

Primate Diversity in the Pannonian Basin: In situ evolution, dispersals, or both?

by

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Abstract

Middle and Late Miocene deposits in the Pannonian Basin contain the greatest diversity of primate taxa of any comparably defined geological region in Europe. Three catarrhine superfamilies, five families, six genera and eleven species are known from MN 6 to MN 13 localities in the basin. This level of diversity within a mammalian infraorder rivals that in most other large mammals from the basin, and testifies to the success of this taxon in the region. In addition, globally, some of the richest Miocene primate localities in terms of numbers and completeness of specimens occur in the Pannonian Basin (Göriach, Děvínská Nová Ves, and Rudabánya). In this paper we explore the evidence for this exceptional diversity. In the case of the both the Hominoidea and the Pliopithecoidea, the occurrence and diversity of these taxa in the Pannonian Basin are probably the products of dispersal events followed by *in situ* evolution, although in their details the history of each taxon is different. Cercopithecoidea appear to disperse into the region late and remain relatively rare and minimally diverse. We attribute the dynamics of the history of all three superfamilies to local, regional and global effects at the faunistic, ecological and geological levels.

Keywords: *Dryopithecus*, *Anapithecus*, Middle and Late Miocene Hominoidea

Kurzfassung

Mittel- und Obermiozäne Ablagerungen des Pannonischen Beckens enthalten die meisten Primaten-Taxa aller vergleichbaren geologischen Regionen innerhalb Europas. Drei Unterfamilien der Catarrhini, fünf Familien, sechs

Genera und 11 Arten kennt man aus den Fundstellen des Pannonischen Beckens, deren stratigraphische Reichweite vom MN 6 bis MN 13 reicht. Diese hohe Diversität einer Unterordnung der Säugetiere kann sich mit der anderer Großsäuger messen und zeugt vom Erfolg dieses Taxons in der hier besprochenen Region. Weltweit betrachtet, liegen einige der reichsten Miozän-Fundstellen für Primaten sowohl im Hinblick auf Artenzahl als auch auf Komplettheit der Fundstücke im Pannonischen Becken (Göriach, Děvínská Nová Ves, and Rudabánya). In diesem Artikel gehen wir den Ursachen für diese außergewöhnliche Diversität auf den Grund. Sowohl im Falle der Hominoidea als auch der Pliopithecoidea sind das Vorkommen und die Diversität dieser Taxa im Pannonischen Becken möglicherweise das Produkt von Separation gefolgt von *in situ*-Evolution obwohl natürlich die entwicklungsgeschichtlichen Details jedes Taxons unterschiedlich sind. Nur die Cercopithecoidea sind relativ spät in diese Gegend eingewandert und dabei recht selten und wenig divers geblieben. Wir schreiben die Dynamik und Geschichte dieser drei Überfamilien den lokalen, regionalen und globalen Effekten auf faunistischem, ökologischem und geologischem Niveau zu.

1. Introduction

Over the past ten years our group has been surveying and documenting Middle and Late Miocene terrestrial localities in the Pannonian Basin, with a view towards describing the dynamics of mammal movements, evolution, and extinction during the time period in which the common ancestors of apes and humans diverged. Preliminary results of this survey work are described in more detail in NARGOLWALLA et al. (2007). Here we review the primates from the Pannonian Basin, focusing on the alpha taxonomy, with the goal of resolving issues regarding the relationship of Pannonian taxa to those outside the region. This is a necessary first step to reconstructing their patterns of dispersals and evolution. The primate fossils discussed here were compared to other Miocene catarrhines from Europe, Asia and Africa, and to a large sample of extant primates.

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1.1. Geological background

The Carpathians, Eastern Alps and Dinarides were uplifted as a result of Mesozoic to Cenozoic continental collision between Europe and Africa, with the development of an extensive thrust and strike-slip system occurring as a response to this collision in the present day area of the basin. In all the surrounding orogenic belts, heterogeneity exists in the times of deformation - with the interior areas deformed during the Mesozoic and the exterior areas deformed during the Cenozoic.

