributed throughout Europe and Asia (being recorded from over forty different localities), pliopithecids are rarely found in association with large hominoids. The localities where they do co-occur include Rudabánya (Hungary), Lufeng (China), Epplesheim (Germany), Castell de Barberà (Spain), and Neudorf-Sandberg (Republic of Slovakia). The observed differences in pliopithecid and large hominoid distribution patterns may possibly reflect inadequate sampling, a conclusion supported to some extent by the fact that two of the sites where a co-occurrence has been established, Rudabánya and Lufeng, are among the most productive primate-bearing localities in Eurasia. However, this explanation seems unlikely in itself, given that pliopithecids and large hominoids co-occur in Europe at only 8.3% of the localities (5 of the 60) from which they are known (see table

12.7), and that some sites with good samples, such as Can Llobateres in Spain and Göriach in Austria, have only yielded the remains of *Dryopithecus* or *Pliopithecus*, respectively. A more likely explanation is that pliopithecids and large hominoids had somewhat different habitat preferences that allowed them only minimal geographical overlap under certain ecological conditions. However, until better data are available on the paleoecology of European Miocene localities, the nature of the ecological partitioning between pliopithecids and large hominoids cannot be resolved.

As mentioned above, the cranio-dental and postcranial anatomy of most pliopithecid species is relatively poorly known. Many of the species are represented by jaw fragments and isolated teeth only. An almost complete cranium of *Pliopithecus vindobonenis* is known from the Republic of Slovakia, and good cranial material of *Laccopithecus robustus* and *Pliopithecus zhanxiangi* has been recovered from sites in China (Zapfe 1958, 1961a; Wu and Pan 1984, 1985; Pan 1988; Harrison et al. 1991). In addition, several partial skeletons of *Pliopithecus vindobonensis* have provided valuable information on postcranial anatomy and its relevance for taxonomic and phylogenetic reconstructions (Zapfe 1958, 1961a; Simons and Fleagle 1973; Fleagle 1983; Harrison 1987a). However, postcranial remains of other species are extremely rare, being limited to a few isolated specimens belonging to *Pliopithecus antiquus*, *Anapithecus hernyaki*, and *Laccopithecus robustus* (Hürzeler 1954; Zapfe and Hürzeler 1957; Kretzoi 1975; Ginsburg and Mein 1980; Begun 1988; Meldrum and Pan 1988). Nevertheless, the available material is adequate to provide a reasonably good assessment of pliopithecid phylogenetic relationships, as well as a sound reevaluation of their alpha-taxonomy.

In the past, authors have argued that pliopithecids bear a close relationship to modern gibbons (Gervais 1849; Hofmann 1893; Hürzeler 1954; Zapfe 1961a; Simons 1972; Simons and Fleagle 1973), and this view has recently received additional support from studies of *Laccopithecus* from China (Wu and Pan 1985; Meldrum and Pan 1988; Fleagle 1988). However, a number of workers have presented a more convincing case that resemblances to hylobatids are due to similarity in overall size and the retention of plesiomorphous features (Remane 1965; Groves 1972, 1974; Delson and Andrews 1975; Ciochon and Corruccini 1977; Szalay and Delson 1979; Ginsburg and Mein 1980; Harrison 1982, 1987a).

It should be further noted that when the family-group name was originally proposed by Zapfe (1961a), the Pliopithecidae also included *Propliopithecus* from the Eo-Oligocene of Egypt. This taxonomic arrangement was widely accepted and expanded on by later workers (Remane 1965; Groves 1972, 1974; Delson and Andrews 1975; Ciochon
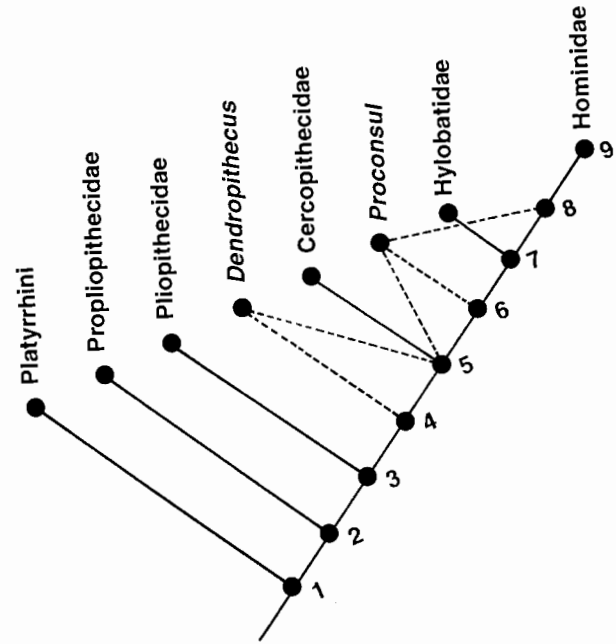


FIGURE 12.1 Cladogram showing the phylogenetic relationships of Pliopithecidae (adapted from Harrison 1987a). Broken lines indicate alternative interpretations of the phylogenetic position of *Dendropithecus* (nodes 4 and 5: Harrison 1982, 1987a) and *Proconsul* (node 5: Harrison 1982, 1987a; node 6: Andrews 1992; node 7: Walker and Teaford 1989).

and Corruccini 1977; Szalay and Delson 1979; Andrews 1980; Fleagle 1986). However, Harrison (1982; 1987a) has demonstrated that the Pliopithecidae, as traditionally conceived, is a paraphyletic group including a number of unrelated, morphologically conservative early catarrhine species. As a result, Harrison includes only Eurasian Miocene genera within the Pliopithecidae, while *Propliopithecus* (including *Aegyptopithecus*) is included in its own family, the Propliopithecidae Straus 1961. This view has received additional support from a number of recent workers (Andrews 1985; Delson 1988; Tattersall et al. 1988; Fleagle 1988), and the nomen Pliopithecidae is used here in this more restrictive sense. The inferred phylogenetic relationships of the Pliopithecidae are shown in figure 12.1.

Cranio-dentally pliopithecid morphology is generally consistent with the ancestral catarrhine morphotype, as inferred by Harrison (1982, 1987a). The partial crania of *Pliopithecus vindobonensis*, *Pliopithecus zhanxiangi*, and *Laccopithecus robustus* show that pliopithecids conform quite closely to the hypothesized ancestral pattern. The pliopithecids share the following key features of the cranium:

1. the face is relatively short and broad
2. the lower face is shallow, with a substantial overlap of

the orbits and nasal aperture in the dorso-ventral plane, and a low subnasal clivus
3. the palate is narrow, especially in the premaxillary region, and the upper toothrows converge anteriorly
4. the region of the incisive canal is represented by a pair of large elliptical openings, located close to the alveolar margin of the incisors, which allow a wide communication between the palate and the nasal fossa
5. the orbits are subcircular, frontally directed, and situated anteriorly over the premolars
6. the orbits have a slightly protruding inferior rim and supraorbital torus (it is uncertain whether this circumorbital rim represents a specialization of the pliopithecids or a feature retained from the primitive catarrhine morphotype)
7. the infraorbital foramen is usually single, and is located close to the inferior margin of the orbit
8. the interorbital region is relatively wide
9. the anterior root of the zygomatic arch originates low on the face, close to the maxillary alveolar margin, just above M1
10. the facial portion of the maxilla bears a distinct canine juga, at least in males, and a shallow canine fossa
11. the maxillary sinus is large, causing inflation of its lateral wall and invading the anterior root of the zygomatic arch, but not so extensively that it penetrates inferiorly between the roots of the cheek teeth
12. the complete postorbital plate retains a wide inferior orbital fissure, but no superior orbital fissure
13. the neurocranium is large in relation to the facial skeleton, and the well-marked temporal lines converge posteriorly, but do not meet to form a sagittal crest, even in males

The structure of the ectotympanic in *Pliopithecus vindobonensis* is critical for determining its phylogenetic status. The ectotympanic forms a short, partially enclosed bony tube, most resembling the condition in some juvenile individuals of extant catarrhine primates. In this respect, *Pliopithecus* is more derived than *Propliopithecus* from the Eo-Oligocene of Egypt, which has a platyrrhine-like annular ectotympanic but is less derived than all extant catarrhines, as well as fossil hominoids such as *Proconsul*, *Sivapithecus*, and *Oreopithecus*, which have a fully enclosed ectotympanic tube (Szalay and Delson 1979; Harrison 1987a). Unfortunately, the ear region of other pliopithecids is completely unknown, so it is uncertain whether this was a characteristic of the entire group. Nevertheless, it is reasonable to assume that *Pliopithecus'* ectotympanic morphology represents an intermediate step in the transformational series between the primitive anthropoid condition and the more derived pattern typical of modern catarrhines (fig. 12.1).

The pliopithecids are characterized by a number of dental specializations that distinguish the family as a monophyletic group. Pliopithecid autapomorphies include:

1. lower incisors are relatively slender and high-crowned (the height of the crown is at least twice that of the mesiodistal length)
2. lower central incisors are waisted toward the base of the crown, giving the tooth a distinctive flask-shaped outline when viewed from the buccal aspect (the lower incisors are broader and more spatulate in *Anapithecus*)
3. p3 is mesiodistally short and high-crowned, with a steeply inclined mesiobuccal honing face for occlusion with the upper canine
4. p4 and lower molars are relatively long and narrow
5. lower molars have a pliopithecine triangle on the talonid basin (except for *Pliopithecus vindobonensis*, which may be secondarily derived in this regard)
6. lower molars increase in size from m1 to m3, with a marked size differential between them
7. upper premolars and molars are relatively short and very broad
8. both M2 and M3 are considerably larger than M1

The postcranium of *Pliopithecus* is generalized and conforms closely to the proposed ancestral catarrhine morphotype (Harrison 1987a). However, in two significant aspects, it is more primitive than all extant catarrhines: the distal humerus is perforated by a large entepicondylar foramen (a feature lacking in all extant and fossil cercopithecids and hominoids, including the early catarrhines from the early Miocene of East Africa, but present in the propliopithecids from the Eo-Oligocene of Egypt); and there is a simple, hinge-like articulation in the carpo-metacarpal joint of the pollex (modern catarrhines have a specialized saddle joint that allows axial rotation of the thumb) (Napier 1961, 1962; Harrison 1987a).

The Pliopithecidae includes two distinct subfamilies, the Pliopithecinae and the Crouzeliinae (see below). The subdivision of the Pliopithecidae into two distinct clades was first proposed by Ginsburg and Mein (1980), who noted that the genus *Pliopithecus* could be distinguished from the other pliopithecids in the morphology of its lower molars. These differences, and additional characteristics used to separate the two subfamilies, are presented in table 12.2 (see also Harrison et al. 1991). The anterior dentition and the facial skeleton are poorly known for most species, especially the crouzeliines, so it is not certain whether consistent morphological differences exist between the subfamilies in these areas. Comparisons of the partial skull of *Laccopithecus* with those of *Pliopithecus* spp., indicate, however, that the cranial morphology of pliopithecids may, in general, be quite uniform. The upper and lower incisors in some of the pliopithecids do exhibit contrasting morphologies, but these appear to be species-specific differences, rather than differences that distinguish the pliopithecids at the subfamilial level. For example, *Laccopithecus robustus* has relatively small incisors, especially the upper central incisors, when compared with those in *Pliopithecus*

spp., while *Anapithecus* apparently has slightly broader, more spatulate lower incisors than other pliopithecids.

From comparisons of the upper dentition of *Laccopithecus robustus*, the only crouzeliine in which the upper molars have so far been described, and given the contrasting lower molar morphology in the two subfamilies, it is likely that the upper molars of crouzeliines differ from those of pliopithecines in the following respects: (1) the cusps are higher and more conical in shape, and are connected by sharper occlusal crests; (2) the trigon forms a larger component of the crown; (3) the distal basin is restricted to a narrow, slit-like fissure; and (4) the hypocone is separated by a deep groove from the trigon, rather than connected by a crest to the protocone, as in pliopithecines.

The dental differences between pliopithecines and crouzeliines presumably reflect a fundamental difference in their dietary behavior. Although the pliopithecids as a group were probably adapted to exploit a range of niches that were predominantly folivorous, the more elongated lower molar crowns of crouzeliines, with their more elevated cusps and relatively longer and sharper occlusal crests, imply that the subfamily may have exploited leaves and other soft fibrous plant materials more intensively than did the pliopithecines, which were probably somewhat more frugivorous. The crouzeliines probably occupied niches most comparable to those seen in some of the more frugivorous colobines, such as *Colobus satanas*, or *Alouatta*, which is strikingly similar to *Anapithecus* in molar morphology.

Harrison (1987a) has previously suggested that crouzeliine dentitions appear to be more conservative than those of *Pliopithecus* in retaining several features of the lower molars characteristic of the ancestral anthropoid morphotype. For example, the long, narrow crowns, the high and sharp occlusal crests and cusps, the relatively elongated mesial foveae, the small size of the hypoconulids, the long and obliquely aligned crista obliquae, and the absence (in some species) of true distal foveae in the lower molars of crouzeliines represent a complex of features that are usually interpreted as being more primitive than the morphological pattern typical of pliopithecines. This view is still maintained by Andrews and Martin, but Harrison is now more inclined to accept the alternative explanation that the crouzeliine molar morphology is a derived pattern, associated with more specialized dietary behaviors, that has in some respects secondarily converged on the ancestral anthropoid morphotype.

## PLIOPITHECINAE

The subfamily Pliopithecinae includes five species (tab. 12.1). The species are morphologically similar, and all of them can be assigned readily to a single genus, *Pliopithecus*. The species of *Pliopithecus* can be distinguished from each other by a combination of dental morphological

TABLE 12.1 *Classification of the European Pliopithecidae*

Pliopithecoidea
  Pliopithecidae
    Pliopithecinae
      *Pliopithecus antiquus* (Blainville 1839)
        (including *P. piveteaui* Hürzeler 1954)
      *Pliopithecus platyodon* Biederman 1863
      *Pliopithecus vindobonensis* Zapfe and Hürzeler 1957
      *Pliopithecus priensis* Welcomme et al. 1991
    Crouzeliinae
      *Plesiopliopithecus lockeri* Zapfe 1961
      *Plesiopliopithecus auscitanensis* (Ginsburg 1975)
        ( = *Crouzelia auscitanensis* Ginsburg 1975)
      *Plesiopliopithecus rhodanica* (Ginsburg and Mein 1980)
        ( = *Crouzelia rhodanica* Ginsburg and Mein 1980)
      *Anapithecus hernyaki* Kretzoi 1975
        Nov gen. et nov. sp. Moyà-Solà, in prep.
  Indeterminate
    "*Semnopithecus*" *eppelsheimensis* Haupt 1935

differences and overall size. Four of the species, *Pliopithecus antiquus*, *Pliopithecus vindobonensis*, *Pliopithecus platyodon*, and *Pliopithecus priensis*, are known from European sites and will be dealt with in detail below. The fifth species, *Pliopithecus zhanxiangi*, recently described by Harrison et al. (1991), is known from middle Miocene (early Tungurian, correlative with the early Astaracian, MN 6) localities in Northern China. Further discussion of this latter taxon is outside the scope of this present review.

*Pliopithecus antiquus*    *Pliopithecus antiquus*, the type species of the genus, was the first extinct non-cercopithecid catarrhine to be described (Blainville 1839). The type specimen, from Sansan (MN 6), France, consists of a mandible with complete lower dentition (Blainville 1839; Gervais 1849; Hürzeler 1954; Bergounioux and Crouzel 1965; Simons 1972; Szalay and Delson 1979). The species is known primarily from localities in France, but several isolated specimens referable to this species have been recovered from similar age localities in Switzerland (Stein am Rhein, MN 6) and Germany (Stätzling, Ziemetshausen, and Gallenboch, MN 6; see Heissig 1987). A well-preserved lower jaw fragment with m1–3 from La Grive-Saint-Alban (possibly from the Peyre et Beau quarry) is clearly referable to this species. The specimen was first described by Depéret (1887) as *Pliopithecus antiquus*, race *chantrei*, and later recognized as a distinct subspecies, *Pliopithecus antiquus chantrei*, by Ginsburg (1986), purportedly characterized as having a somewhat reduced m3. The molars, however, are remarkably similar in size and morphology to those of the type specimen from Sansan, differing in a few minor details. The size difference between m2 and m3 is insignificant given the range of variation seen in modern catarrhine species.

The slightly older material from the Faluns de Touraine, Anjou, Pontlevoy-Thenay, and Manthelan in the Loire Valley of France (all correlated with MN 5), was previously attributed to a different species, *Pliopithecus*

*piveteaui* (Hürzeler 1954; Ginsburg 1964, 1975, 1986; Collier 1978, 1979; Szalay and Delson 1979; Ginsburg and Mein 1980). However, the major purported distinction, the smaller relative size of m3 in the Loire Valley sample, is not supported by more recent discoveries. The type specimen, a mandibular fragment of an immature individual with m2 in occlusion and m3 partially erupted, from the locality of Manthelan, is certainly unusual for a pliopithecid in having an m3 smaller in size than m2: the occlusal area of m3 is only 89.4% of that of m2, while in all other pliopithecids it ranges from 101.1% to 127.8%. However, several factors indicate that this difference may be explained as the result of normal pliopithecid intraspecific variation. Firstly, unlike the Göriach sample, which formerly comprised most of the *Pliopithecus antiquus* hypodigm, and in which m3 is substantially larger than m2 (the occlusal area of m3 is 114.8% of m2 on average), the two specimens with m2–3 from Sansan, the type locality for *Pliopithecus antiquus*, have a much smaller discrepancy in size between m2 and m3 (the occlusal area of m3 is 107.8% of m2 in Sansan I and can be reliably estimated to be only 104.3% in Sansan II). Secondly, other species of pliopithecids, including those in which only small samples are available for study, exhibit quite wide ranges of variation in relative m3 size (e.g., *Pliopithecus vindobonensis*, 101.1–127.7%; *Pliopithecus platyodon*, 109.3–127.8%; *Laccopithecus robustus*, 103.2–118.0%). Thirdly, the range of variation in extant catarrhine relative m3 size is great, and more than adequate to encompass the range of variation exhibited by the Sansan sample and the Manthelan specimen. Finally, a number of isolated m3s from the Loire Valley, previously attributed to *Pliopithecus piveteaui*, are as large or even larger than m3 in the type specimen of *Pliopithecus antiquus*, and from this evidence it would seem that m3 reduction in the Manthelan specimen is an isolated case, not typical of the Loire Valley sample as a whole (see figure 4 in Ginsburg and Mein 1980 for a graphic illustration of this point). As a consequence, *Pliopithecus piveteaui* is considered to be insufficiently distinct to merit the recognition of a separate taxon and is included as a junior synonym of *Pliopithecus antiquus* (Harrison 1991a; see also Bergounioux and Crouzel 1965).

A number of additional specimens from France (Meigné-le-Vicomte and Doué-la-Fontaine, MN 9), Spain (Castell de Barberà, MN 9), Switzerland (Kreuzlingen and Rümikon, MN 6), Germany (Diessen am Ammersee, MN 6), and Poland (Opole, MN 7, and Przeworno II, MN 8) can be assigned tentatively to *Pliopithecus antiquus* (Hürzeler 1954; Kowalski and Zapfe 1974; Crusafont-Pairo 1978; Ginsburg 1986, 1989). If these identifications are confirmed, they would greatly extend the species geographic and temporal range. Most of the specimens consist of isolated teeth that are difficult to assign with any degree of taxonomic certainty, although they appear to be mor-

phologically and metrically consistent with *Pliopithecus antiquus*.

The best of the late material referred to this taxon originates from Castell de Barberà, which is considerably younger in age than that from the type locality (Crusafont-Pairo 1978; Crusafont-Pairo and Golpe-Posse 1981). At least two individuals are represented. One individual consists of an associated series of isolated teeth, comprising upper and lower partial toothrows of a subadult female. The second individual is represented by an isolated right p3. The specimens are similar to material from France attributed to *Pliopithecus antiquus*. The minor morphological differences and slightly smaller size of the Castell de Barberà material, when compared with the type specimen from Sansan (a male individual), are easily interpreted as the result of sexual dimorphism. It is worthwhile noting, in this regard, that the lower check teeth from Castell de Barberà are closest in size to the dentition in the smaller mandibular fragment from Sansan, which may have belonged to a female individual of *Pliopithecus antiquus*. Nevertheless, the lower molars from Castell de Barberà are relatively narrower than those assigned to *Pliopithecus antiquus* from France, and this feature may later prove to be of some taxonomic significance. However, given the overall similarity in general size and morphology of the material, and the small samples available, it seems best to include the Castell de Barberà specimens in *Pliopithecus antiquus*, and to regard the minor differences as due to intraspecific variation.