Thinning of the continental lithosphere began in the Ottnangian (Early Miocene), resulting in general but moderate subsidence across the region. During the Badenian, north-south orientated compression led to the development of a major east-west trending tensional stress field that resulted in the establishment of an extensional Pannonian Basin system (KÁZMÉR, 1990). This Middle Miocene system consisted of deep, half-grabens and pull-apart basins bounded by listric synthetic and antithetic growth faults that were representative of syn-rift structural features (SZTANÓ & TARI, 1993). Late Miocene to recent post-rift sedimentation occurred during basin-wide subsidence caused by the combined effects of isostatic compensation and lithospheric thermal contraction (KÁZMÉR, 1990, SZTANÓ & TARI, 1993).

The uplift of the Carpathian Mountains had a profound influence on basin sedimentation and potential faunal migration pathways. The overall trend of mountain building due to northeasterly directed thrust tectonics was from northwest to southeast during the Neogene (ROYDEN, 1988, CSONTOS, 1992), following the arc of the present day Carpathians. Lowland or flooded regions were located in the Vienna Basin, west of the uplifted southern extent of the Eastern Carpathians and in the South Carpathians in the Sarmatian and early to middle Pannonian. These regions are thought to provide evidence for potential migration pathways at this time (see NARGOLWALLA et al. (2007), for a more in depth review of these pathways).

Volcanic activity in the Pannonian Basin region occurred in almost every epoch of the Mesozoic and Cenozoic, and reached a climax during the Miocene (TRUNKÓ, 1996). Vast quantities of acidic (rhyolitic) and intermediate (andesitic/dacitic) lavas, ignimbrites and pyroclastics were extruded over much of the northern areas of the Pannonian Basin, where thicknesses exceeded 2000 m (POPOV et al., 2004). In the Middle Miocene, large blankets of rhyolite tuff (useful for stratigraphic correlations and radiometric dating) were deposited mainly in the northern areas of the Pannonian Basin, where they interfingered with syn-rift sediments (CSATÓ, 1993). This volcanic activity was associated with subsidence within the Pannonian Basin, and was the magmatic response to continued subduction of the European plate under the East Carpathians.

Diachronous Neogene sedimentation in the Pannonian Basin occurred during the final stages of thrusting and folding in the outer parts of the Carpathians (BÉRCZI et al., 1988, ROYDEN, 1988). In much of the basin system during the Middle Miocene (Badenian), sedimentation was unable to

keep pace with subsidence and marine conditions prevailed. Clastic supply was derived from the uplifting Alps and Carpathians, with southerly sediment transport occurring from the north, west and east towards the centre of the Pannonian Basin (KÁZMÉR, 1990). BÉRCZI et al.'s (1988) study of Neogene sedimentation in Hungary concluded that the five basal Miocene stages each represent a transgressive-regressive cycle (i.e. Eggenburgian, Ottnangian, Karpatian, lower Badenian and upper Badenian/Sarmatian), although this is disputed by TRUNKÓ (1996). NARGOLWALLA et al. (2007) provide a detailed description of these latter cycles in relation to palaeoenvironmental change in the Pannonian Basin during the Miocene.

Following the isolation (and a salinity reduction – see NARGOLWALLA et al., 2007) of Lake Pannon from the Paratethys due to the final uplift of the East Carpathians and/or regression during the late Badenian to Sarmatian (~14 & 12 Ma), the lake then experienced a gradual transgressive phase (until 9.5 Ma) followed by a terminal regression during the Late Miocene (MAGYAR et al., 1999). Since significant faunal turnovers occur in Europe during the Pannonian (i.e. the mid-Vallesian Crisis), it is interesting to note that during the time period assigned to this 'crisis', a dramatic shrinkage of Lake Pannon occurred between 9.5 and 9 Ma (MAGYAR et al., 1999, POPOV et al., 2004). Complete infilling of the Pannonian Basin system due to post-rift delta progradation began in the northwesterly Vienna Basin, and proceeded southeasterly during the Late Miocene and Pliocene, with the deep basins of the Pannonian being formed more basin-ward during the transgression than the Sarmatian Basins (MAGYAR et al., 1999). A wide variety of sedimentary environments were established at the lake margins, consisting of shallow lacustrine, swamp and fluvial sandstone, mudstone and lignite facies.