Ginsburg (1989) has described a right mandibular fragment preserving a portion of m1 and the well-preserved crowns of m2–3 from Meigné-le-Vicomte, France (MN 9), which he has assigned to *Pliopithecus antiquus*. In addition, a number of *Pliopithecus* isolated teeth have been recovered from Doué-la-Fontaine, a locality of similar age to Meigné-le-Vicomte (Ginsburg 1986, 1989, 1990). These specimens are morphologically and metrically very similar to *Pliopithecus antiquus* from Sansan, and they may thus provide further evidence that the species extended its temporal range from the early Astaracian (MN 5) to the early Vallesian (MN 9).

*Pliopithecus vindobonensis*    The type specimen of *Pliopithecus vindobonensis* is from Neudorf-Spalte in the Slovakian Republic (MN 6). It is the best-known pliopithecid species, being represented at the type locality by three partial skeletons, in addition to some isolated bones of other individuals (Zapfe and Hürzeler 1957; Zapfe 1958, 1961a). *Pliopithecus vindobonensis* is slightly larger than the type species but comparable in size to *Pliopithecus platyodon*. It is distinguished morphologically from both of these species in the following respects: (1) the lower incisors are relatively higher-crowned; (2) the upper central incisor has a notched lingual cingulum and is relatively

broad; (3) the p4 and lower molars tend to be slightly narrower; (4) the pliopithecine triangle on the lower molars is absent or indistinct; (5) the upper molars are slightly broader, with a relatively smaller trigon basin and a less well developed buccal cingulum; and (6) the size differential between the teeth in the upper and/or lower molar series is greater.

In their initial description of *Pliopithecus vindobonensis*, Zapfe and Hürzeler (1957) referred all the material in a new subgenus, *Pliopithecus* (*Epipliopithecus*). However, Zapfe (1958, 1961a) expressed justified reservations about its level of distinctiveness, and most subsequent authors have tended to abandon the use of a separate subgeneric rank for the taxon (Szalay and Delson 1979; Ginsburg and Mein 1980; Harrison et al. 1991).

*Pliopithecus platyodon*    The extensive collections of *Pliopithecus* from Göriach, Austria (MN 6) were referred to *Pliopithecus* cf. *antiquus* by Hürzeler (1954). However, these specimens differ from *Pliopithecus antiquus* in their significantly larger size, broader p3, slightly narrower and more rectangular lower molars, and greater size increase from m1 to m3. Although the Göriach specimens are similar in overall size to *Pliopithecus vindobonensis*, they differ in the following characters:

1. upper and lower incisors are lower-crowned
2. I1 has a continuous lingual cingulum without a distinct notch
3. upper premolars are broader
4. p3 is relatively broader with subequal mesial and distal crests
5. the upper molars are somewhat narrower, with better development of the buccal cingulum and a relatively larger trigon
6. P4 has a better-developed lingual cingulum
7. lower molars tend to be slightly broader, with a well-developed pliopithecine triangle.

It is evident from these comparisons that the Göriach sample should be assigned to a separate species of *Pliopithecus*. Sera (1917) referred the Göriach material to a separate species, *Pliopithecus goeriachensis*. However, as noted earlier by Hürzeler (1954), the Göriach sample is very similar in morphology to a crushed palate from Elgg (Switzerland; MN 5), the type specimen of *Pliopithecus platyodon* Biedermann 1863. As a consequence, *Pliopithecus platyodon* has been resurrected as the valid name for the Göriach and Elgg samples, and *Pliopithecus goeriachensis* is considered a junior synonym (Harrison 1991a; Harrison et al. 1991).

*Pliopithecus priensis*    Welcomme et al. (1991) recently described a new pliopithecid species, *Pliopithecus priensis*, from Priay II, France (upper MN 9) The type specimen is a right mandibular fragment with m1–2. Based on the published illustration of m1, the specimen appears to have its closest affinities with the pliopithecines and is probably referable to the genus *Pliopithecus*. The species is somewhat larger than the other pliopithecines from Europe but is comparable in its size to the early middle Miocene taxon *Pliopithecus zhanxiangi* from Tongxin, China (MN 6). However, it differs from the latter in having relatively more elongated lower molars and a less pronounced size differential between m1 and m2. Additional material will be needed before the precise affinities of *Pliopithecus priensis* can be established with confidence.

*Neudorf-Sandberg*    An isolated right m3 of a pliopithecid was recovered from Neudorf-Sandberg in the Slovakian Republic (MN 6) at the end of the last century. It has usually been regarded as belonging to *Pliopithecus antiquus* (Glaessner 1931; Pia and Sickenberg 1934; Hürzeler 1954; Zapfe 1961a, 1969; Szalay and Delson 1979). The specimen can be readily identified as belonging to *Pliopithecus*, but its allocation to a particular species is uncertain (see also Hürzeler 1954).

CROUZELIINAE

Compared with the pliopithecines, the crouzeliines are taxonomically more diverse. The European representatives of the subfamily comprise at least six species, belonging to three or four different genera (tab. 12.1); as noted above, the differences between crouzeliines and pliopithecines are summarized in table 12.2. In addition to these species, a late surviving crouzeliine, *Laccopithecus robustus*, is known from the late Miocene of China. The three species of *Plesiopliopithecus* are the earliest recorded crouzeliines in Eurasia, being known from sites in France and Austria correlated with MN 6 and MN 7. *Anapithecus*, a larger and more specialized crouzeliine from Hungary, and possibly also Austria, occurs later in time (late MN 9; ca. 10–9.5 Ma; Bernor et al., this volume). A pliopithecid from Terrassa in Spain (MN 10) probably belongs to an additional, as yet unnamed, genus of crouzeliine.

*Plesiopliopithecus lockeri*    The holotype of *Plesiopliopithecus lockeri*, a left mandibular fragment with p3–m1, and associated i1 and i2, was recovered from Trimmelkam, Austria (MN 6), in 1959. The block of lignite that originally contained the jaw fragment also preserves the impression of a lower canine, just anterior to p3. From the size of the canine one can be fairly certain that the holotype represents a male individual. This is the only known specimen belonging to the species. The species was first described by Zapfe (1961b) as belonging to the genus *Pliopithecus*, but on the basis of its distinctive premolar and molar morphology he established a new subgenus, *Plesiopliopithecus*. The distinctiveness of the species has

TABLE 12.2 *Differences in the Lower Molars That Distinguish the Pliopithecinae from the Crouzeliinae*

|  | Pliopithecinae | Crouzeliinae |
|---|---|---|
| $M_{1-2}$ | Crown more or less rectangular | Crown narrows mesially in $M_1$ |
|  | No buccolingual waisting | Buccolingual waisting |
|  | Mesial fovea short and broad | Mesial fovea elongated |
|  | Mesial transverse crest slightly oblique | Mesial transverse crest strongly oblique |
|  | Trigonid slightly more elevated than talonid | Trigonid more markedly elevated than talonid |
|  | Cristid obliqua short and more or less mesially directed | Cristid obliqua long and obliquely directed |
|  | Crown moderately long and narrow; breadth-length index of $M_1$ ($\bar{X}$ = 85.8; Range = 78.3–96.8; N = 23) and $M_2$ ($\bar{X}$ = 87.9; Range = 77.3–97.1; N = 20) | Crown very long and narrow; breadth-length index of $M_1$ ($\bar{X}$ = 77.5; Range = 72.3–81.2; N = 8) and $M_2$ ($\bar{X}$ = 77.3; Range = 72.2–81.4; N = 5) |
|  | Hypoconulid large | Hypoconulid reduced in size |
|  | Hypoconulid situated bucally to the midline of the crown | Hypoconulid situated in the midline or slightly lingually to the midline of the crown |
|  | Distal fovea moderately large and well defined | Distal fovea restricted in size (and poorly defined in *Plesiopliopithecus*) |
| $M_3$ | Mesial fovea transversely aligned | Mesial fovea slightly obliquely aligned |
|  | Buccal cusps tend to be arranged almost in a line | Hypoconulid more linqually placed than the protoconid and hypoconid |
| Lower molars | Cusps tend to be low and rounded and voluminous | Cusps tend to be high, conical, and well spaced |

been confirmed by subsequent workers who generally prefer to recognize *Plesiopliopithecus* as a separate genus (Ginsburg and Mein 1980; Ginsburg 1986; Harrison 1987a, 1991a; Harrison et al. 1991).

*Plesiopliopithecus auscitanensis*   A second species of pliopithecid was discovered at Sansan, France (MN 6), during the early 1960s. The type specimen, a mandibular fragment with p4–m2, is the only known specimen assigned to this species. Begounioux and Crouzel (1964, 1965) described the specimen in some detail, and noted a number of distinct differences that separate it from the type specimen of *Pliopithecus antiquus*, including the small size of the teeth, the elongated lower molars with very small hypoconulids, open distal foveae, and a reduced buccal cingula. Bergounioux and Crouzel (1964, 1965) regarded these differences as being of only intraspecific significance, referring the specimen to a new "variety," *Pliopithecus antiquus*, var. *auscitanensis*. Ginsburg (1975) included the specimen in a new genus, *Crouzelia*, and at the same time made the species name *auscitanensis* available (names proposed for varieties or races are unavailable under the provisions of the International Code of Zoological Nomenclature). However, the dentition is very similar in size and morphology to the crouzeliine pliopithecid from Trimmelkamm, and their inclusion in a single genus, *Plesiopliopithecus*, seems justified. With the recovery of further material, they may even prove to be conspecific. The minor differences between the two known specimens provide sufficient justification to recognize two different species. For example, the m1 of *Plesiopliopithecus auscitanensis* can be distinguished from that of *Plesiopliopithecus lockeri* in be-

ing slightly relatively shorter, in having a less well-developed buccal cingulum, and in having a well-defined distal fovea set off from the talonid basin by a distinct crest linking the hypoconulid to the entoconid.

Collier (1978) has described a few isolated teeth from Liet, France (MN 6), which he has referred to *Crouzelia auscitanensis*, as well as to *Pliopithecus antiquus*. Ginsburg and Mein (1980) contend, however, that all of the Liet teeth are referable to *Pliopithecus antiquus*, and this assessment is followed here. Although the placement of this species in *Plesiopliopithecus* results in synonymizing the genus *Crouzelia* within it, the family group taxon based on that genus retains its original name because the type genus was available at the time Crouzeliinae was named by Ginsburg and Mein (1981).

*Plesiopliopithecus rhodanica*   Ginsburg and Mein (1980) named a second species of *Crouzelia*, *C. rhodanica*, based on an isolated lower molar germ from La Grive-Saint-Alban (Fissure L7), France (MN 7). The presence of a well-defined pliopithecine triangle in the talonid basin and posterior crown narrowing suggests that the tooth is an m2 rather than an m1. It differs from the m2 in *Plesiopliopithecus auscitanensis* in being considerably smaller in size (the *P. auscitanensis* m2 has an occlusal area that is 38.7% larger than that of the La Grive specimen), the crown is relatively narrower (the breadth-length index is 75.0 in the m2 from La Grive, and 79.7 in that from Sansan), the mesial fovea is relatively shorter, and the hypoconulid is reduced to only a vestige. The La Grive specimen is possibly a small individual or an unusual m1 of *Plesiopliopithecus auscitanensis*, but until additional material is avail-

able, the La Grive specimen is distinctive enough to be retained as a separate species within the genus *Plesiopliopithecus*.

*Anapithecus hernyaki* *Anapithecus hernyaki* is represented by an extensive series of cranio-dental specimens and some isolated postcranials. It is the best-known crouzeliine from Europe (Kretzoi 1975; Begun 1988). The species is known principally from Rudabánya, although some specimens recently recovered from Götzendorf, Austria (MN 9/10, ca. 9.5 Ma; Zapfe 1992; Bernor et al. 1993; Rögl et al. 1993), may also prove to be referable to *Anapithecus hernyaki* (Andrews and Bernor, personal observation). Although *Anapithecus* was originally described as a subgenus of *Pliopithecus* by Kretzoi (1975), its relatively large size and distinctive dental features allow the recognition of a separate genus (Ginsburg and Mein 1980; Kretzoi 1984; Harrison 1987a, 1991a; Harrison et al. 1991).

*Anapithecus* is the largest crouzeliine, having an average lower molar occlusal area 10% larger than that of *Laccopithecus*, 34% larger than that of the Terrassa crouzeliine, and 85%, 89%, and 122% larger than that of *Plesiopliopithecus lockeri*, *Plesiopliopithecus auscitanensis*, and *Plesiopliopithecus rhodanica*, respectively. In fact, *Pliopithecus zhanxiangi* from China is the only pliopithecid larger than *Anapithecus* in dental size (the occlusal areas of its lower molars are on average about 8% larger than those of *Anapithecus*).

*Anapithecus hernyaki* can be distinguished from the Terrassa crouzeliine in having broader and much more

molariform premolars, and relatively broader molars with a more elongated trigonid, a better-defined pliopithecine triangle, a hypoconulid that is more centrally placed, and a smaller, less-distinct distal fovea. It differs from *Laccopithecus* in having a broader p3, with a much more strongly developed metaconid, a broader p4 with a relatively longer talonid basin, and narrower lower molars, with a more distinct buccal cingulum, less pronounced buccolingual waisting of the crown, a more distally positioned hypoconulid, and a correspondingly more obliquely oriented distal fovea. *Anapithecus* can be distinguished from *Plesiopliopithecus* in having a broader p3 with a much more pronounced development of the metaconid, a more molariform p4 with a relatively longer talonid basin and a well-developed pair of distal stylids, and lower molars with a less well-developed buccal cingulum and a hypoconulid located closer to the midline. Table 12.3 summarizes some of the key features that serve to distinguish the different crouzeliine species.

*Terrassa* Three jaw fragments from "Torrent de Febulines" near Terrassa, northern Spain (MN 10), apparently belonging to a previously undescribed genus and species of crouzeliine, represent the latest occurrence of pliopithecids in Europe (Golpe-Posse 1982; Moyà-Solà, in prep.). The material includes associated mandibular fragments with right p3–m3 and left p3–m2, a right maxillary fragment with P3, and a symphyseal fragment of a subadult female individual, with right and left canines exposed in their crypts and the roots of left i1–2 and right p3–4. The

TABLE 12.3 *Some Key Features of the Lower Dentition That Distinguish the Different Species of the Crouzeliinae*

| | Nov. gen. et sp. (Terrassa) | Ples. lockeri (Trimmelkamm) | Ples. auscitan. (Sansan) | Ples. rhodanica (La Grive) | Anapithecus (Rudabánya) | Laccopithecus (Lufeng) |
|---|---|---|---|---|---|---|
| Size of $P_3$ metaconid | Prominent | Small tubercle | — | — | Prominent | Prominent |
| Length of $P_4$ talonid | Talonid much longer than trigonid | Talonid somewhat longer than trigonid | Talonid and trigonid subequal | — | Talonid much longer than trigonid | Talonid somewhat longer than trigonid |
| Development of distal stylids on $P_4$ | Prominent | Small | Small | — | Prominent | Prominent |
| Length-breadth proportions of lower molars* | $M_1$: 81.2 $M_2$: 72.2 $M_3$: 62.1 | $M_1$: 78.3 — — | $M_1$: 78.0 $M_2$: 79.7 — | — $M_2$: 75.0 — | $M_1$: 77.6 $M_2$: 79.9 $M_3$: 69.8 | $M_1$: 86.0 $M_2$: 83.6 $M_3$: 72.6 |
| Trigonid length of lower molars | Short | Quite short | Long | Long | Long | Long |
| Development of pliopithecine triangle | Indistinct or absent | Well developed | Well developed | Well developed | Vestigial to well developed | Indistinct or absent |
| Development of buccal cingulum on lower molars | Moderately well developed | Well developed | Well developed | Well developed | Moderately well developed | Poorly developed |
| Size and position of hypoconulid | Small, buccally placed | Small, buccally placed | Very small, buccally placed | Vestigial, buccally placed | Small, midline | Small, close to midline |
| Structure of distal fovea | Small, well defined | Small, well defined | Communicates directly with talonid basin | Communicates directly with talonid basin | Very small, well defined | Very small, well defined |

*The indices given for *Anapithecus* and *Laccopithecus* are mean values.

p3 is relatively short, quite high-crowned, with a steep honing face for occlusion with the upper canine. One interesting feature of p3 is that the metaconid is quite prominent, being linked to the protoconid by a sharp, obliquely oriented crest. The p3 is small in relation to p4. The p4 is a long narrow molariform tooth, in which the talonid basin is almost twice as long as the trigonid and the distal margin bears a pair of distinct stylids. The m1 and m2 are long and narrow, and exhibit the following morphological characteristics: a small mesial fovea, with an oblique transverse crest linking the protoconid and metaconid; an elongated talonid basin, with no indication of a pliopithecine triangle (but possibly obliterated by wear); a small, buccally placed hypoconulid; a narrow but distinct distal fovea on m1–2; a narrow ledge-like buccal cingulum mesially and distally. The m3 is much longer than the m2, but slightly narrower. It has broad, almost transversely aligned mesial fovea. The talonid basin is very elongated, and there is a small pit beside the protoconid and hypoconid that may represent a worn trace of the pliopithecine triangle. The hypoconulid is quite small, but distinct and well-developed, and it is situated more or less in line with the protoconid and hypoconid. The distal fovea forms a large heel, which is partially filled by a tuberculum sextum.

The molar morphology confirms that the Terrassa material is referable to the Crouzeliinae, while the size and distinctive characteristics of its teeth provide adequate justification for the recognition of a new species, and probably also a separate genus (Moyà-Solà, pers. comm.; in prep.). In terms of its overall size, the Spanish material is somewhat larger than *Plesiopliopithecus lockeri*, *Plesiopliopithecus auscitanensis*, and *Plesiopliopithecus rhodanica*, but is slightly smaller than *A. hernyaki* and *L. robustus*. Morphologically, it can be distinguished from all other crouzeliines by its unique combination of features of the lower premolar and molar characters (see tab. 12.3). It is interesting that the Terrassa specimens share with *Anapithecus* and *Laccopithecus* the possession of more molariform lower premolars, which includes a combination of a well-developed p3 metaconid, and an elongated talonid with well-developed p4 distal stylids. Because this character complex is not found in the crouzeliine *Plesiopliopithecus*, it could be used as a synapomorphy to support a close relationship between *Anapithecus*, *Laccopithecus*, and the Terrassa species. However, it seems more likely that these shared traits are independently derived, reflecting similar dietary specialization and their larger size. This conclusion is supported by the fact that parallel developments can also be recognized among the pliopithecines.

*Can Feliu*    In addition to the Terrassa material, an isolated dp4 of a medium-sized crouzeliine has been recovered from Can Feliu, Spain (MN 8). Although the specimen is older than the Terrassa material, it is concordant in size and form, and may belong to the same species. However, until adequate comparative material is available, it is probably best to refer this specimen to Crouzeliinae gen. and sp. indet.

*Pliopithecidae from Eppelsheim and Salmendingen*    An isolated pliopithecid upper male canine was collected from Eppelsheim, Germany (MN 9; >10 Ma; Bernor et al. 1993; Swisher, this volume; Woodburne et al., this volume). It was initially identified as being a cercopithecid and named *Semnopithecus eppelsheimensis* (Haupt 1935). It was later identified as a pliopithecid by Hürzeler (1954). Koenigswald (1956) argued that the canine should be included, along with the contemporary small dryopithecine material from Wissberg in Germany, in a new genus *Rhenopithecus*. Szalay and Delson (1979) also argued for its dryopithecine affinities, preferring, however, to assign the specimen to *Dryopithecus brancoi*. More recently, Begun (1989) has once again reaffirmed the pliopithecid affinities of the Eppelsheim canine.

Further comparisons establish that the canine is certainly referable to the Pliopithecidae. However, male pliopithecid upper canines are generally similar in morphology, making any attempt to assess their alpha-taxonomic affinities very difficult. The specimen is somewhat larger than male canines of *Pliopithecus vindobonensis*, and comparable in size to those of *Pliopithecus platyodon*, *Laccopithecus robustus*, and *Anapithecus hernyaki*. Given the close correspondence in age, and the Central European location of both Rudabánya and Eppelsheim, the similarity in size and morphology of the Eppelsheim canine to that of *Anapithecus* may be significant. Pertinent here is the fact that *Rhenopithecus eppelsheimensis* (Haupt 1935; von Koenigswald 1956) has priority over *Anapithecus hernyaki* (Kretzoi 1975).

Begun (1989; 1992b) has further suggested that the femur from Eppelsheim, originally described as *Paidopithex rhenanus* Pohlig 1895, and most commonly attributed to *Dryopithecus*, should also be identified as a pliopithecid. The reasoning behind this claim can be briefly summarized as follows:

1. one of the lower teeth from Salmendingen, Germany (probably MN 11), identified as a dryopithecine dp4 by most previous workers (Branco 1897; Schlosser 1901, 1902; Abel 1902; Simons and Pilbeam 1965), has been misidentified, and is really an m1 of a large-bodied crouzeliine, tentatively identified as an m1 of *Anapithecus* cf. *hernyaki* (Begun 1989)
2. this attribution is supported by the fact that the tooth co-occurs at Salmendingen with a dryopithecine, *Dryopithecus brancoi*, that is very similar to the large hominoid that co-occurs with *Anapithecus* at Rudabánya

3. the supposed crouzcliine molar corresponds in size with the *Paidopithex* femur, which is also derived from a late Miocene site in close geographical proximity to Salmendingen

4. the femur shares a number of morphological and morphometric similarities to the femora of *Pliopithecus vindobonensis* from the Republic of Slovakia

5. the referral of the isolated upper canine from Eppelsheim to the Pliopithecidae, the only other fossil catarrhine from the site, strengthens the case that the *Paidopithex* femur is also a pliopithecid.

Begun's (1989) referral of this material to the Pliopithecidae is intriguing, and requires careful consideration. After all, the correct taxonomic placement of the Eppelsheim femur has implications for determining the appropriate nomenclature for several species of Central European catarrhine. For example, the prior name *Paidopithex rhenanus* Pohlig 1895 could enter into synonymy with either *Anapithecus hernyaki* Kretzoi 1975 or *Dryopithecus brancoi* (Schlosser 1901). However, in Harrison's view (1991b), there are good reasons to accept the earlier suggestion that the Salmendingen tooth is a dp4, rather than an m1, in which case it would fit metrically and morphologically with the dryopithecine material already known from the site (but see below). If this is the case, then Begun's attempt to show that the tooth is consistent in size with the Eppelsheim femur has little relevance for deciding on the pliopithecid affinities of the latter. The tooth is consistent in size with the femur, so they both may belong to a dryopithecine. Moreover, if we exclude the possibility that the Salmendingen tooth belongs to an undescribed species of pliopithecid, which is larger than all other known pliopithecids, then the *Paidopithex* femur is much too large to be attributed to *Anapithecus hernyaki* or to the species represented by the pliopithecid canine from Eppelsheim. On the available evidence, it seems most reasonable to assume that the Eppelsheim femur belongs to a dryopithecine, rather than a pliopithecid. And even if this Salmendingen tooth is an *Anapithecus hernyaki* permanent molar, this says nothing about the identification of the Eppelsheim femur.

There is another problematic specimen from Salmendingen, an isolated m3. It was originally named *Anthropodus brancoi* Schlosser 1901 and then *Neopithecus brancoi* (Abel 1902). It was then referred to *Dryopithecus rhenanus* by Remane (1921) before being transfered to *Dryopithecus* as *D. brancoi* by Abel (1931). It was reassigned to *Pliopithecus* by Hürzeler (1954) and then transfered back to *Dryopithecus* by Szalay and Delson (1979). Despite the fragmentary nature of the type specimen, Szalay and Delson (1979) referred this species to the Spanish MN 8–10 hominoids originally described as *Hispanopithecus laietanus* Villalta and Crusafont 1944 and "*Rahonapithecus sabadel-*

*lensis*" Crusafont and Hurzeler 1961. Begun (1992c) removed all the Spanish material from *brancoi* and used the name instead for the dryopithecine collection from Rudabánya. New material from Götzendorf and Mariathal assigned to *Dryopithecus brancoi* (Thenius 1982; Zapfe 1989) further complicates the matter because at least some of it is clearly pliopithecid and may come to be grouped with *Anapithecus hernyaki* (Zapfe, pers. comm.). In our view, the Salmendingen m3 cannot be attributed with certainty to either pliopithecids or dryopithecines, and our solution to this is to leave aside the type specimen of *brancoi* as incertae sedis and not apply to it the name for any primate group.

## Hominidae

An African origin can be postulated for the Hominidae, which is used here sensu Goodman (1963, 1974) and Andrews (1985, 1992) to include all the great apes and humans (Delson and Andrews [1975] and Szalay and Delson [1979] had included gibbons as well). Early Miocene records for pre-hominid fossils are restricted to Africa, and the earliest known hominoids are from the late Oligocene locality of Lothidok (Eragaleit Beds), Kenya, dated 27.5 to 24.0 Ma (Boschetto et al. 1992). Additionally, the first hominids are also known from Africa with the appearance of the Afropithecini. The earliest hominoid record outside Africa is in Turkey and the Vienna Basin, with the basal MN 6 appearance of the kenyapithecin *Griphopithecus* (ca. 15 Ma; Bernor and Tobien 1990).

The family Hominidae is divided into four subfamilies. The earliest-known members of the family are provisionally included in the Dryopithecinae, which is a paraphyletic group encompassing three tribes (Andrews 1992): the Afropithecini, the Kenyapithecini, and the Dryopithecini. The Afropithecini are restricted to Afro-Arabia. The other subfamilies of the Hominidae are the Ponginae for the orang utan clade, Oreopithecinae for the late Miocene hominoid from Italy, and Homininae for the African ape-human clade. All three of these subfamilies are represented in the European and Southwest Asian Miocene. Their relationships with each other, and with possible ancestral populations of fossil apes, are far from clear at present, and the three subfamilies will therefore be presented here as separate entities (tab. 12.4).

The earliest known tribe of the Dryopithecinae is the Afropithecini. This tribe includes *Afropithecus, Heliopithecus,* and some of the fossils previously attributed to *Kenyapithecus* (for example the samples from Maboko Island and Nachola in Kenya; Andrews 1992). It is possible that the Moroto sample (Pilbeam 1969) and *Otavipithecus* (Conroy et al. 1992) are also referable to this tribe, giving it a geographic distribution from Southwestern Africa (*Otavipithecus*) as far north as the Saudi Arabian plate (*Heliopith-*

TABLE 12.4 *Classification of European and Southwest Asian Hominidae*

Hominidae
  Dryopithecinae
    Kenyapithecini
      *Griphopithecus alpani* Tekkaya 1974
        ( = *Sivapithecus alpani* Tekkaya 1974)
        ( = *Sivapithecus darwini* Abel 1902)
      *Griphopithecus darwini* (Abel 1902)
        ( = *Dryopithecus darwini* Abel 1902)
        ( = *Austriacopithecus weinfurteri* Ehrenberg 1937)
        ( = *Austriacopithecus abeli* Ehrenberg 1937)
        ( = *Griphopithecus suessi* Abel 1902)
    Dryopithecini
      *Dryopithecus fontani* Lartet 1856
      *Dryopithecus laietanus* (Villalta and Crusafont 1944)
        ( = *Hispanopithecus laietanus* Villalta and Crusafont 1944)
        ( = *Sivapithecus occidentalis* Villalta and Crusafont 1944)
        ( = *Rahonapithecus sabadellensis* Crusafont and Hürzeler 1961)
        ( = *Dryopithecus piveteaui* Crusafont and Hürzeler 1961)
      *Dryopithecus carinthiacus* Mottl 1957
        ( = *Rudapithecus hungaricus* Kretzoi 1975)
        ( = *Bodvapithecus altipalatus* Kretzoi 1975)
      *Dryopithecus crusafonti* Begun 1992
        ( = *Dryopithecus fontani* Smith-Woodwood 1914 partim)
  Ponginae
    *Sivapithecus meteai* (Ozansoy 1957)
      ( = *Ankarapithecus meteai* Ozansoy 1957)
  Oreopithecinae
    *Oreopithecus bambolii* Gervais 1872
  Homininae
    *Graecopithecus freybergi* von Koenigswald 1972
      ( = *Dryopithecus macedoniensis* de Bonis and Melentis 1974)
      ( = *Ouranopithecus macedoniensis* |de Bonis and Melentis 1974|)
  *Incertae sedis*
    *Udabnopithecus garedziensis* Burtschak-Abramovich & Gabachvili 1950
    *Paidopithex rhenanus* Pohlig 1895
    *Dryopithecus? brancoi* Schlosser 1901
      ( = *Anthropodus brancoi* Schlosser 1901)
      ( = *Neopithecus brancoi* Abel 1902)

*ecus*). It is beyond the scope of this contribution to discuss this further, but it is important to note that the second dryopithecine tribe, the Kenyapithecini, shares many similarities with the Afropithecini and may indeed be derived from it. The earliest kenyapithecins are only slightly later in time than the afropithecins, and there are thus strong indications that the kenyapithecins originated in Africa. The case of the third tribe, the Dryopithecini, is more problematic. There are substantial morphological differences, as well as a long temporal hiatus, between kenyapithecins and dryopithicins, and it does not appear that they shared an immediate common ancestor.

The second subfamily of the Hominidae to be considered here, Ponginae, is represented by a single species, for which only two specimens are known from Europe and Southwestern Asia. These come from the Sinap Formation in Turkey, from a site dated 9.8 Ma ( = latest MN 9; Kappelman et al., this volume), and the species is attributed to the Indo-Pakistan genus *Sivapithecus*. The charac-

ters that are used to assign the fossil species of this genus to the orang utan clade are based on the morphology of the face and palate, and a suite of synapomorphies have been listed (Andrews and Cronin 1982) and subsequently defined in some detail (Ward and Pilbeam 1983; Ward and Kimbel 1983; Ward and Brown 1986). Recent work showing that the postcrania lacked shared great ape characters that would have been expected to be present in an orang utan ancestor (Pilbeam et al. 1990) have been claimed to cast doubt on the affiliation of *Sivapithecus* to the orang utan clade, but in our view the palatal-facial characters are more robust because they encompass several independent functional complexes of the skull, and we maintain the pongine status of the Turkish and Indo-Pakistan specimens. The implication here is that the postcranial characters shared by the orang utan and the African apes, but absent from *Sivapithecus*, are convergent for the orang utan and the African apes; alternatively, there may have been a "reversal" in *Sivapithecus* related to its modified locomotor adaptations.

The third subfamily present in Europe is the Oreopithecinae. It is represented by a single species, *Oreopithecus bambolii*, know from late Miocene sites in Tuscany and Sardinia, Italy (MN 12 and MN 13). This taxon has a uniquely specialized dentition, and previous attempts to elucidate its phylogenetic relationships based on dental morphology alone have produced conflicting results (see Szalay and Delson 1979; Harrison 1987b). However, the postcranial adaptations are clearly very close to those characterizing extant great apes and humans, and several important synapomorphies of the cranium clearly associate *Oreopithecus* with the Hominidae. As the precise relationship of *Oreopithecus* to other hominids is still uncertain, and given the divergent nature of its cranio-dental specializations, we have included it in a separate subfamily.

Homininae is represented by a single genus and species in the Miocene, *Graecopithecus freybergi*, and its place in this subfamily is based on characters such as the African ape pattern of incisive canal and the enlarged supra-orbital tori and glabella (Andrews 1990, 1992; Dean and Delson 1992). Unlike the other subfamilies of Hominidae, which are well represented in other parts of the world, even if rare in Europe, hominine fossils are rare everywhere until the early fossils on the human lineage are known from the Pliocene of Africa.

## DRYOPITHECINAE, KENYAPITHECINI

The genus *Kenyapithecus* is known only from Africa, the type species being *Kenyapithecus wickeri* from Fort Ternan, Kenya. The similarities of the Turkish middle Miocene hominoids from Paşalar to *Kenyapithecus* have been recognized since their first description (Andrews and Tobien 1977). They are also similar to the four specimens

from middle Miocene deposits of the Vienna Basin at Neudorf Sandberg (MN 6): left and right m3, left M1 and M2 (Abel 1902; Steininger 1967) and to an isolated left m3 from Engelswies (MN 5) in southern Germany (Heizmann 1992). Although originally assigned to two genera and species, we consider that in fact they all belong to the one species, which as first revisers we have identified as *Griphopithecus darwini* (Begun 1987, 1992b; Martin and Andrews 1993). We have attempted a resolution of these similarities by using the genus name available from Neudorf, *Griphopithecus*, for the Paşalar sample, while at the same time grouping this genus with *Kenyapithecus* in the Kenyapithecini (Andrews 1992; Martin and Andrews 1993). Two species of *Griphopithecus* are recognized here, *G. alpani* for the Çandir and Paşalar samples and *G. darwini* for the Neudorf sample. In addition, an unnamed third species is also known, based on a morphologically distinct sample from Paşalar.

*Griphopithecus* The type locality of *Griphopithecus alpani* is Çandir (MN 6), and the type specimen is a well-preserved mandible with the crowns of left p3 to m3 and right p4 to m3, described by Tekkaya (1974) as *Sivapithecus alpani*. Andrews and Tekkaya (1976) reassigned the mandible to *Ramapithecus* (now *Kenyapithecus*) *wickeri*, and when material from Paşalar (MN 6; Bernor and Tobien 1990) in Turkey was described, part of the sample was put in the same species (Andrews and Tobien 1977). Later, the Turkish material was recognized as distinct from the African, and, together with much more abundant remains from Paşalar, they were transfered back to *Sivapithecus* (Alpagut et al. 1990). The discovery of more complete material, including several mandibles and maxillae and a portion of premaxilla, now show the presence of a broad incisive canal and a short premaxilla, similar to that seen in early Miocene species of *Proconsul*. The retention of this primitive morphology of the subnasal region, and the absence of the elongated premaxilla and long, narrow incisive canal present in *Sivapithecus* (Ward and Pilbeam 1983), is taken to demonstrate that this taxon does not belong in *Sivapithecus*. The descriptions of the new specimens are in preparation (Andrews, Alpagut, and Martin, in prep.). Discovery of more complete material may show the presence of some of the synapomorphies of the orang utan clade, for example in the orbital region of the skull, but in the absence of such information we see no reason to link the Paşalar hominoids with the orang utan clade.

There is good evidence for the presence of two species at Paşalar. This was originally assessed on the basis of size (Andrews and Tobien 1977), but with increasing collections (Alpagut et al. 1990) it has become apparent that there is extensive overlap in the size distributions of the two species. The overall variability of the Paşalar sample is too great to encompass a single species (Martin and An-



FIGURE 12.2 The two incisor morphs from Paşalar. On the left is one of the largest specimens of incisor with a central lingual pillar, identified here as *Griphopithecus alpani*, and on the right is one of the smallest specimens lacking a pillar. The greater relative breadth of the latter and its lower crown are correlates of this morphology.

drews 1993), and the morphology of teeth like the I1 (fig. 12.2) shows two distinct morphologies, with large and small (male and female) samples of each (in preparation). The common species, about 90% of the sample, is believed to be that recognized from Çandir, and the second species at Paşalar is therefore left without a name. It is possible that it may still be referred to the genus *Sivapithecus*, for the incisor morphology is similar to that described for the Indo-Pakistan specimens (Tattersall and Simons 1969), but the other body parts needed to distinguish this genus from *Griphopithecus* are not known for this species, for which only a few isolated teeth are known. On the other hand, on the basis of its extreme similarity to *alpani*, so great that most teeth cannot be distinguished one from the other, it seems most likely that it should be attributed to the same genus as *alpani*. This is the course we are adopting here.

The similarity of the Paşalar hominoids with the Neudorf Sandberg *Griphopithecus darwini* has also been recognized (Andrews and Tobien 1977). The four Neudorf Sandberg teeth described by Abel (1902) were originally assigned to two genera and species, *Dryopithecus darwini*

and *Griphopithecus suessi*. The former species was subsequently transfered to *Sivapithecus darwini* by Lewis (1937; Andrews and Tobien 1977). The attribution to *Sivapithecus* was based on the inferred presence of thick enamel on the molar crowns, and this was also one of the reasons that the Paşalar sample was grouped with this material, combined with the presence of buccal cingula on the lower molars. It is now recognized that these are primitive characters for the hominid clade and do not support the attribution of any part of the Neudorf or Paşalar samples to *Sivapithecus*. An unpublished isolated m3 has been recovered in previous years from Engelswies and may be referable to the same species, although it is believed to come from MN 5 horizons (Heizmann, 1992). If the systematic and age attributions prove to be so, this record would represent the oldest-known entry of hominoids into Europe.

One last point to be considered here is the identification of "*Austriacopithecus weinfurteri*" and *A. abeli* described by Ehrenberg (1937) from Klein Hadersdorf (MN 6) in Austria. Begun (1992b) has shown that these postcranial bones are different from specimens associated with *Dryopithecus* species. The humerus shaft is not as straight and more robust, with a prominent and convex deltoid tuberosity that imparts some degree of anterior convexity to the shaft. On the other hand, the curvature is not as great as in earlier afropithecins, such as the humerus from Maboko Island, and it is also less than that of the two *Sivapithecus* humeri from Pakistan (Pilbeam et al. 1990). Similarly, the olecranon fossa is deeper than that of the Maboko humerus, but not as deep as that from St. Gaudens. It seems very likely, therefore, that these specimens could belong to *Griphopithecus darwini*, as suggested recently by Begun (1992b), on the grounds that the Klein Hadersdorf deposits are similar in age to Neudorf Sandberg and their morphology is different from slightly earlier (e.g., Maboko Island) and slightly later (e.g., St. Gaudens) specimens.

We therefore recommend the following taxonomic changes:

1. synonymize the two taxa from Neudorf, with *suessi* being recognized as the junior subjective synonym of *darwini*

2. include the Klein Hadersdorf taxa *Austriacopithecus weinfurteri* and *A. abeli* in *darwini* (Szalay and Delson 1979; Begun 1992b)

3. retain the genus *Griphopithecus* for the Neudorf and Klein Hadersdorf taxon, hence *Griphopithecus darwini* (Begun 1987, 1992b; Martin and Andrews 1993)

4. transfer the Paşalar and Çandir taxa from *Sivapithecus* to *Griphopithecus* on the basis of their similarity to the Neudorf Sandberg specimens

5. recognize two species of *Griphopithecus* from Paşalar, one referred to the Çandir taxon, now *Griphopithecus*

*alpani*, and the other to an unnamed species of the same genus

6. group the Neudorf and Paşalar/Çandir specimens in the tribe Kenyapithecini in recognition of their close similarity to the East African genus *Kenyapithecus*

DRYOPITHECINAE, DRYOPITHECINI

The species of the Dryopithecini have thinner enamel than the kenyapithecines, comparable to that seen in early Miocene hominoids (Martin 1985; Andrews and Martin 1991). The skull of dryopithecins show some similarities with living great apes, for example in the enlarged glabella (Begun 1992c), and the postcrania also show resemblances to modern apes and humans (Begun 1992b). Begun has interpreted this to indicate sister-group relationship between dryopithecins and the great ape and human clade, but there is a further possibility that they may share characters with the African ape and human clade, what we term here the Homininae (tab. 12.4).

The cranial characters uniting *Dryopithecus* with the hominine clade center on the interpretation of klinorhynchy being present (Shea 1985; Begun 1992c). The klinorhynchous state of basicranial flexion is said to be associated with the presence of a prominent supraorbital torus, prominent glabella, shallow supratoral sulcus, and the development of frontal sinuses (Shea 1985). However, it is still equivocal whether any or all of these characters are present in *Dryopithecus*. Begun (1992c) considers that these characters are present in the common ancestor of all great apes and humans, including the orang utan, which lacks them, but we think it more likely that they were unique to the African ape and human clade (see also Dean and Delson 1992). On the basis of this and other characters of the subnasal region, we suggest below that *Graecopithecus freybergi* belongs to the hominine clade, but it would appear that the cranial characters present in *Dryopithecus* do not support hominine relationship.

Of particular significance here is the interpretation of the polarity of the subnasal morphology of hominines. There is general agreement that the subnasal morphology of hominines is probably convergent on that of the orang utan (Begun 1992c), and while the pongine morphology is known for several *Sivapithecus* species, the hominine morphology is only known for the single species of *Graecopithecus* and is not present in *Dryopithecus*. The condition in *Oreopithecus* also appears to be more similar to the hominine pattern than the condition in *Dryopithecus*, and postcranially it is very much closer. At the very least, therefore, it would appear that both *Oreopithecus* and *Graecopithecus* are more closely related to living African apes and humans than is *Dryopithecus*.

In another significant paper, Begun (1992b) has reviewed the postcranial evidence for hominoid evolution.

He identified two postcranial groups for the European dryopithecines: the Klein Hadersdorf specimens, which he links with earlier, primitive hominoids like *Proconsul* on the basis of symplesiomorphous characters; and *Dryopithecus* from Rudabánya and St. Gaudens (see below), which he claims share advanced characters with the extant great apes, such as straight humeral shafts, flat deltoid planes, and distal humerus modifications for enhanced mobility of the elbow.