Frequent movement of the lake's northern shoreline during the Sarmatian and Pannonian is attributed to minor climatic fluctuations (MAGYAR et al., 1999) or localized tectonics, with the southern margin remaining in a relatively constant location on the northern flanks of the Dinarides. Unlike the fluvially-dominated deltas prograding from the north, clastic and freshwater input was relatively low in the southern lake due to the prevailing carbonate terrain surrounding the lake margins. However, freshwater input from the north exceeded rates of evaporation, and by the Early Pliocene, Lake Pannon's salinity had decreased from brackish (15-20‰ at the Sarmatian/Pannonian boundary) to freshwater (8-15‰ in the late Pannonian – KÁZMÉR, 1990).

During the late Early Pliocene, large scale tectonic reorganization, together with major thrusting and folding (uplifting the south Carpathians) came to an end in the Pannonian realm (POPOV et al., 2004). In the remaining depressions of the Pannonian Basin up to 1000 m of Middle and Upper Pliocene sediments were deposited. Further decreases in salinity are observed from the molluscan fauna, with the appearance of viviparids and melanopsids characterizing fluvial/shallow lacustrine and marginal freshwater environments, respectively (KÁZMÉR, 1990). Alkali-basaltic volcanism also occurred in the Pannonian Basin during the Plio-Pleistocene.

1.2. History of discovery

Primates were first recorded from Pannonian Basin sediments in the late 19th Century. ABEL (1902) described a small sample of isolated teeth from Děvinská Nová Ves (known at the time and occasionally to this day as Neudorf an der March) in what was then Austria and what is now Slovakia, which he assigned to a new genus and species, *Griphopithecus darwini*. A second species, *G. suessi*, also named by ABEL, is generally considered to be a junior subjective synonym of the first (REMANE, 1921). *Griphopithecus* was quickly subsumed under the pre-existing nomen *Dryopithecus* (GREGORY & HELLMAN, 1926), and was almost completely forgotten [an exception is found in (STEININGER, 1967)] until more complete collections of similar looking apes were found in Turkey. EHRENBURG (1938) described a well-preserved humeral shaft and ulna with a portion of the proximal end preserved from Klein Hadersdorf, which he attributes to *Austriacopithecus*, but which has more recently been assigned to *Griphopithecus* (BEGUN, 1992).

While the history of the resurrection of *Griphopithecus* is complex, much of the credit goes to Peter Andrews, who with Heintz Tobien published a paper on thickly enameled hominoids from Turkey, to which they linked the small sample from Central Europe (ANDREWS & TOBIEN, 1977). In the years that have followed a consensus has emerged of a phylogenetic connection between the Central European and Western Asian primate faunas (ANDREWS et al., 1996; HEIZMANN & BEGUN, 2001; BEGUN et al., 2003). Many researchers also favor the hypothesis that the “griphopiths” are the earliest members of the great ape and human clade (hominids) (see below).

Hominines (African apes and humans) make their first appearance in the Pannonian Basin at St. Stefan, in MN 7/8, represented by *Dryopithecus fontani* (BEGUN, 2002a). MOTTI (1957) described this mandible and associated isolated teeth as *D. fontani carinthiacus*, but some authors have sought to elevate Motti’s subspecies to the level of the species, and have suggested that it is conspecific with other Pannonian Basin hominids, though the latter are of considerably younger age (e.g. ANDREWS et al., 1996). In this paper, following BEGUN & KORDOS (1993) and BEGUN (2002a), we attribute the St. Stefan specimen to *D. fontani* (see below).