This is potentially stronger evidence than the cranial evidence, but two issues need to be addressed. One is that these dryopithecine characters are present in all living great apes, i.e., the Hominidae as a whole, including both pongines and hominines, and they are not necessarily diagnostic of the latter. Many of these characters are present in *Oreopithecus*, and some, although not all, are present in *Sivapithecus* species, but the humeral shaft morphology of *Sivapithecus* lacks the great ape characters present on the *Dryopithecus* humerus (Pilbeam et al. 1990). As a result, the polarity of the postcranial features is difficult to interpret, and it may be questioned whether the changes observed on the *Dryopithecus* postcrania indicate phylogenetic relationship or functional adaptation resulting in convergence.

*Dryopithecus fontani*   The type species of *Dryopithecus*, this species is known from three mandibles representing male individuals from St. Gaudens, France, MN 8. There are also several isolated teeth from southern Germany and an upper molar (Depéret 1911) and a previously undescribed upper central incisor from La Grive (see below). The Seu d'Urgell (El Firal, Lerida) mandible is included here, but the St. Stephan (Austria) mandible, previously assigned to this species (Simons and Pilbeam 1965), is removed from *D. fontani* (see below).

The Seu d'Urgell mandible has generally been attributed to *D. fontani* since the time of its first description (Smith Woodward 1914; Simons and Pilbeam 1965). Recently, Begun (1992b) has grouped it with the Can Ponsic material in a new species, *Dryopithecus crusafonti*. We agree that these specimens differ from the other Spanish hominoid material that is generally assigned either to *D. laietanus* or to *D. brancoi*, but we do not consider that the case has been made distinguishing them from the type sample of *D. fontani* (see below). This is particularly true of the Seu d'Urgell mandible, which differs in some minor details from *D. fontani*, such as the lower molar cusp proportions and mandibular body proportions. Begun (1992a) argues that these differences justify species separation of the Seu d'Urgell jaw from *fontani*. This view might be justified by additional material, but with existing specimens we do not consider it to be so. Begun (1992a) wisely did not include this specimen in the species hypodigm for *D. crusafonti*, and with only three isolated teeth from the type site (Can Ponsic) with which to compare



FIGURE 12.3 The La Grive upper central incisor, which has a morphology similar to G. *alpani* from Paşalar (see fig. 12.2) and also to the Rudabánya and Can Ponsic specimens.

it, there is little reason for including it in that species.

The La Grive incisor (fig. 12.3) is an isolated left I1 described here for the first time. The crown is intact, but the root is broken buccally from the base of the crown. The root's lingual surface is damaged, but part of the root extends for some distance from the base of the crown. Its dimensions are as follows:

mesiodistal length: 8.6
buccolingual breadth: 7.1
buccal crown height: 11.4
length of root preserved: 10.6

The crown is slender and tall, the breadth/length index being 0.83 and the height/length index 1.3. These values compare closely with those for the Can Ponsic hypodigm of *D. crusafonti* (see tab. 12.5), while the robusticity of the Can Llobateres incisors is greater and the height/length index is lower. There is a prominent lingual pillar arising from a massive lingual swelling at the base of the crown to three quarters of the way along the crown. It is medially placed on the lingual surface, and it is broadly rounded, ending in a rounded apex.

There is reason to believe that the La Grive incisor's

TABLE 12.5 *Comparative Data on Incisor Proportions for Four Samples of* Dryopithecus

|  | H/L | H/B | B/L |
|---|---|---|---|
| D. crusafonti | 1.5–1.6 | 1.8–1.9 | 0.82–0.86 |
| D. laietanus* | 1.3 | 1.4 | 0.93 |
| D. carinthiacus** | 1.3–1.4 | 1.4–1.6 | 0.88 |
| D. fontani*** | 1.3 | 1.6 | 0.93 |

H = buccal height
B = buccolingual breadth
L = mesiodistal length
*Can Llobateres sample—D. *brancoi* in Szalay and Delson's (197) usage.
**Rudabánya sample—D. *brancoi* in Begun's (1992c) usage.
***Specimen from La Grive, our data.

morphology is representative of *Dryopithecus fontani*, although in the absence of associated material this cannot be proved. It will be so taken in this paper, and the morphology will form the basis for comparison with other species of *Dryopithecus*. It should be noted in this regard, that the same morphology is seen in the Can Ponsic and Rudabánya samples, but the significance of this will be discussed below.

*Dryopithecus carinthiacus*    There is good evidence for a second species of *Dryopithecus* in Central Europe, and there are diverse opinions about its proper taxonomic referral. Begun (1992c), following Szalay and Delson (1979), has assigned it to *Dryopithecus brancoi*, which is based on the isolated worn m3 from Salmendingen in southern Germany. Andrews and Martin think that the Salmendingen specimen may be pliopithecid (following Hürzeler 1954, but see above). If it is indeed pliopithecid, the name *brancoi* is unavailable as a species name for *Dryopithecus*. Alternative names available are *Dryopithecus rhenanus*, based on an isolated lower molar from Salmendingen (Schlosser 1901), *Rudapithecus hungaricus*, based on the excellent series of fossils described from Rudabánya, Hungary (Kretzoi 1975; Kordos 1987, 1991), and *Dryopithecus carinthiacus*, based on the mandible from St. Stephan, Austria (MN 8) (Mottl 1957). Kelley and Pilbeam (1986) advocate the retention of the nomen *Rudapithecus hungaricus*, but this has been criticized by Begun and Kordos (1993) on the grounds that the characters identified as being of generic significance by Kelley and Pilbeam are in fact too variable and do not reliably distinguish the Rudabánya sample from other samples of *Dryopithecus*.

Begun and Kordos (1993) have recently redescribed the type specimen of *Dryopithecus brancoi* (from Salmendingen), and argue for differences in its degree of elongation from other species referred to that genus. Within *Dryopithecus* on the other hand, they argue that the Salmendingen molar shares its greatest similarity with the Rudabánya m3 sample and suggest its referral to *D. brancoi*. This interpretation is supported by Delson and Harrison. Andrews, Bernor, and Martin, however, would accept this proposal if indeed the Salmendingen specimen could clearly be attributed to *Dryopithecus*. The nomen *D. brancoi* could be used for the Rudabánya sample, but there remains the possibility that it may be an advanced pliopithecid, as suggested by Hürzeler (1954). For this reason, Andrews, Bernor and Martin are suggesting here that the nomen *Dryopithecus carinthiacus* be applied for all of the Rudabánya *Dryopithecus* material. Finally, Begun and Kordos (1993) have demonstrated that there is no good reason to recognize more than one species of *Dryopithecus* from Rudabánya (contra Andrews and Martin 1987).

The type specimen of *D. carinthiacus* consists of a right mandibular fragment with the crowns of p3 to m1 in place,



FIGURE 12.4 The mandible from St. Stephan, Austria: *Dryopithecus carinthiacus*. The fragment of mandible on the right has the crowns of p3 to m1 in place, the crown of the lateral incisor displaced, and the left tooth row has c1-m1 with a broken m2 but no part of the mandibular body.

and a displaced right central incisor (fig. 12.4). Associated with this specimen are five isolated teeth, the intact crowns of left c1-m1 and a broken m2 (Mottl 1957). It is similar to the type material of *D. fontani*, differing mainly in its smaller size. In this respect it could be considered a female of this species, as has generally been the case (Simons and Pilbeam 1965). The canine and p3 are small and low crowned in both the type specimen and the Rudabánya material, the former also having a short mesial ridge indicative of female morphology (Kelley and Xu 1991): the *carinthiacus* canine falls in the female range of great ape canines very close to the mean of chimpanzee females. The molars are similar in size and morphology, but the p4 of the *carinthiacus* specimen is narrow and elongated, differing from the corresponding teeth in the Rudabánya sample (and also from the *fontani* type material). This is interpreted for the present as intraspecific variation (but see below).

The large hominoid sample from Rudabánya, Hungary, has been divided in the past into two species (Kretzoi 1975). The majority of the specimens are readily referable to the type specimen of *Rudapithecus hungaricus*, and this group has been in turn referred to *Dryopithecus brancoi* (Szalay and Delson 1979; Begun 1992c), but in view of the possible pliopithecid affinities of the type specimen of *brancoi* (see above), Andrews and Martin reject this assignment. In terms of molar size and morphology it is closer to the *carinthiacus* specimen, and it is recognized as such here. The type specimen of a second species described from Rudabánya, *Bodvapithecus altipalatus*, is distinguished only by its slightly larger size, and it is also synonymized with *carinthiacus*. There appears to be no good reason for the recognition of more than one species.

The size and morphology of the upper central incisor is similar to that of the Can Ponsic material from Spain, and it is also similar to the La Grive incisor, with a broadly rounded but prominent lingual tubercle and similar crown proportions (see below). The distal humerus is similar to the humerus from St. Gaudens with morphology significantly advanced over that of earlier Miocene hominoids (Begun 1992b).

*Dryopithecus laietanus*    The type site is La Tarumba in Spain (MN 10). We have referred to this species almost all of the Spanish MN 8–10 hominoids, including *Hispanopithecus laietanus* Villalta and Crusafont 1944, "*Rahonapithecus sabadellensis*" Crusafont and Hürzeler 1961, and *Dryopithecus piveteaui* Crusafont and Hürzeler 1961, but we exclude the Can Ponsic material that Begun (1992a) has recently assigned to a new species, *D. crusafonti*. Even with that exclusion, this combination produces a large range of variation for this species.

There is some evidence for more than one species being present at Can Llobateres, particularly when the types of "sabadellensis" and "piveteaui" are compared. There is also some evidence of two morphologies that have similar size distributions. One morphology has upper molars with prominent cusps and ridges, elongated crowns, second and third molars not morphologically reduced, and traces of cingulum on the upper molars. The second morphology differs in having broader crowns with rounded cusps, no cingulum, second and third molars with considerable distal reduction, and the third molar very small. Despite these differences, we do not consider them sufficient to distinguish two species on present evidence, so that we conclude that only one species appears to be represented at Can Llobateres, and the same species is present at La Tarumba, Can Vila, and Sant Quirze, and probably also at Polinya, Can Mata, and Castell de Barberà (Begun 1990; Harrison 1991b).

Another suggestion is that the Can Ponsic material can also be divided into two species, but Begun (1992a) provides good evidence that this is not the case. Begun also shows that the Can Ponsic material belongs to a different species from the Can Llobateres sample (Begun et al. 1990), an observation supported by those of Martin and Andrews when they studied the Spanish collection in 1984.

*Dryopithecus crusafonti*    This species was described by Begun (1992a) from the type site of Can Ponsic, Spain (MN 9). Begun referred the Seu d'Urgell mandible to this species, but its affinities appear to us to lie with *D. fontani*, as originally described by Smith Woodward (1914; Simons and Pilbeam 1965; see above). Compared with the Can Llobateres and La Tarumba specimens, the Can Ponsic material has I1 high crowned and with a prominent lingual pillar, upper canine crenulated and without a lingual groove, P3 with less buccal flare, upper molars increasing in size posteriorly, p4 long and narrow, and lower molars with a long metaconid.

Harrison (1991b) has observed that the apparent differences between the Can Ponsic and Can Llobateres samples have been accentuated by differential wear and that they are minor differences that do not justify the recognition of a separate species. This may not be true of the incisor and p4 morphologies, which are the most distinctive features of *D. crusafonti*, and in the view of Martin and Andrews, they are sufficient to justify separation from *D. laietanus*, especially the contrast with the Can Llobateres I1, which is low crowned and lacks a lingual pillar (see fig. 12.5). However, in this respect the Can Ponsic incisors are similar to the isolated incisor from La Grive (see figs. 12.4 and 12.5) which we attribute to *Dryopithecus fontani*. Begun (1992a: fig. 9 and tab. 6) provides good comparative data on the distinctiveness of the central incisor.

The crown dimensions are similar in the La Grive and Rudabánya samples and slightly larger than the Can Ponsic teeth, but the crowns of the Can Ponsic specimens are higher and narrower than in *D. fontani*. They share the presence of a lingual pillar, but on the Can Ponsic specimens the pillar is narrow and pointed, with deeply incised grooves on either side and arising from nearer the base of the crown. On the Rudabánya and La Grive specimens the tip of the pillar is more rounded and the base is broader. The presence of a lingual pillar is probably primitive for hominoids (Andrews 1985) so that the similarity in morphology in the La Grive and Can Ponsic samples is probably not systematically significant.

The narrow p4 is also not as distinct on the Can Ponsic specimen as Begun (1992a) suggests. Apart from the fact that there is only one specimen of this notoriously variable tooth, it is similar in shape and morphology to the p4 on the St. Stephan mandible (see fig. 12.4), which is also relatively elongated and only slightly larger in size (L x B is 7.8 x 7.3 mm for the St. Stephan p4 compared with 7.4 x 6.6 mm for the Can Ponsic specimen). Both specimens are longer than broad, an unusual feature for hominoid p4s and distinct from both the Rudabánya and St. Gaudens samples attributed to *D. fontani*.

Another problem with the *D. crusafonti* hypodigm is the combination of the Seu d'Urgell mandible with the Can Ponsic specimens. There are only two teeth in the latter sample that can be compared with the Seu d'Urgell mandible, and although they are similar in size and morphology (sharing broad buccal cusps, restricted and shallow talonid and trigonid basins, and long post-metaconid cristids), this is not strong evidence for association, particularly because the diagnostic features of the species (i.e., upper central incisor and p4 morphology) are missing from the mandible. Begun (1992a) describes the robustness of
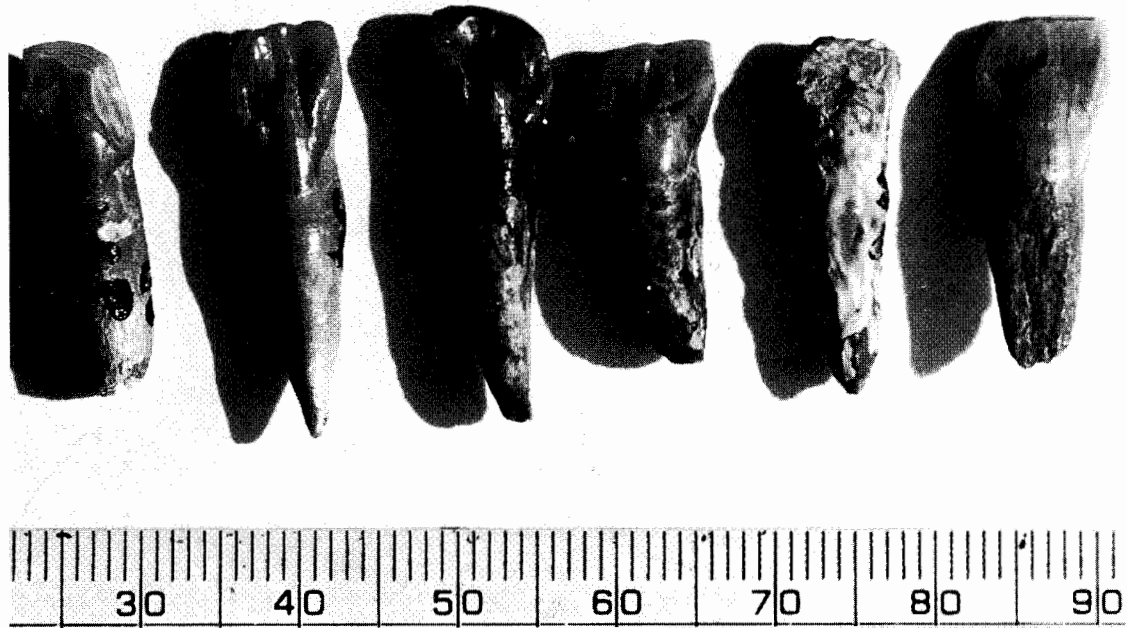
FIGURE 12.5 Incisor morphology from middle Miocene Western European sites. The three specimens on the left are *Dryopithecus laietanus*; next to them are two specimens of *Dryopithecus crusafonti* from Can Ponsic; and on the far right is the La Grive specimen, which we attribute to *Dryopithecus fontani*.

the mandibular ramus by means of the relationship between molar width and ramus width in the Seu d'Urgel mandible, and he concludes that the mandible is remarkably robust (or the molars extremely small relative to mandibular size), so much so as to be distinct from all other species of *Dryopithecus*, but since this feature cannot be measured for the Can Ponsic material it does not necessarily associate the material from the two sites.

To summarize these conclusions for the genus *Dryopithecus*, we make the following attributions, of which we have some confidence in the first three but less in the fourth: (1) *D. fontani* includes the type material from St. Gaudens, as well as La Grive, some isolated teeth from Germany, and the Seu d'Urgell mandible; (2) *D. carinthiacus* includes the St. Stephan mandible and the whole of the Rudabánya hominoid sample; (3) *D. laietanus* includes the samples from most of the Spanish Miocene sites, most notably Can Llobateres, but excluding Can Ponsic and Seu d'Urgell; (4) *D. crusafonti* includes the material from Can Ponsic; this has similarities to, and potentially is synonymous with, *D. laietanus* (Harrison's 1991b view), *D. fontani* (Andrews and Martin's view), or *D. carinthiacus*, in all cases giving the relevant taxon an MN 8–9 range in time. The chronologic range would be ca. 12.5–9.5 Ma (see Rögl and Daxner-Höck, this volume).

Some samples could not be taxonomically assigned, including the *Paidopithex* femur (see discussion at the end of the Pliopithecidae section), and the isolated teeth of

*Udabnopithecus*. Both of these would appear likely to be *D. fontani*. These apart, it would appear that the four species of *Dryopithecus* recognized here are closely related, so much so that it is difficult to determine the pattern of relationship.

PONGINAE, SIVAPITHECINI

With the removal of the Turkish middle Miocene and Greek thick-enameled hominoids from the orang utan lineage, there remains only a single taxon referred to the Ponginae in Europe and Southwestern Asia: the Turkish species *Sivapithecus meteai*. The type specimen is a fragmentary mandible from the Sinap Formation near Yassi-ören, Kazan, Turkey; these late MN 9 deposits have a preliminary date of 9.8 Ma (Kappelman et al., this volume). It was originally described as *Ankarapithecus meteai* by Ozansoy (1957), and a maxilla and lower face was described by Andrews and Tekkaya (1980), at which time the species was assigned to the genus *Sivapithecus*. It was suggested later that the Greek material described as *Graecopithecus freybergi* (including "*Ouranopithecus macedoniensis*"—see below) was conspecific with *meteai* (Szalay and Delson 1979; Martin and Andrews 1984), but this view has now to be abandoned because the Turkish face shares characters of the nose and palate with sivapithecins (Andrews and Cronin 1982) and these characters are absent in the Greek sample (de Bonis and Melentis 1978; de Bonis et al. 1990a).

The morphological differences separating *Sivapithecus meteai* from the Indo-Pakistan sivapithecins include characters of the dentition and lower face: (1) the upper central incisors of *S. meteai* are low crowned and extremely broad mesiodistally compared with the robust and high crowned incisors of *S. sivalensis*; (2) the upper lateral incisors of *S. meteai* are more pointed and caniniform; (3) the upper molars are more squared with less constricted occlusal basins; (4) the zygomatic region is broader and has a stronger flare than in *S. sivalensis*. These characters suggest at least a species difference between the Turkish and Indo-Pakistan samples, and it may be that they are generically distinct (in which case the name *Ankarapithecus* is available). With respect to the cranial material, they show a number of similarities that justify their inclusion within the orang utan clade (see addendum).

### OREOPITHECINAE

Although usually placed in a separate family of the Hominoidea, we recognize the postcranial similarities shared with the extant great apes and humans, and place *Oreopithecus* in its own subfamily within the family Hominidae. *Oreopithecus bambolii* is a large-bodied arboreal primate adapted for vertical climbing and forelimb suspension (Harrison 1991c). The postcranial similarities shared with the extant hominids, and inferred to be ancestral for the clade, include a suite of characters combined by Harrison into eleven functional complexes, as follows:

1. strongly differentiated usage of fore- and hind-limbs
2. increased potential for raising the forelimb above the head
3. increased potential for full extension and powerful flexion of the forelimb at the elbow
4. greater potential for circumduction at the shoulder and pronation-supination at the elbow and wrist joints
5. increased range of abduction/adduction of the wrist
6. increased potential for powerful grasping with the hands
7. adoption of more orthograde posture
8. increased potential for full extension of the hip and knee joints
9. greater ranges of rotation at the hip and knee, and inversion-eversion at the ankle joint
10. increased potential for body weight to be supported by a single hindlimb
11. increased ability of the foot to grasp and provide powerful push-off from large diameter vertical supports

If this suite of character complexes is shared by oreopithecines and the living great apes and humans, it indicates that it was present also in the common ancestor between them in the middle/late Miocene, and this in turn has implications for the interpretation of the apparently similar characters on the humerus of *Dryopithecus*. It would also support the view that the apparently primitive morphology of *Sivapithecus* is in fact a secondary reversion toward the primitive character state as a result of functional convergence.

*Oreopithecus bambolii*    The type specimen consists of a mandible from Monte Bamboli, Italy (MN 13). In addition, this species is known from other localities in Maremmia, Tuscany, correlated with MN 12 (Bacinello V1, Casteani, Montemas, and Ribolla), MN 12 or MN 13 (Baccinello *Cardium* horizon), and MN 13 (Baccinello V2) (Szalay and Delson 1979; Azzaroli et al. 1987; Rook et al., 1996). Several isolated teeth of *Oreopithecus bambolii* have also recently been recovered from Fiume Santo in Sardinia (MN 13) (Cordy and Ginesu 1994). An earlier report of *Oreopithecus* from the late Miocene of Russia appears to be unsubstantiated (Laskarev 1909; Hürzeler 1958; Szalay and Delson 1979; Harrison 1986).

*Oreopithecus bambolii* is one of the best-known fossil catarrhine species, being represented by over fifty individuals (mostly from Baccinello V1), comprising numerous upper and lower jaws, and an almost complete skeleton (Hürzeler 1958; Szalay and Delson 1979; Harrison 1987b, 1991c). Although a number of workers have suggested a possible relationship between *Oreopithecus* and cercopithecids, based on dental evidence (Delson 1979; Szalay and Delson 1979; Rosenberger and Delson 1985), Harrison (1987b, 1991c) and others (Sarmiento 1987; Rose 1988, 1993) have established that postcranially its affinities are with the Hominoidea (see above). Delson (Rosenberger and Delson, in prep.) continues to maintain the possibility that the dental similarities between *Oreopithecus* and the cercopithecid morphotype (such as molar elongation and mirror image symmetry between uppers and lowers, details of cingulum reduction and cusp placement, and development of notches and clefts) reflect unique shared ancestry. In that case, the numerous postcranial similarities noted above would represent convergences due to locomotor adaptation, as has been suggested above for the situation with *Sivapithecus* and *Pongo*. However, the possibility of functional convergence in the postcranium does not take into account the occurrence of derived cranial characters linking *Oreopithecus* with the extant hominids. These include the reduced size of the subarcuate fossa and the morphology of the incisive canal, which is similar to the African ape pattern. These clearly support the relationship of *Oreopithecus* with the Hominidae.

### HOMININAE GRAECOPITHECINI

The fourth subfamily of the Hominidae is the Homininae, which is represented in the European Miocene by a single species, *Graecopithecus freybergi* von Koenigswald

1972. This has an unknown relationship with the two extant hominine tribes, Gorillini and Hominini, and it is therefore placed as indeterminate in the Homininae.

*Graecopithecus freybergi*  The type is a fragmentary mandible from Pyrgos (near Athens, Greece) of uncertain age, probably MN 10 described by Koenigswald (1972). Martin and Andrews (1984), following Szalay and Delson (1979) included in this taxon the more complete material from Ravin de la Pluie, and later collections from Xirochori I (de Bonis et al. 1990) and Nikiti (Koufos 1993, 1994) belong here also (see fig. 12.6). These localities are correlated with MN 10 ca. 9.5–9.0 Ma (Rögl and Daxner-Höck, this volume; Bernor et al., 1993). The northern Greek sample was originally described as *Dryopithecus macedoniensis* (de Bonis et al. 1974) and later placed in a new genus, *Ouranopithecus* de Bonis and Melentis 1977a.

A new partial skull has recently been described (de Bonis et al. 1990a) that confirms the distinction between this taxon and *Sivapithecus*. Schwartz (1990) has described some features linking it with the orang utan lineage, and there is also some evidence linking it with the human and African ape clade (de Bonis et al. 1990a; Dean and Delson 1992). Of particular significance for the latter are the morphology of the subnasal region and the conformation of glabella and the brow ridge development. The premaxilla is elongated and rotated supero-anteriorly, overlapping the maxilla so as to restrict the size of the incisive canal, which may have been the ancestral condition of the great ape and human clade, subsequently retained by the African apes with only minor modification. The further change in the orang utan lineage could therefore have been an additional change from this shared character state (Andrews and Martin 1987). An alternative interpretation, however, is that the unique orang utan morphology developed independently of the African apes from a *Dryopithecus*-like morphology (Begun 1992c), in which case the *Graecopithecus* morphology could be interpreted as an African ape and human synapomorphy.

Similarly, the glabella morphology and the development of the supraorbital torus represent advances over the primitive hominoid condition. The prominent glabella and supraorbital torus in *Graecopithecus* (de Bonis et al. 1990a) are characters shared only with the African apes and hu-



FIGURE 12.6 The type specimen of *Graecopithecus freybergi* from Pyrgos in Greece. The crown of right m2 is intact, with the broken and heavily worn crowns of p4-m1 and roots of m3.

mans in the hominoid clade. These characters have been claimed to be present also in *Dryopithecus* (Begun 1992b, 1992c), whose humeral morphology Begun (1992b) has also interpreted as indicating a link with the African ape and human clade. It is therefore possible that *Dryopithecus* as well as *Graecopithecus* could belong to the African ape and human clade, the Homininae as classified here. Interestingly, *Graecopithecus freybergi* has very thick enamel (Andrews and Martin 1991), which distinguishes it from all other hominoids except for robust australopithecines.

The characters just discussed have been used by de Bonis et al. (1990a) to support the relationship of *Graecopithecus* with the human lineage alone. This view does not appear justified on this evidence (the characters are mainly conservative for all hominids), but they have also put forward the claim for canine reduction that needs to be considered. This claim rests on the identification of the skull XIR-1 as a male. There are several upper canines known from the Greek sites, all of which appear to belong to the one species, and the canine from XIR-1 corresponds to the large end of the range of variation for this tooth. On the other hand, the canine/M1 ratio for this specimen is 94%, which is below the range for males of all extant large hominoids but is within the range for females (Andrews 1990). Two interpretations of these data are possible: either the skull represents a female with a normal sized canine; or it represents a male with reduced canine, as de Bonis has claimed. A new maxilla from Nikiti has been described by Koufos (1994) that is clearly a female and supports the second of these two alternatives. If this is the case, it must then be determined if this is evidence of relationship with the human lineage or is an independent development in this 9.5–9.0 Ma fossil.

Some researchers (e.g., de Bonis et al. 1990a) have suggested that *Ouranopithecus* and *Graecopithecus* should be systematically separated on the grounds that the Pyrgos mandible is too incomplete to use as a type specimen. This runs counter to the Code of Zoological Nomenclature, and moreover the Pyrgos mandible is not that incomplete (see fig. 12.5). Parts of the mandibular body are preserved together with the crown of the right second molar, the damaged crowns of the right p4 and m1, and the roots of the right m3 and left p3–m3 (Martin and Andrews 1984). The size and proportions of both teeth and mandibular body are similar to the female mandibles from Ravin de la Pluie (de Bonis and Melentis 1977b), although the teeth are somewhat larger and the corpus shallower in the Pyrgos specimen. It appears most likely that the latter represents a large female that, perhaps because of its size, appears similar in corpus depth and alveolar planum shape to the Ravin de la Pluie males. Other apparent differences (Begun, pers. comm., 1994) may be the result of deformation of the Pyrgos jaw. In our opinion, there are no distinguishing

features separating these two taxa and therefore no reasonable grounds for recognizing two genera or even species. We have used the same argument for relating the Turkish middle Miocene hominoids to the Vienna Basin taxon *Griphopithecus darwini*, which is based on four isolated teeth, and it might also be claimed that the same argument applies to the use of *brancoi* for the mid-European small dryopithecins, although in the latter case Andrews and Martin consider the family affinities of the type specimen of *brancoi* to be too uncertain for its use as a species of *Dryopithecus*.

*Hominid relationships* The relationships of the hominoid higher taxa known from Europe and Southwestern Asia during the middle to late Miocene are depicted here in figure 12.7. Two positive statements are made here: *Graecopithecus freybergi* is recognized as a hominine, related to the African ape and human clade and possibly close to the ancestry of the living species of this group; and *Sivapithecus meteai* is recognized as a member of the pongine clade related to other sivapithecins and the living orang utan. The third subfamily recognized here, Oreopithecinae, contributes to the interpretation of postcranial evolution of the hominids, but these interpretations are still provisional because of the possibility of functional convergence in different hominoid lineages. The fourth subfamily, Dryopithecinae, is even more problematic inasmuch as it is based on the concept of grade rather than clade. The Kenyapithecini has a geographic range from East Africa to Turkey and implicitly the Vienna Basin, and its links are probably with the earlier afropithecins, which are also grouped in Dryopithecinae (Andrews 1992). Dryopithecins appear more advanced, both cranially and postcranially (Begun 1992c), but not sufficiently to warrant grouping with either the pongine or the hominine clade (Begun 1992c; Andrews 1992). They are of similar grade to afropithecins and kenyapithecins and for this reason we maintain their grouping in Dryopithecinae.

## Cercopithecidae

The cercopithecid monkeys do not appear in the European fossil record until the late Miocene. Only one of the two subfamilies, the Colobinae, is represented until the end of the epoch, but these are widespread across Europe and extend into Southwestern Asia. The earliest record is a single upper premolar from Wissberg, in deposits of probable MN 9 age (Delson 1973; Tobien 1986), but all the other European records are Turolian age (late Miocene, MN 11–13; ca. 9–5.3 Ma; Steininger et al. this volume).

Three species are represented, two of *Mesopithecus* and one referred to *Macaca*. The *Mesopithecus* species are closely similar, and only one is common, *M. pentelicus* (tab. 12.6). *Mesopithecus monspessulanus* is known from
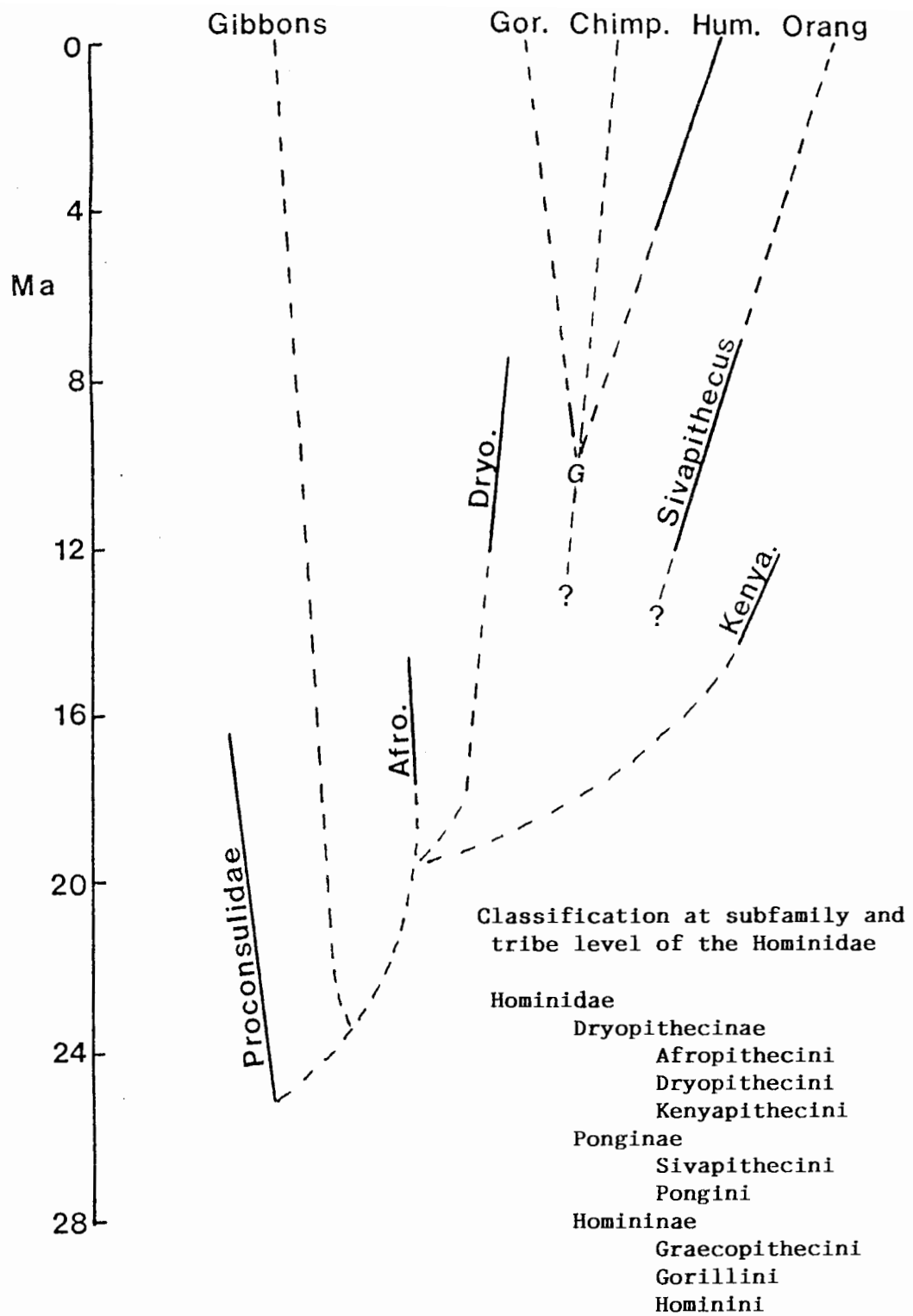
FIGURE 12.7 Phylogeny of the Hominoidea with classification of the Hominidae. The solid lines signify known ranges of fossil taxa, and the dashed lines indicate possible relationships.

TABLE 12.6 *Classification of the European Neogene Cercopithecidae*

Cercopithecidae
  Colobinae
    Colobini
      Subtribe Indet. (??Presbytina)
        *Mesopithecus pentelicus* Wagner 1839
          ( = *M. major* Roth and Wagner 1845)
          ( = *M. delsoni* de Bonis et al. 1990b)
          ( = *M. p. microdon* Zapfe 1991)
        *Mesopithecus monspessulanus* (Gervais 1849)
          ( = *Semnopithecus monspessulanus* Gervais 1849)
        *Dolichopithecus ruscinensis* Depéret 1889:
          (*D. cf arvernensis* Depéret 1929: Kretzoi 1954)
  Cercopithecinae
    Papionini
      Macacina
        *Macaca* sp. indet.

fragmentary material, although it is more common in the Pliocene. Both show some evidence of terrestrial adaptation, the more extreme being found in *M. pentelicus*. In contrast to this, *Macaca* has a more restricted distribution, having been recovered at only one MN 13 locality, but occurring more widely through Europe during the Pliocene (see below). *Dolichopithecus* has been reported from the late Miocene (e.g., by Szalay and Delson 1979), but the locality now appears to be early Pliocene (MN 14?) in age; the material will be briefly discussed to clarify the situation.

COLOBINAE

*Mesopithecus*    The type species of *Mesopithecus* is *M. pentelicus*, known mainly from Southeastern Europe, MN 11–13. The type locality is Pikermi, Greece, which has also yielded the largest sample. Zapfe (1991) designated a new subspecies for a single mandible from the Chomateri locality near Pikermi, distinguished on the basis of relatively small tooth size. Specimens from southern Yugoslavia, Bulgaria, and Northern Greece have generally been referred to the Pikermi species, but recently de Bonis et al. (1990b) have described a small sample from Ravin des Zouaves 5 (RZO, Greece) as *M. delsoni*, which they distinguished by larger m3, longer lower molar and premolar rows, and several mandibular corpus differences. In addition to the specimens from RZO, de Bonis et al. (1990b) reported *Mesopithecus* fossils from the apparently younger Dytiko localities that were tentatively allocated to either *M. pentelicus* or *M. monspessulanus*; these will be discussed under the latter species below.

In order to test the distinctiveness of the putative new species *M. delsoni*, statistical tests were carried out on metrical data obtained from casts of three mandibular specimens kindly provided by L. de Bonis (see comparisons in fig. 12.8). Additional specimens referred to *M. pentelicus* were recovered previously from the nearby localities of

Vathylakkos and Ravin X (Arambourg and Piveteau 1929), as well as from the Titov Veles localities in ex-Yugoslavia (now Macedonia; Schlosser 1921; Ciric 1957) that derive from the valley of the same river (named differently across the border). Moreover, Bakalov and Nikolov (1962) described similar material from three sites in Bulgarian Macedonia.

All of these original specimens were measured by Delson, and these data were combined with those obtained from the RZO casts to form a "Macedonian" sample of *Mesopithecus*, with 9–12 individuals for each lower molar measure (mesial width, distal width, and length) and 2–5 individuals for the upper molars; these were compared to a sample of 32–42 individuals per measure for Pikermi. A series of 18 t-tests reveals that although each of these small samples averages slightly larger than the 40–50 specimens from Pikermi measured by Delson, few are statistically different (the 99% confidence level is employed to take into account the large number of t-tests evaluated): m1 length differed at the 98.5% level (even greater distinction was found for the few teeth from RZO and Vathylakkos) and m3 length at the 99.7% level; no other variates approached significance. De Bonis et al. (1990b) reported that both m3 length and [mesial?] breadth differed "highly significantly" (without definition) between the Pikermi and RZO samples, but they included both antimeres of the two large male jaws from RZO, and their measurements were rather larger than those Delson obtained on casts using the same techniques employed for the larger Pikermi sample.

Referring now to the tooth rows, de Bonis et al. (1990b) again found "highly significant" differences between the (bilateral) RZO and Pikermi samples for p3–4 and m1–3 lengths. Molar length was significant at the 99.8% level when both Pikermi sexes were included, but no distinction was found when the two RZO (and Maragheh, see below) males were compared only to seven Pikermi males; the difference in premolar length was not significant even when sexes were combined (Pikermi sample of only four).

Given the few statistically significant differences between the Pikermi and Macedonian samples, a species distinction between *M. delsoni* and *M. pentelicus* is not supported. In terms of the corpus features, the two RZO specimens appear to show plastic deformation leading to an increase in depth, and other characters are not deemed indicative of major taxonomic separation. As all the specimens are of broadly similar age (see below), it is unlikely that even a subspecific distinction is warranted at this time. De Bonis (pers. comm.) rejects this interpretation, arguing that the corpora are not deformed and noting that Delson's measurements on casts differ from his on the originals; in response, the same techniques were used on the whole sample studied here, so that these potential differences in measurement technique cancel out. Delson and de Bonis have agreed to disagree on the status of *M. delsoni* for the
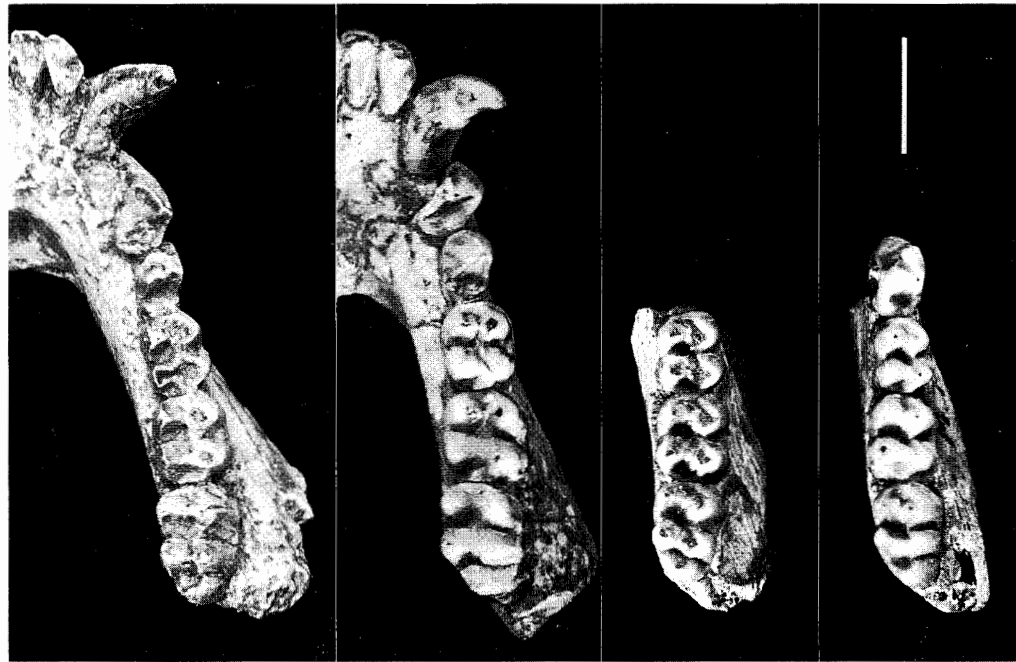
FIGURE 12.8 Right mandibular dentitions of *Mesopithecus* species. Left to right: *M. pentelicus* male from Ravin des Zouaves, i1-m3 (holotype of *M. "delsoni,"* cast); *M. pentelicus* male from Pikermi, i1-m3; *M. cf. pentelicus* (sex unknown) from Baltavar, m1-3; *M. monspessulanus* (sex unknown) from Montpellier, p4-m3. Scale bar = 1 cm.

present. Similarly, the distinction of *M. p. microdon* as a subspecies (from the probably younger Chomateri locality) proposed by Zapfe (1991) based on small teeth in a deep corpus cannot now be supported.