Probably the most celebrated locality in the Pannonian Basin, in terms of hominoid paleontology, is Rudabánya, in Hungary (BEGUN & KORDOS, 1993; BERNOR et al., 2004; KORDOS & BEGUN, 2002). Rudabánya is well known for its large sample of *Dryopithecus*, represented by numerous cranial and postcranial remains, but it is also the source of the largest collection of the intriguing pliopithecoid *Anapithecus*. The first primate specimens were collected from Rudabánya in the late 1960s, and in the following decades four genera were named, *Rudapithecus*, *Bodvapithecus*, *Anapithecus*, and *Ataxopithecus* (KRETZOI, 1969, 1975, 1984). These have subsequently been reduced to two taxa, the first two being attributed to the hominine *Dryopithecus brancoi* and the latter two to the pliopithecoid *Anapithecus henyaki* (BEGUN & KORDOS, 1993; KORDOS

& BEGUN, 2002). Both taxa from Rudabánya are also known from other Pannonian Basin and non Pannonian localities. *Anapithecus* is found at Götzendorf in Austria and Salmendingen in Germany, and *Dryopithecus brancoi* is known from Mariatal in Austria, and Salmendingen as well, and possibly other localities in Germany and Georgia (BEGUN, 2002a; BEGUN & KORDOS, 1993; KORDOS & BEGUN, 2002; THENIUS, 1982; ZAPFE 1989) (see below).

Somewhat less attention has been lavished on the rich sample of pliopithecoid primates recovered from Pannonian Basin sediments, apart perhaps from the spectacular skeletons described by ZAPFE (1960) from the Děvinská Nová Ves fissures (Slovakia). Relatively large samples of pliopithecoids are known from Göriach (Austria), described in some detail by HÜRZELER (1954), but first published as far as we can tell by HOFMANN (1886, 1893). In addition to the pliopithecoids mentioned above from Rudabánya and Götzendorf, published specimens include a complete but isolated phalanx of a pliopithecoid is known from Felsőtárkány in Hungary, and a single molar of *Pliopithecus* cf. *P. antiquus* is identified from the Děvinská Nová Ves sands in association with *Griphopithecus* (GLÄSSNER, 1931; HÜRZELER, 1954; KORDOS & BEGUN, 2003; KRETZOI, 1982). In addition, an unpublished deciduous premolar of a crouzelid is known from Taut, in the Transylvanian Basin (DELSON & McNULTY, personal communication, and personal observations of the authors). It should be noted in passing that the stratigraphic relationship between the Děvinská Nová Ves sands and fissures, which are separated structurally and geographically, is unclear.

1.3. Primate Diversity

Three primate superfamilies are found in Middle and Late Miocene deposits in the Pannonian Basin, a level of Miocene primate diversity that rivals any region in the world. Many other mammals are also represented by large and diverse assemblages. Table 1 is a list of all currently known primates from the Pannonian Basin. All primate subfamilies and most genera from the Pannonian Basin are also known from localities outside the Basin. In most cases, genera or species from outside the region that belong to Pannonian Basin subfamilies are either more primitive, older, or both. This suggests that the basin was repeatedly invaded by primate taxa that had evolved elsewhere, and that *in situ* evolution of endemic forms occurred. In the Middle Miocene advanced pliopithecids appear in the Pannonian Basin, and in the Late Miocene a highly derived crouzelid pliopithecoid appears. In both cases the more primitive sister taxon is known from localities in Western Europe. Middle Miocene hominoids include the stem hominid *Griphopithecus* and the most primitive member of *Dryopithecus*, *Dryopithecus fontani*. Late Miocene hominids are represented by the more derived *D. brancoi*. *Dryopithecus brancoi* first appears in the Pannonian region in MN 9, and persists possibly until MN 10 in Germany and possibly Georgia, suggesting possible *in situ* evolution and subsequently one or more