None of these localities has been well dated, and there is disagreement among authors concerning their relative dates. Previous estimates of the age of the main Pikermi locality as early Turolian (MN 11?, e.g., Delson 1973, 1975) were replaced by younger estimates of MN 12/13 (e.g., Mein 1989), based on rodents collected from Chomateri; these do not appear reasonable, given the lack of continuity between the two localities, and the most recent research (Bernor et al., this volume) seems to imply an age equivalent to the lower levels at Maragha and Samos, that is near the MN 11/12 boundary. De Bonis et al. (1987, 1990b) suggested that the Ravin des Zouaves (RZO) locality might be older than Pikermi, while the Dytiko localities would be younger, but local superposition, and unequivocal faunal comparisons outside the Axios Valley are still awaited (but see de Bonis et al. 1992). The ages of the "Saloniki" (Vathylakkos), Bulgarian, and Yugoslav Macedonian localities are even less defined (but see Forstén and Garevski 1989).

Outside this region of Southeastern Europe, Miocene fossil cercopithecids are far less common. One isolated upper premolar from Wissberg (fig. 12.9) was identified by Delson (1973; see also Tobien 1986) as belonging to a colobine of the size of *M. pentelicus*; it is important only in registering the earliest presence (MN 9?) of the family

in Eurasia. Although some workers (e.g., Tobien 1980) have accepted the Wissberg sample as indicative of an early Vallesian age, Bernor among others suggests caution because several of the "Dinotherium-Sands" localities include an admixture of younger faunal elements, of which this tooth could be one. A maxilla from the Meotian (early Turolian) of Grebeniki-1 (Ukraine) has been tentatively termed *M. ukrainicus* by Gremyatskii (1961), but no substantive distinctions were provided, and the specimen is indistinguishable metrically (or morphologically) from any of the above; the same is true for a mandible from Molayan (Afghanistan). On the other hand, the long-known mandible from Maragheh (Iran; middle horizon, basal MN 12, ca. 8.24 Ma, Bernor et al., this volume) was indicated to be possibly distinctive by Delson (1973) and Heintz et al. (1981), and de Bonis et al. (1990b) have referred it to *M. delsoni*. As noted above, it is large but no more likely than the RZO fossils to represent a different species. Its corpus is shallow, rather than deep, as the RZO jaws are said to be. Fragmentary colobine remains from the Indo-Pakistan Siwaliks (see Barry 1987) may be younger but are hard to distinguish from *M. pentelicus*; the possible presence of an earlier late Miocene (MN 11–12) paleoenvironmental/paleogeographic filter in the Baluchi Hills region between Afghanistan and Pakistan should give rise to caution in synonymizing these taxa (see Bernor 1983, 1984; Brunet et al. 1984; Barry 1987; Delson 1994). De Bonis et al. (1994) have reconsidered the question of this barrier, but we must note that at least for the primates their faunal list is incor-

rect: *Mesopithecus* is wrongly indicated to occur at Lufeng (perhaps based on an early reference to a cercopithecid, never confirmed) and Taraklia (perhaps based on references such as Simionescu 1930, which confused Taraklia and the nearby Grebeniki); moreover, the presence of *Sivapithecus* at Yassiören does forge a link between the Potwar sequence and Turkish sites.

Several probably latest Miocene (MN 13) colobines are known from Baltavar (Hungary; fig. 12.8), Baccinello V-3, Brisighella, Casino, and Gravitelli (Italy). Only two m3s remain of the Casino sample (see Ristori 1890) and a single dP3 from Baccinello has recently been discussed, but Rook (pers. comm.) indicates that other specimens have been found; all the Gravitelli specimens have been lost. In the past they have usually been referred to *M. monspessulanus* (e.g., Delson 1973; Szalay and Delson 1979), but re-evaluation of tooth size here (see above) suggests that Casino and Baltavar at least are better grouped with *M. pentelicus*; the other Italian fossils must be termed only *Mesopithecus* sp. The exact biochronologic placement of Casino (which cannot be relocated) and Baccinello V3 is questioned, but Gravitelli (now covered by urban development) appears to predate the deposition of gypsum brought on by Mediterranean desiccation, and Baltavar is associated with the "Unio wetzleri" horizon in the terminal Pontian. Two isolated teeth from MN 13 localities in Hungary (Hatvan and Polgardi) were tentatively referred to this species by Delson (1973 et seq.); they are somewhat large for *M. pentelicus*, but much smaller than *D. ruscinensis*, to whose origin they may conceivably relate (see below).

*Mesopithecus pentelicus* has been described in detail by Gaudry (1862), Delson (1973), Szalay and Delson (1979), and Zapfe (1991). It is a relatively terrestrially adapted form, probably most similar to the living *Semnopithecus entellus*, and recent studies suggest that its Greek habitats were more forested than previously thought (see Solounias and Dawson-Saunders 1988 and Delson 1994; but compare de Bonis et al. 1992).

*Mesopithecus monspessulanus*'s type locality is Montpellier, southern France. It is basal Pliocene age (early MN 14), and most of the species' range lies within the Pliocene (MN 14–17), from France and England through Romania (see fig. 12.8). Several latest Miocene (or earliest Pliocene) localities have yielded fragmentary dental remains previously assigned to this species but transferred above to *M. pentelicus*. However, de Bonis et al. (1990b) indicated that specimens from the Dytiko localities near Ravin des Zouaves included some which are small for *M. pentelicus* and perhaps best referred here.

The reanalysis of dental metrics discussed above demonstrated that lower molars (and the single known M1 and M2) of Pliocene *M. monspessulanus* are smaller than those of *M. pentelicus* at greater than 99.5% probability (except m2 length at 97.5% and m3 length not distinct). A proba-
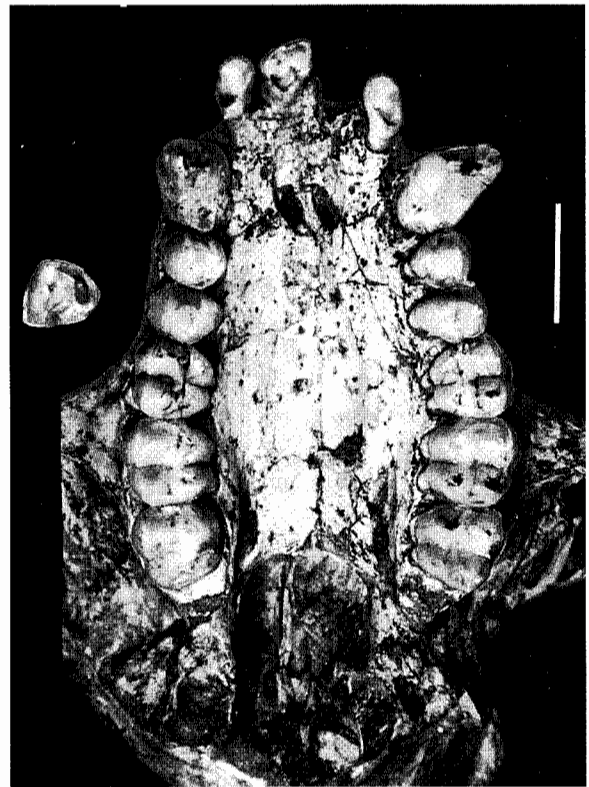


FIGURE 12.9 Upper dentition of *Mesopithecus pentelicus:* palate of male from Pikermi, compared to P4 from Wissberg. Scale bar = 1 cm.

ble female corpus fragment from Dytiko 1 with a measurable m3 differs from *M. pentelicus* in both widths (but not length) at the 99% level but can not be separated from *M. monspessulanus*. A male corpus from Dytiko 2 differs in widths from *M. pentelicus* at greater than 99% and in m3 length at 97%, but is not distinct from *M. monspessulanus*. Both specimens are referred to the latter species. De Bonis et al. (1990b) had suggested that some but not all of the Dytiko 2 specimens be so referred, but attributed most of the other Dytiko remains to *M. pentelicus*. Further study is needed to determine if indeed both species are represented in the Dytiko area, but it is interesting to note the rough (MN 13) contemporaneity of larger individuals identified as *M. pentelicus* in Hungary and Italy and at least some smaller individuals referred to *M. monspessulanus* in Northern Greece. This suggests that the latter may have originated at the end of the Miocene from small population(s) of *M. pentelicus*, which adapted to a more arboreal niche.

*Mesopithecus monspessulanus* is distinguished by smaller size, especially narrower teeth, and somewhat less terrestrial adaptation of the postcranium (elbow joint). It apparently inhabited mainly more forested environments (in the Pliocene) than did its congeners.

The morphology, evolution, and biogeography of *Mesopithecus* is summarized as follows:

1. *Mesopithecus delsoni* is formally synonymized with *M. pentelicus*, in that it shows few significant size differences, the supposed greater corpus depth may be due to crushing, and other distinctions do not appear to warrant specific (or subspecific) separation.
2. The premolar from Wissberg is potentially the oldest *M. pentelicus*, but the veracity of its MN 9 age has been brought into question by Bernor (here). Specimens from Pikermi, various Macedonian sites, Maragheh, Molayan, and Grebiniki form the homogeneous core of this species. Late MN 13 specimens from Baltavar (Hungary) and Casino (Italy; age less definitive) are transferred to this species, and some material from Dytiko (Greece) may also belong here; MN 13 specimens from Gravitelli and Brisighella and MN 13/14 teeth from Baccinello V3 (Italy) are not determinable to species at present.
3. The Pliocene age *Mesopithecus monspessulanus* is clearly distinct from *M. pentelicus* in its tooth size and elbow morphology. Of the Miocene assemblage, two jaws from Dytiko (Greece) appear best referred to this taxon.
4. Fragmentary evidence suggests that at the end of the Miocene, *M. pentelicus* gave rise (allopatrically and/or vicariantly?) to the smaller *M. monspessulanus* and the larger, more terrestrial forest-dwelling *Dolichopithecus* (see below).

*Dolichopithecus ruscinensis*   The type locality of this species is at Serrat d'en Vacquer (near Perpignan), Roussillon, southern France, and all specimens come from deposits that are Pliocene in age (MN 14–17?). A single nearly complete ulna from the locality of Pestlörinc (previously Pestszentlörinc, Hungary; Kretzoi 1954, 1969a) can be securely identified as this taxon due to the highly terrestrially adapted nature of its postcranium (fig. 12.10). In previous reviews, Delson (1975; Szalay and Delson 1979) followed Kretzoi (1969a) in dating this locality to early MN 13, but Kordos (pers. comm.; Jasko and Kordos 1990) has now shown that the fauna and stratigraphic position of the site place it in the earlier Pliocene, in MN 14 or 15. Previously, it was suggested that *Dolichopithecus* might have arisen in the more forested region of northern Central Europe at the end of the Turolian, when southern areas saw some diversification of *Mesopithecus*. However, the younger date for Pestlörinc deprives this hypothesis of any direct paleontological support. Similarly, the two large teeth from other Hungarian sites mentioned above (see *M. pentelicus*) might have supported the idea of a large and eventually more terrestrial population of the latter species giving rise to *Dolichopithecus*, but Polgardi (MN 13) only yielded a partial upper canine, and the lower molar from Hatvan is probably comparable in age to Pestlörinc (Kordos, pers. comm.). Further morphological details on the species are
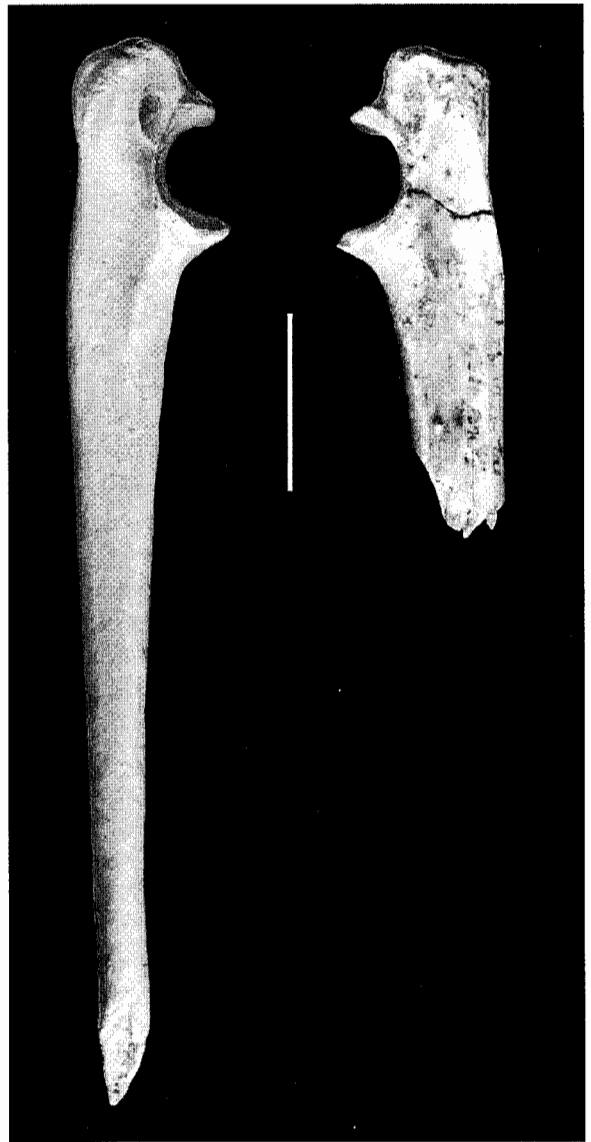


FIGURE 12.10  Medial view of ulnae of ?male *Dolichopithecus ruscinensis*, left to right: Pestszentlôrinc (left), Perpignan (right). Scale bar = 3 cm.

provided by Delson (1973) and Szalay and Delson (1979) as well as Depéret (1890), but at present it is not known from any Miocene site and thus is outside the scope of this chapter.

## CERCOPITHECINAE

The most recent addition to the European Miocene primate fauna is the presence of macaque in the karst fissure of Casablanca M, in eastern Spain (*Macaca* sp.; Moyà-Solà et al. 1992). The deposits are correlated with late MN 13 on the basis of rodent and other fauna, but the macaque specimens have not yet been described. *Macaca sylvanus* "subspecies" are known throughout Europe and into Southwestern Asia from early Pliocene through late

Pleistocene, and the species is extant in Northwestern Africa and on Gibraltar.

## Chronology and Biogeography

We have reported here twenty-three taxa of Miocene European and Southwest Asian catarrhine primates. Table 12.8 gives our present knowledge of species chronologic ranges by province, while figure 12.11 gives biogeographic ranges by species to identify patterns of biogeographic connections and disconnections. Figures 12.12–12.14 map fossiliferous localities by taxon for three time intervals: middle Miocene, Vallesian, and Turolian. European and West Asian catarrhine primates reveal a complex pattern of biogeographic first occurrences, interprovincial range extension, and vicariance. We attempt to interpret the various lines of evidence for these observations by evolutionary group below.
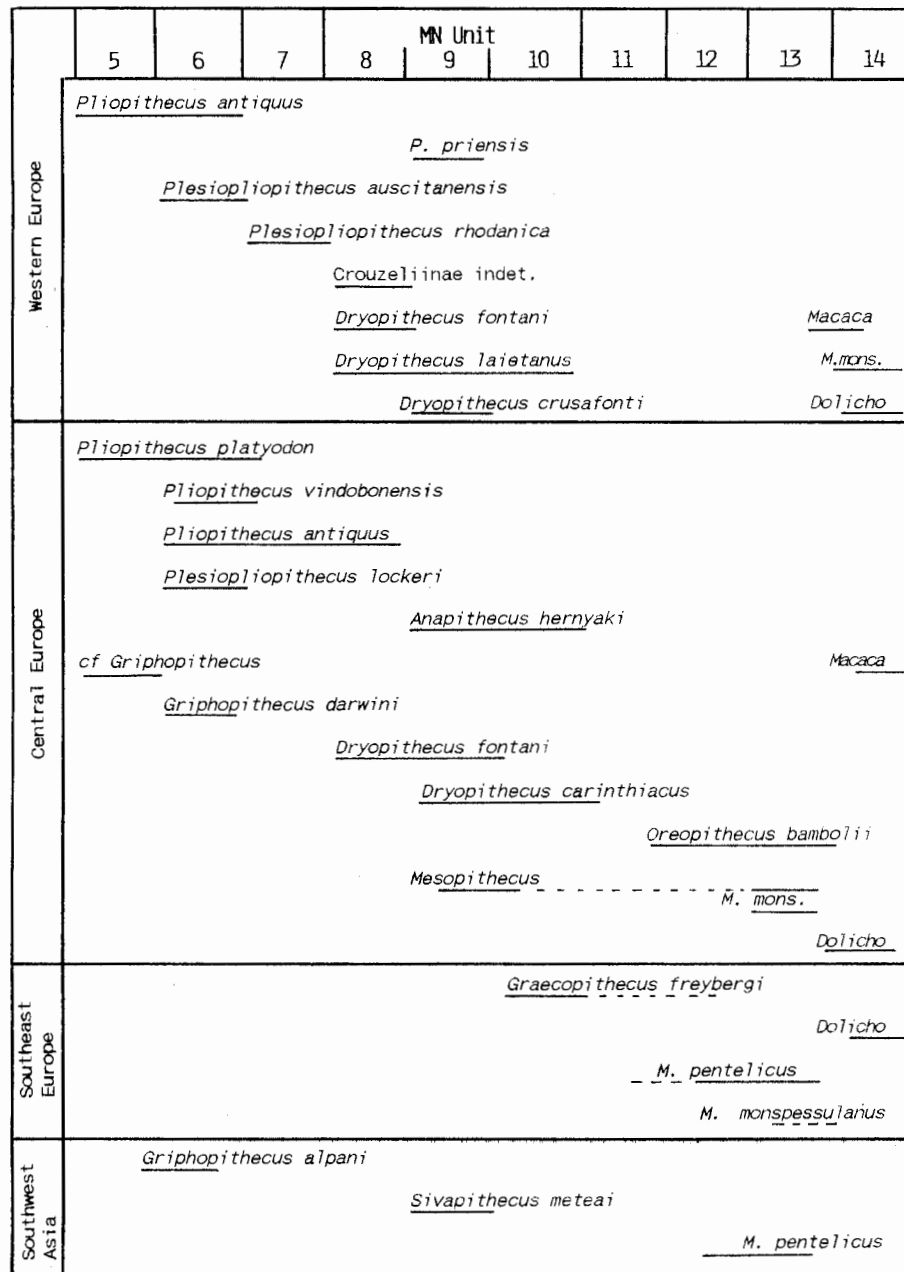


FIGURE 12.11 Distributions of Miocene catarrhine primates in Europe and Southwest Asia. The time scale is given in MN units across the top; four geographic regions are indicated on the left, and the MN ranges of fossil taxa are shown by the solid lines, with uncertain or controversial ranges shown by dashed lines.
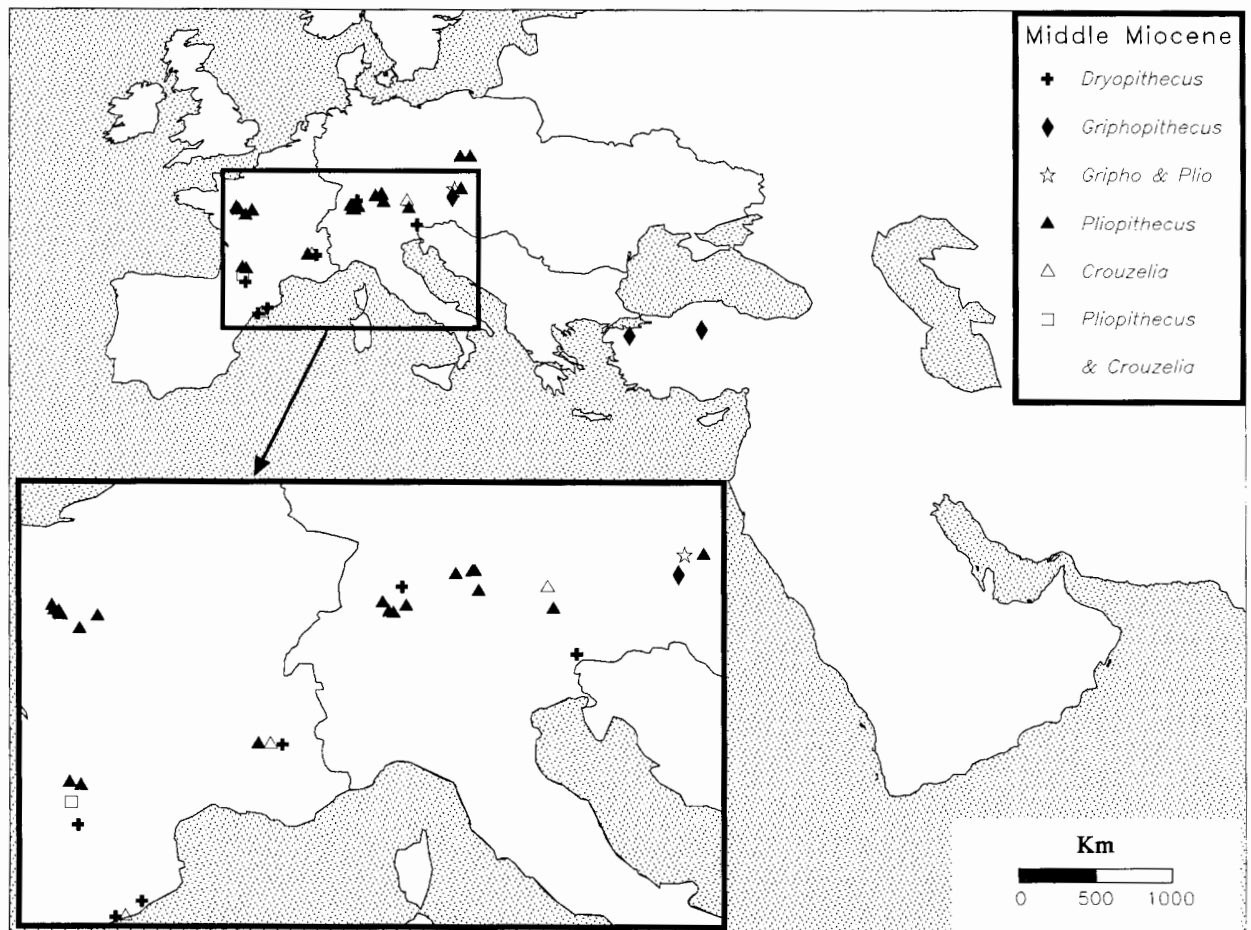
FIGURE 12.12 Distribution of middle Miocene sites yielding catarrhine primates in Europe and Southwest Asia. Central Europe is outlined. The inset enlarges the area boxed on the main map; symbols in the key indicate which taxa are present at each site.

The Pliopithecidae made their first appearance in Europe during MN 5, and became established and geographically widespread by MN 6. The collision of the Afro-Arabian plate with Eurasia during the late Oligocene/early Miocene established a land corridor across which extensive faunal interchange occurred (Adams et al. 1983; Bernor 1983; Whybrow 1984; Thomas 1985; Steininger et al. 1989). The pliopithecids were the earliest catarrhines to migrate into Europe (Thomas 1985; Barry et al. 1985, 1987; Bernor et al. 1988a; Harrison et al. 1991a), and although they almost certainly originated in Africa during the Oligocene, their evolutionary history is unknown until after their arrival in Europe. Pliopithecids are unknown from the Eastern Mediterranean and Southeastern Europe, but they are common and have a wide distribution across Western and Central Europe.

The earliest pliopithecid-bearing localities in Europe are correlated with MN 5. Three species of *Pliopithecus* are represented during the period MN 5–6 interval: *Pliopithecus antiquus* from sites in France and possibly also

Switzerland and Germany; *Pliopithecus vindobonensis* from Neudorf-Spalte, the Republic of Slovakia; and *Pliopithecus platyodon* from Elgg, Switzerland. The earliest crouzeliines, *Plesiopliopithecus lockeri* from Trimmelkam in Austria and *Plesiopliopithecus auscitanensis* from Sansan in France, are probably slightly later, correlated with MN 6, and according to Harrison they were probably derived from the pliopithecines. Andrews's (1980) view that the crouzeliine dental morphology was primitive is receiving support from new analysis of *Anapithecus* material from Rudabánya (Kordos, in prep.).

Harrison et al. (1991a) have recently suggested that the high taxonomic diversity at the time of pliopithecid first appearance may indicate that their initial migration involved multiple species that were derived from a diverse community of pliopithecids that existed prior to their arrival in Europe. If this proves to be the case, it would have important implications for understanding the zoogeographic relationships of Eurasian pliopithecids. On the other hand, there could have been a considerable period
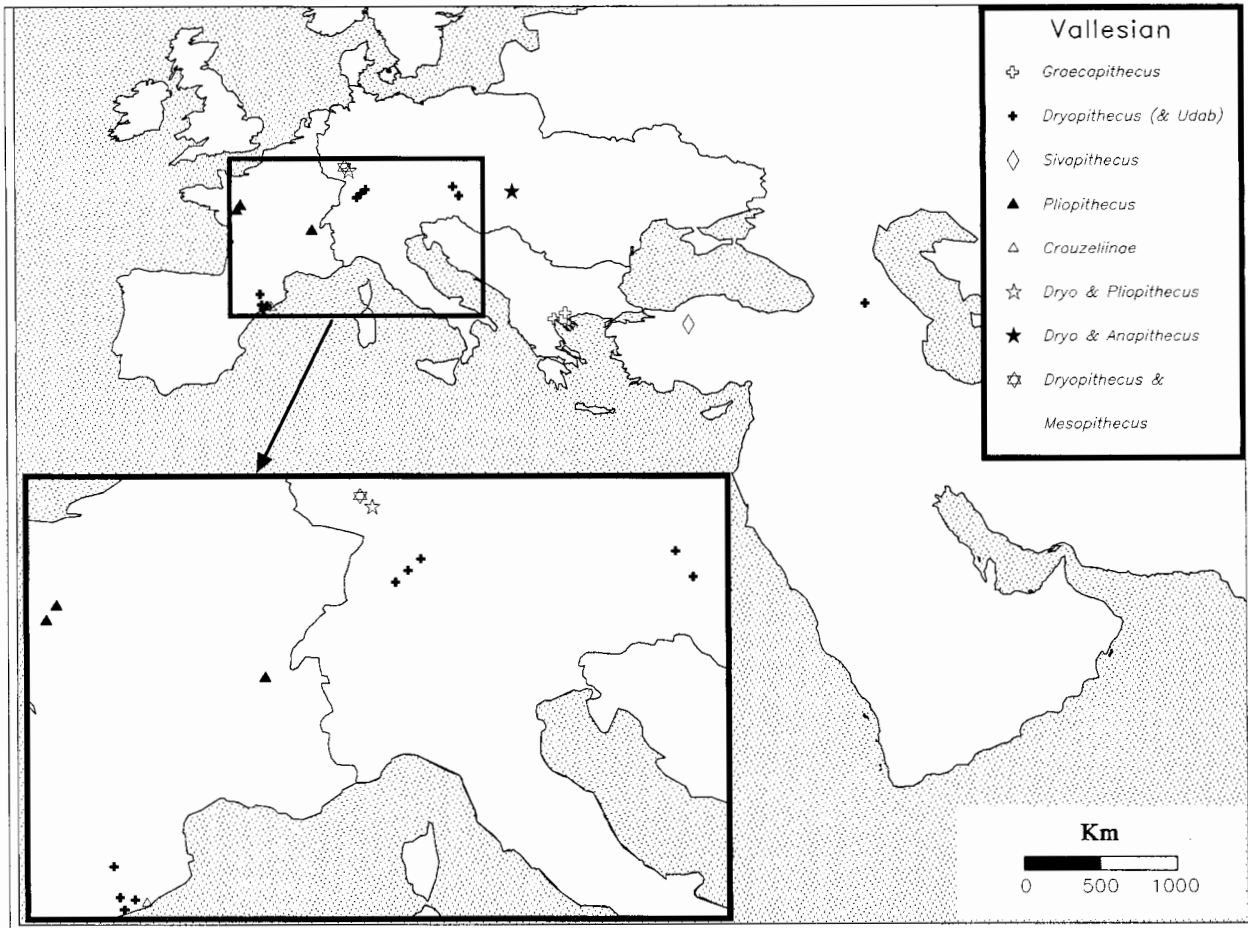
FIGURE 12.13 Distribution of Vallesian sites yielding catarrhine primates in Europe and Southwest Asia. Central Europe is outlined. The inset enlarges the area boxed on the main map; symbols in the key indicate which taxa are present at each site.

of speciation in Southern Europe that is still unknown in the fossil record. Unfortunately, these hypotheses can only be tested with the discovery of ancestral pliopithecids in Europe or Africa.

Although there is a general decline in their relative abundance and species diversity during the middle and late Miocene, pliopithecids remained widespread in Europe throughout the late Astaracian and early Vallesian (MN 7–9). A number of specimens tentatively referred to *Pliopithecus antiquus* are recorded at sites in Poland (Opole, MN 7 and Przeworno II, MN 8), Spain (Castell de Barberà, MN 9) and France (MN 9). If these identifications are confirmed by additional material, they greatly extend the geographic and temporal range of this species, covering most of Europe with a latitudinal range from 42° N to 50° N, and ranging from MN 5 to MN 9. The pliopithecines began to decline in Europe before the crouzeliines, which continue well into the late Miocene of Europe, being represented by abundant remains of *Anapithecus hernyaki* from Rudabánya (MN 9) and an undescribed species from Terrassa, Spain (MN 10). However, the absence of pliopi-

thecids from Turolian sites (MN 11 to 13) strongly suggests that the family had become extinct in Europe by the close of the Vallesian. Nevertheless, a large and specialized crouzeliine, *Laccopithecus robustus*, did survive in China until Turolian correlative time (Wu and Pan 1984; Harrison 1987a; Pan 1988; Pan et al. 1989).

The hominoids made their first appearance in Europe during MN 5 or 6. There is a single lower molar of a large hominoid from Engelswies, which is correlated with MN 5 (Heizmann 1992), and the middle Miocene fauna from Paşalar in Turkey is early MN 6, similar in age to the Neudorf-Sandberg fauna (Steininger et al., this volume). The hominoid recognized from these sites is the genus *Griphopithecus*, which forms a distinct clade with three species, *G. darwini* in Central Europe and *G. alpani* and *G sp* in Southwestern Asia. Andrews and Martin (here; Andrews and Tobien 1977; Andrews 1992) and Begun (1992c) argue for a close evolutionary relationship between *Griphopithecus* and the East African early/middle Miocene form *Kenyapithecus wickeri*. Following Bernor and Tobien (1990) it would appear that their first occurrence corres-
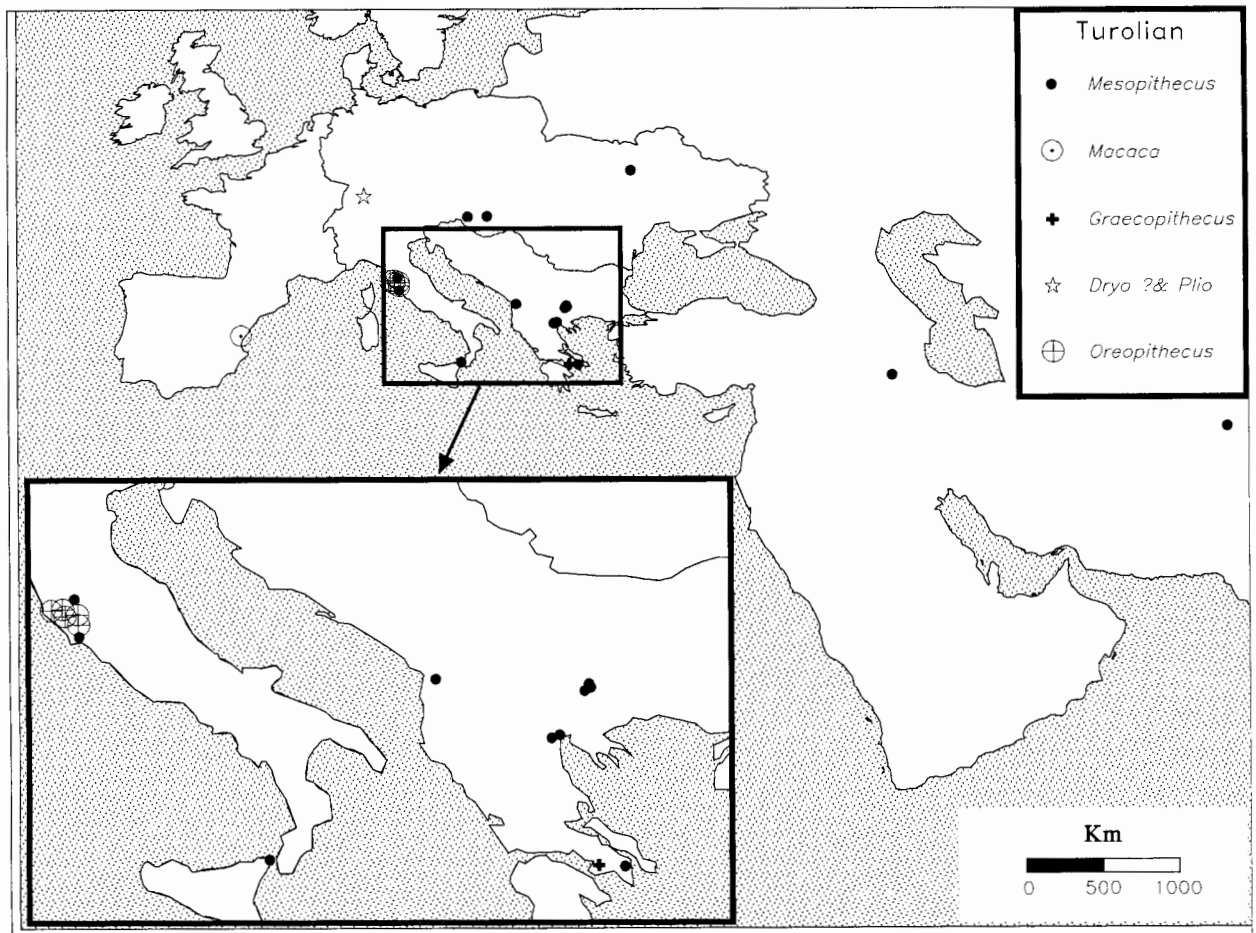
FIGURE 12.14 Distribution of Turolian sites yielding catarrhine primates in Europe and Southwest Asia. Central Europe is outlined. The inset enlarges the area boxed on the main map; symbols in the key indicate which taxa are present at each site.

ponds with the late Langhian regression (= basal MN 6), when a broad continental shelf was exposed between Eurasia and Africa-Arabia.

Begun (1992a, 1992c) has argued that the Kenyapithecini (what Begun refers to as "griphopiths") represent the sister-taxon of all later hominids. We take the opposing view that kenyapithecins are the sister-group to the earlier afropithecins, locating the origin of the former securely in Africa. Moreover, there is a chronologic hiatus between *Griphopithecus* (earlier MN 6) and the first occurrence of *Dryopithecus* (MN 7 + 8) (see: Steininger et al. 1989 and this volume) that apparently witnessed major changes in cranio-dental and postcranial anatomy. For these reasons we consider that the radiations of kenyapithecins and dryopithecins are independent of each other in evolutionary terms, while at the same time we group them together taxonomically on the basis of their common evolutionary grade.

The *Dryopithecus*-group first appears in Western Europe (St. Gaudens, MN 8; Mein 1989; Steininger et al. 1989) and Central Europe (St. Stephan, MN 8, lower Sarmatian s.s. of Vienna-Pannonian Basins, Steininger et al. 1989 and this volume). Whether these first occurring *Dryopithecus* are referable to *D. fontani* alone, or to *D. fontani* (St. Gaudens) and *D. carinthiacus* (St. Stephan), is currently debated, but the latter course is followed here.

There is good evidence for at least two species of western *Dryopithecus* by MN 8, including *D. fontani* from St. Gaudens and *D. laietanus* from Spain. Begun (1992b) has provided evidence for an additional Spanish species, *D. crusafonti*, in MN 8/9, but we are uncertain about the validity of this species (i.e., its distinction from *D. fontani*) and in any case, the specimen from Seu d'Urgell is best identified as *D. fontani*.

The evolutionary pattern of *Dryopithecus* suggests that there was an early MN 8 separation of the Spanish dryopithecines (except for the specimen from Seu d'Urgell, which is on the southern flanks of the Pyrenees) from other Western and Central European species. This suggests a possible MN 7 + 8 dispersal of a primitive member of *Dryopithecus*. *Dryopithecus carinthiacus* is recognized as a clade distinct from Spanish and French taxa, revealing a vicari-

TABLE 12.7. *Miocene Primate Localities in Austria (Au), Germany (G), and Switzerland (S)(Continued)*

Primate Localities in Austria (Au), Germany (G), and Switzerland (S)

| Locality | MN Zone | Species | References for dates |
|---|---|---|---|
| Mariathal (Au) | MN 9 | *Dryopithecus carinthiacus* | Mein 1986, 1990; Thenius 1982 |
| Eppelsheim (G) | MN 9 | cf. *Dryopithecus* sp. ( = *Paidopithex rhenanus*) Pliopithecid indet. ("*Semnopithecus*" *eppelsheimensis*) [type locality] | Mein 1986, 1989 |
| Wissberg (G) | MN 9 | *Dryopithecus* sp. cf. *Mesopithecus pentelicus* | Mein 1986, 1989 |
| Melchingen (G) | MN 9 | *Dryopithecus* sp. | Mein 1986, 1989 |
| Götzendorf (Au) | MN 9/10 | *Anapithecus hernyaki* | Zapfe 1989 |
| Salmendingen (G) | MN 11 | ?*Dryopithecus brancoi* ( = *Neopithecus brancoi*;) type locality; = pliopithecid or dryopithecine??) ?Pliopithecid (?*Anapithecus hernyaki*) | Mein 1986, 1989 |
| Trochtelfingen (G) | ? | *Dryopithecus* sp. | |
| Ebingen (G) | ? | *Dryopithecus* sp. | |

Primate Localities in Italy

| Locality | MN Zone | Species | References for Dates |
|---|---|---|---|
| Baccinello V1 | MN 12 | *Oreopithecus bambolii* | Hürzeler and Engesser 1976); Azzaroli et al. 1986; Harrison and Harrison 1989 |
| Casteani | MN 12 | *Oreopithecus bambolii* | Hürzeler and Engesser 1976; Azzaroli et al. 1986; Harrison and Harrison 1989 |
| Montemassi | MN 12 | *Oreopithecus bambolii* | Hürzeler and Engesser 1976); Azzaroli et al. 1986; Harrison and Harrison 1989 |
| Ribolla | MN 12 | *Oreopithecus bambolii* | Hürzeler and Engesser 1976; Azzaroli et al. 1986; Harrison and Harrison 1989 |
| Baccinello *Cardium* horizon | MN 12/13 | *Oreopithecus bambolii* | Rook et al. 1995 |
| Monte Bamboli | MN 13 | *Oreopithecus bambolii* [type locality] | Hürzeler and Engesser 1976; Azzaroli et al. 1986; Harrison and Harrison 1989 |
| Baccinello V2 | MN 13 | *Oreopithecus bambolii* | Hürzeler and Engesser 1976); Azzaroli et al. 1986; Harrison and Harrison 1989 |
| Fiume Santo | MN 13 | | Cordy and Ginesu 1994; Kotsakis et al. 1995 |
| Gravitelli | MN 13 | *Mesopithecus* sp. | Seguenza 1902 |
| Baccinello V3 | MN 13/14 | *Mesopithecus* sp. | Mein 1989 |
| Casino | MN 13/14 | *Mesopithecus* cf. *pentelicus* | Mein 1989 |

Primate Localities in Bulgaria (B), the Republic of Slovakia (S), Hungary (H), Poland (P), Ukraine (U), and ex-Yugoslavian Macedoni (Y)

| Locality | MN Zone | Species | References for Dates |
|---|---|---|---|
| Neudorf-Spalte (S) | Upper MN 5 | *Pliopithecus vindobonensis* [type locality] | Mein 1986; Steininger 1986; Ginsburg and Mein 1980; Ginsburg 1986 |
| Neudorf-Sandberg (S) | MN 6 | *Griphopithecus darwini* ( = *Dryopithecus darwini*) ( = *Griphopithecus suessi*) | Mein 1989 |
| Przeworno II (P) | MN 8 | *Pliopithecus* cf. *antiquus* | Kowalski and Zapfe 1974; Ginsburg 1986 |
| Opole (Oppeln) (P) | MN 7 | *Pliopithecus* cf. *antiquus* | Steininger 1986; Ginsburg 1986 |
| Rudabánya (H) | Upper MN 9 | *Dryopithecus carinthiacus* ( = *Rudapithecus hungaricus*) ( = *Bodvapithecus altipalatus*) *Anapithecus hernyaki* ( = *Rangwapithecus [Ataxopithecus] sericus*) [type locality] | Mein 1986, 1989; Steininger 1986; Kordos 1987 |
| Grebeniki [1] (U) | MN 11/12 | *Mesopithecus pentelicus* ( = *M. "ukrainicus"*) | Mein 1989 |
| Titov Veles (Y) | MN 12/13 | *Mesopithecus pentelicus* | Ciric 1957 |
| Kalimanci 2 (B) | MN 12/13 | *Mesopithecus pentelicus* | Bakalou and Nikolov 1962 |
| Kromidovo 2 (B) | MN 12/13 | *Mesopithecus pentelicus* | Bakalou and Nikolov 1962 |
| Gorna Susica (B) | MN 12/13 | *Mesopithecus pentelicus* | Bakalou and Nikolov 1962 |
| Polgardi (H) | MN 13 | cf. *Mesopithecus pentelicus* | Mein 1989 |
| Baltavar (H) | MN 13 | *Mesopithecus* cf. *pentelicus* | Mein 1989 |

TABLE 12.7. *Miocene Primate Localities in Europe and Southwest Asia*

| Primate Localities in France | | | |
|---|---|---|---|
| Locality | MN Zone | Species | References for dates |
| Pontlevoy-Thenay | MN 5 | *Pliopithecus antiquus* | Ginsburg 1986 |
| Manthelan | MN 5 | *Pliopithecus antiquus* (= *Pliopithecus piveteaui*) | Ginsburg 1986 |
| La Condouc | MN 5 | *Pliopithecus antiquus* | Baudelot and Collier 1978 |
| Faluns of Touraine and Anjou[1] | Upper MN 5 | *Pliopithecus antiquus* | Ginsburg 1986, 1989 |
| Liet | Lower MN 6 | *Pliopithecus antiquus* | Collier 1978, 1979 |
| Sansan | MN 6 | *Pliopithecus antiquus* [type locality] *Plesiopliopithecus auscitanensis* (= *Crouzelia auscitanensis*) [type locality] | Ginsburg 1986 |
| La Grive-Saint-Alban (Peyre and Beau) | MN 6 | *Pliopithecus antiquus* | Ginsburg 1986 |
| La Grive–Saint-Alban (L7) | MN 7 | *Plesiopliopithecus rhodanica* (= *Crouzelia rhodanica*) [type locality] | Ginsburg 1986 |
| St. Gaudens | MN 8 | *Dryopithecus fontani* [type locality] | Mein 1986, 1989 |
| La Grive–Saint-Alban (L3) | MN 8 | *Dryopithecus fontani* | Mein 1986, 1989 |
| Doué-la-Fontaine | Lower MN 9 | *Pliopithecus antiquus* | Ginsburg 1986, 1989 |
| Meigné-le-Vicomte | MN 9 | *Pliopithecus antiquus* | Ginsburg 1989, 1989 |
| Priay II Upper | MN 9 | *"Pliopithecus" priensis* [type locality] | Welcomme et al. 1991 |

[1] Including the following localities: Channay, Denezé, Hommes, Lasse, Noyant-sous-le-Lude, Ponbrault, Pont-Boutard, Pontigné, Rillé, Savigné-sur-Lathan

| Primate Localities in Spain | | | |
|---|---|---|---|
| Locality | MN Zone | Species | References for Dates |
| Sant Quirze | MN 8 | *Dryopithecus laietanus* | Mein 1986, 1989 |
| Can Vila | MN 8 | *Dryopithecus laietanus* (= *Sivapithecus occidentalis*) | Mein 1986 |
| Can Feliu | MN 8 | Crouzeliine indet. | Ginsburg 1986 |
| Seu d'Urgell (El Firal) | Lower MN 9 | *Dryopithecus fontani* | Mein 1986 |
| Can Mata 1 | MN 9 | *Dryopithecus laietanus* | Mein 1986, 1989 |
| Can Ponsic | MN 9 | *Dryopithecus crusafonti* [type locality] | Mein 1986, 1989 |
| Castell de Barberà | MN 9 | *Dryopithecus laietanus* | Mein 1986 |
| | | *Pliopithecus* cf. *antiquus* | Mein 1986 |
| Can Llobateres | MN 9 | *Dryopithecus laietanus* (= *Dryopithecus piveteaui*) (= *Rahonapithcus sabadellensis*) | Mein 1986, 1989 |
| La Tarumba 1 | MN 10 | *Dryopithecus laietanus* (= *Hispanopithecus laietanus*) [type locality] | Mein 1986, 1989 |
| Polinya II | MN 10 | *Dryopithecus laietanus* | Mein 1986 |
| Terrassa | MN 10 | Crouzeliine Gen. et sp. nov. | |
| Casablanca-M | Upper MN 13 | *Macaca sp.* | Moyà-Solà et al. 1992 |

| Primate Localities in Austria (Au), Germany (G), and Switzerland (S) | | | |
|---|---|---|---|
| Locality | MN Zone | Species | References for dates |
| Elgg (S) | MN 5 | *Pliopithecus platyodon* [type locality] | Ginsburg 1986 |
| Engelswies (G) | MN 5–6 | ?*Griphopithecus sp.* | Heizmann 1992 |
| Kreuzlingen (S) | MN 6 | *Pliopithecus* cf. *antiquus* | Ginsburg 1986 |
| Rümikon (S) | Lower MN 6 | *Pliopithecus* cf. *antiquus* | Engesser et al. 1981 |
| Stein am Rhein (S) | MN 6 | *Pliopithecus antiquus* | Ginsburg 1986 |
| Göriach (Au) | Upper MN 6 | *Pliopithecus platyodon* | Steininger 1986 |
| Trimmelkam (Au) | MN 6? | *Plesiopliopithecus lockeri* [type locality] | Ginsburg 1986 |
| Diessen am Ammersee (G) | MN 6 | *Pliopithecus* cf. *antiquus* | Ginsburg 1986 |
| Stätzling (G) | MN 6 | *Pliopithecus antiquus* | Ginsburg 1986 |
| Klein Hadersdorf (Au) | MN 6 | *Griphopithecus darwini* (= *Austriacopithecus weinfurteri*) (= *Austriacopthecus abeli*) | Mein 1989 |
| Gallenbach 2(a?) (G) | MN 6 | *Pliopithecus antiquus* | Heissig 1989 |
| Ziemetshausen (G) | MN 6 | *Pliopithecus antiquus* | Heissig 1989 |
| St. Stephan (Au) | MN 8 | *Dryopithecus carinthiacus* [type locality] | Mein 1986, 1989; Mottl 1957 |

| Locality | MN Zone | Species | References for Dates |
|---|---|---|---|
| | | Primate Localities from Greece (Gr), Iran (Ir), Afganistan (Af), Turkey (T), and Georgia (Ge) | |
| Paşalar (T) | MN 5–6 | *Griphopithecus alpani* | Mein 1989 |
| | | *Griphopithecus* sp. | Andrews 1989 |
| Çandir (T) | MN 6 | *Griphopithecus alpani* | Mein 1989 |
| | | [type locality] | |
| Yassiören (T) | MN 9 | *Sivapithecus meteai* | Mein 1989 |
| | | [type locality]; | |
| Ravin de la Pluie (Gr) | MN 10 | *Graecopithecus freybergi* | Mein 1986 |
| | | ( = *Ouranopithecus macedoniensis*) | |
| Xirochori 1 (Gr) | MN 10 | *Graecopithecus freybergi* | de Bonis et al. 1990 |
| | | ( = *Ouranopithecus macedoniensis*) | |
| Udabno (Ge) | MN 10? | *Udabnopithecus garedziensis* | Mein 1986 |
| | | [type locality] | de Bonis et al. 1990 |
| Pyrgos (Tour La Reine) (Gr) | MN 10? | *Graecopithecus freybergi* | Mein 1986 |
| | | [type locality] | |
| Ravin des Zouaves 5 (RZO) (Gr) | MN 11/12 | *Mesopithecus pentelicus* | de Bonis et al. 1987, 1989; Mein 1989 |
| Pikermi (Gr) | MN 11/12 | *Mesopithecus pentelicus* | Mein 1989 |
| | | [type locality] | Bernor et al. this volume |
| Vathylakkos (and Ravin X) (Gr) | MN 12/13 | *Mesopithecus pentelicus* | de Bonis et al. 1987, 1990; Mein 1989 |
| Pikermi "II"-Chomateri (Gr) | MN 12/13 | *Mesopithecus p.* "microdon" | Zapfe 1991; Mein 1990 |
| Dytiko locs (1DTK, 2 DIT, 3 DKO) (Gr) | MN 12/13 | *Mesopithecus* cf. *pentelicus?* and *Mesopithecus* cf. *monspessulanus* | de Bonis et al. 1987, 1989; Mein 1989 |
| Maraghah (Middle) Beds (Ir) | MN 12/13 | *Mesopithecus pentelicus* | |
| Molayan (Af) | MN 12/13 | *Mesopithecus pentelicus* | Heintz et al. 1981 |

TABLE 12.8 *Biogeographic Ranges of Middle and Late Miocene European and Southwest Asian Catarrhine Primates. Ranges are shown by continuous x's if they cross geographic boundaries. Age ranges are indicated by MN zones, with U signifying upper part of the zone, and L signifying lower part of the zone.*

| Taxon | Western Europe | Central Europe | SE Europe | SW Asia | Age Range |
|---|---|---|---|---|---|
| *Pliopithecus platyodon* | | x | | | MN 5–6 |
| *Pliopithecus antiquus* | xxxxxxxxxxxxxxx | | | | MN 5–9 |
| *Pliopithecus vindobonensis* | | x | | | UMN 6 |
| *Pliopithecus priensis* | x | | | | UMN 9 |
| *Plesiopliopithecus auscitanensis* | x | | | | MN 6 |
| *Plesiopliopithecus lockeri* | | x | | | MN 6 |
| *Plesiopliopithecus rhodanica* | x | | | | MN 7 |
| *Anapithecus hernyaki* | | x | | | UMN 9–?11 |
| Pliopithecidae indeterminate | | x | | | MN 9 |
| *Oreopithecus bambolii* | | x | | | MN 12–13 |
| cf. *Griphopithecus* sp. | | | | x | MN 5–6 |
| *Griphopithecus alpani* | | | | x | MN 5–6 |
| *Griphopithecus darwini* | | x | | | MN 6 |
| *Sivapithecus meteai* | | | | x | MN 9 |
| *Graecopithecus freybergi* | | | x | | MN 10–?12 |
| *Dryopithecus fontani* | xxxxxxxxxxxxxx | | | | MN 8–9 |
| *Dryopithecus carinthiacus* | | x | | | MN 8–9 |
| *Dryopithecus laietanus* | x | | | | MN 8–10 |
| *Dryopithecus crusafonti* | x | | | | MN 9 |
| *Mesopithecus pentelicus* | | xxxxxxxxxxxxxxxxxxxxxxxxxxx | | | MN 11?–13 |
| *Mesopithecus monspessulanus* | xxxxxxxxxxxxxxxxxxxxxxxxxxx | | | | MN 13–15 |
| *Dolichopithecus ruscinensis* | xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx | | | | MN 14–15 |
| *Macaca* sp. | x | | | | MN 13 |
| *Macaca* sp. | xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx | | | | MN 13–17 |

ance of Western and Central European *Dryopithecus* by MN 9. This corresponds to a marked shift in palaeovegetation and climates at the middle/late Miocene boundary (Bernor et al. 1988b, 1990), closely equivalent to the Astaracian/Vallesian boundary (MN 8/9; Swisher, this volume).

*Dryopithecus* persisted across its range through MN 9 and perhaps into MN 10/11 in Central Europe only. Its extinction coincided with the shift from warm temperate forests to more seasonal and open country biotopes (Bernor 1983; Bernor et al. 1988b).

Coinciding with the temporal range of *Dryopithecus* was the first appearance of a member of the orang utan clade, the Ponginae. The genus *Sivapithecus* is first reported in the Siwaliks as occurring roughly equivalent to the late Astaracian (MN 7 + 8) in the European sequence (Kappelman et al. 1991). The only species with a distribu-

tion including the biogeographic regions under consideration in this paper is *Sivapithecus meteai*, from latest MN 9 horizons in Turkey (Kappelman et al., this volume).

A significant morphologic advance is seen in *Graecopithecus*, first known in Southeastern Europe during MN 10. *Graecopithecus* shares a number of characters in common with hominines, although it is uncertain whether they are true synapomorphies, plesiomorphies, or homoplasies. If *Graecopithecus* does prove to share a unique relationship with the African ape-human lineage, then a hitherto undocumented late Miocene biogeographic connection must have existed between Southeastern Europe and East Africa during MN 11 time. It must also be considered that this age is close to the postulated divergence within the African ape and human clade (Andrews 1986) on the basis of molecular clocks (Bailey et al. 1993).

The data presented here are not inconsistent with the hypothesis that both the Homininae and Ponginae may be derived from a European-Southwest Asian early middle Miocene kenyapithecin, close to that known here as the genus *Griphopithecus*. Asian Ponginae would appear to have been phylogenetically distinct by the later half of the middle Miocene. This hypothesis does not necessarily directly support Sen's (1982) argument based on rodent lineages that there was late middle Miocene biogeographic separation between eastern Greece and Western Anatolia.

To summarize, the early middle Miocene East African kenyapithecins would appear to have extended their range into Central Europe and Southwestern Asia during the late Langhian regression, ca. 15.5–15 Ma (Bernor and Tobien 1990). This clade, currently recognized in Eurasia as species of a single genus, *Griphopithecus*, may have evolved into two broadly vicariant clades: the Southeast European hominine species *Graecopithecus freybergi* and the Southwest and South Asian (Siwaliks) clade *Sivapithecus*. If *Graecopithecus* indeed shares synapomorphies with the African great ape-human clade, an early late Miocene biogeographic connection would have to be recognized between the Eastern Mediterranean and East Africa.

Regardless of the competing phylogenetic arguments that would alter the large hominoid paleobiogeography developed here, Eurasian forms are currently best considered to be a natural group, and do show a strong pattern of biogeographic extension followed by vicariance within the middle and late Miocene intervals. This vicariance is plausibly due to the replacement of subtropical and warm temperate forests with increasingly seasonal open country habitats (Bernor 1983).

The hominoid primate *Oreopithecus bambolii* is known from sites in Italy (i.e., Maremmia in Tuscany and Sardinia) tentatively correlated with MN 12 and MN 13 (Hürzeler and Engesser 1976; Harrison and Harrison 1989; Rook 1993; Cordy and Ginesu 1994; Rook et al., 1996). The geographical range of the species, and its association

with an endemic vertebrate fauna, indicates that it was an insular form, restricted to a small island chain in the Northern Tethys (Hürzeler and Engesser 1976; Harrison and Harrison 1989). From a biogeographical perspective, much of the fauna (e.g., the rodents, lagomorphs, insectivores, lutrines, and aquatic reptiles) appears to have its closest affinities with taxa from continental Europe that presumably arrived by swimming or rafting across the narrow channel that connected the Ligurian Sea with the Adriatic (Harrison and Harrison 1989). However, the neotragine and alcelaphine bovids probably originated in Africa, and appear to have made their way to Italy via an intermittant trans-Tethyan land connection (Thaler 1973; Hürzeler 1983; Thomas 1984a, 1984b; Harrison 1986; Cordy and Ginesu 1994). Previously, Harrison (1986; Harrison and Harrison 1989) has suggested that *Oreopithecus* may have followed the same route as the bovids, having been derived from an oreopithecine ancestral stock in sub-Saharan Africa. However, an alternative explanation is that *Oreopithecus* was descended from one of the Eurasian hominids, possibly even *Dryopithecus*, and that it survived as a specialized, relictual taxon in an insular setting, long after all other hominids had become extinct in mainland Europe (Harrison and Rook, in prep.). Although provincially quite distinct, these *Oreopithecus*-bearing localities are placed for convenience into the Central European biogeographical province.

Among monkeys, the colobines are a group with low species diversity at any given time in the European and Southwest Asian late Miocene–early Pliocene. The first unequivocal occurrence of colobines is *Mesopithecus pentelicus* reported from Southeastern Europe (Greece) and Southwestern Asia. According to Bernor et al. (this volume), Pikermi would be the oldest certain *Mesopithecus*-bearing locality (MN 11/12, ca. 8.3–8.2 Ma). The age of the single tooth from Wissberg needs clarification, but if it is indeed MN 9 (ca. 10 Ma), it compares with the oldest African colobine *Microcolobus tugenensis* (Benefit and Pickford 1986).

*Mesopithecus pentelicus* is abundantly represented from MN 11–13 of Central Europe, Southeastern Europe, and Southwestern Asia. It appears to have continued to the end of MN 13 in Italy and Hungary, but was perhaps replaced in Greece by *M. monspessulanus* (known in the Pliocene from Western and Central Europe, MN 14–16/17). A new colobine lineage, *Dolichopithecus ruscinensis*, also was thought to first appear in MN 13 before becoming even more widespread in the Pliocene (Western, Central, and Southeastern Europe, MN 14–16/17), with an apparent congener in Northeastern Asia (see Delson 1994). However, as discussed above, the relevant localities of Pestlörinc and Hatvan are probably earlier Pliocene rather than Miocene in age, vitiating this argument. Although Strasser and Delson (1987) rejected Delson's earlier (1973 et seq.)

hypothesis of the *M. pentelicus* ancestry of *Dolichopithecus* because of apparent polarity reversal of some pedal traits, this hypothesis was resuscitated by Delson (1994) based on the variability of these features in Strasser's modern taxa (Strasser 1988). The widespread occurrence of *D. ruscinensis* in the more "forested" early Pliocene and the possible identification of *M. monspessulanus* at Dytiko suggest that environmental changes at the end of the Miocene could well have led to vicariant character displacement and the allopatric origin of the two mainly Pliocene taxa from *M. pentelicus* (as in Delson 1973). More material from these and other latest Miocene sites would be of great interest in testing this hypothesis, which is rather similar to the pattern observed in the other European catarrhines discussed above.

The presence of a few *Macaca* teeth in the latest MN 13 site of Casablanca-M, eastern Spain, presages the broad geographic occurrence of this genus throughout the Pliocene and Pleistocene as far north as Britain and eastward into the Caucasus, Israel, and Greece. Living species of the genus occur from Pakistan eastward to Japan, in North Africa and Indonesia, but neither fossils nor extant populations occupy the area between the Levant and the Siwaliks. North African late Miocene and early Pliocene cercopithecines are referred to *Macaca*, but definitive diagnosis of the genus on dental and even mandibular morphology is not realistic. The most interesting question, perhaps, is the geographic origin of the Casablanca M fossils.

Various authors have discussed trans-Mediterranean and peri-Gibraltarean dispersal of North African mammals into Europe at the end of the Miocene or early in the Pliocene, often related to Messinian desiccation. Aguilar et al. (1984), for example, found that an assemblage of rodents from the latest Miocene of southern Spain included no North African taxa but only those with closest relatives in Asia or eastern Africa. They thus rejected the possibility of a migration into Spain from North Africa during the Messinian/late Turolian in favor of a route along the northern edge of the Mediterranean.

On the other hand, Benson and Rakic-El Bied (1991; Benson, pers. comm.) discussed in detail the paleoceanography of the Western Mediterranean during the Messinian. They suggested that in the pre-desiccation phase, Mediterranean water flowed out to the Atlantic through the Betic region of southern Spain (north of Gibraltar), while Atlantic water entered the Mediterranean through the Rif passage(s) in Morocco, between the Atlas and the Tangier areas. The region between these two passages probably alternated between being submerged, island arcs or being connected to continental platforms. It is possible that some mammalian and other terrestrial species, including hippopotamus and cercopithecine monkeys, might have traversed this "sweepstakes route" to enter southern Spain and dispersed northward during MN 13. With the refilling

of the Mediterranean by the Zanclean Deluge at the beginning of the Pliocene, whether by dint of a "Gibraltar Waterfall" or less spectacular Moroccan waterway, such transit became impossible, sealing the allopatric isolation of various European vertebrate taxa.

## Addendum

Since this article was written, a skull and partial skeleton has been discovered in the Sinap deposits in Turkey (Alpagut et al. in progress). The skull is from a female individual of the same species as the previously described lower face of a male individual from the same site (Andrews and Tekkaya 1980). Originally named *Ankarapithecus meteai*, it was synonymized with *Sivapithecus* as *S. meteai* by Andrews and Tekkaya (1980) as described in this article, but the evidence from the new skull shows it to be lacking several of the key sivapithecin characters linking the group with the orangutan. For example, the orbits are as broad as high, unlike the condition in *Sivapithecus indicus* (Pilbeam 1982), and the brow ridges are relatively well developed, especially for a female individual. The facial profile is only moderately concave and is different from the airorhynch condition in *Sivapithecus*. For this reason we now remove the Turkish species from this genus and resurrect the original name, *Ankarapithecus meteai* (Ozansoy 1957).

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# The Evolution of
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