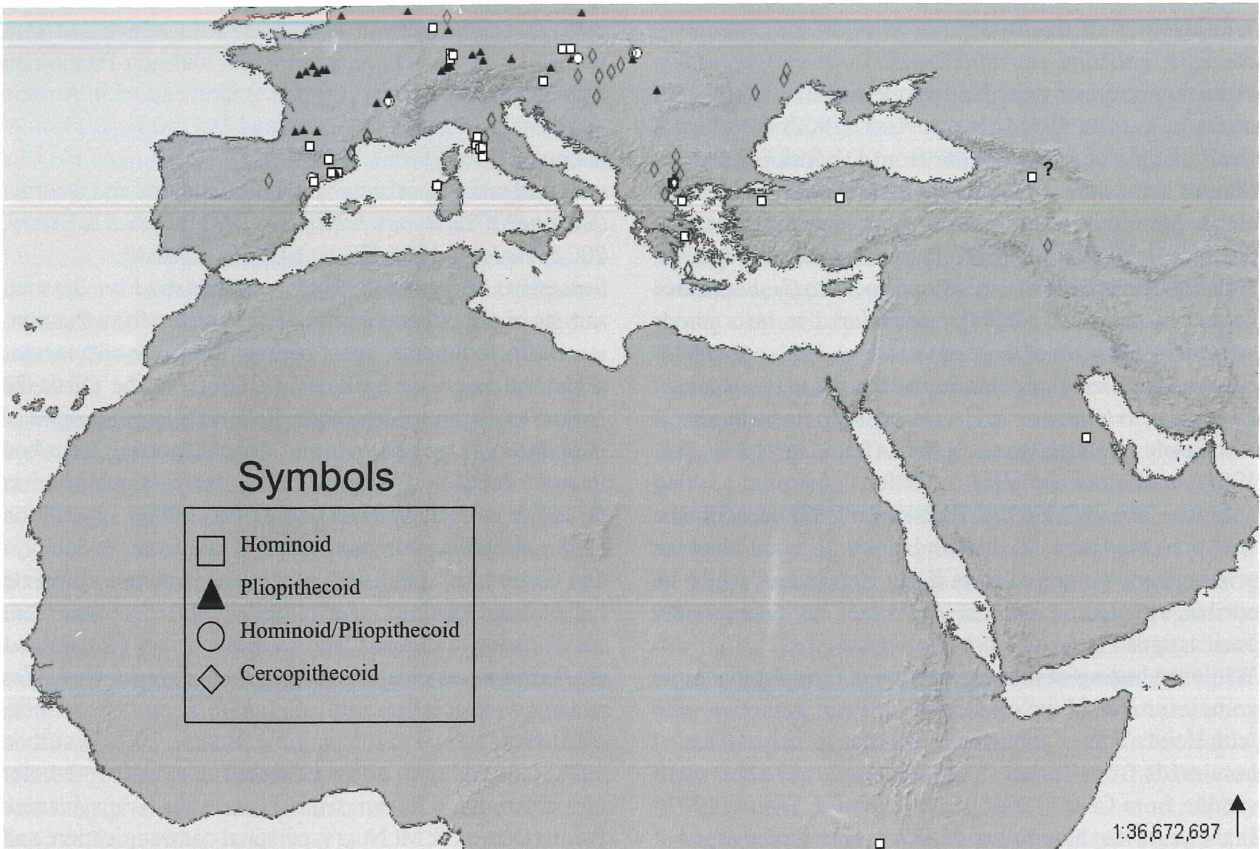


Figure 1: Distribution of primate localities in Europe, Western Asia and Africa during the late early Miocene to the late Miocene. African localities include Kalodirr (*Afropithecus*) in the south (small square), Toros Menalla (*Sahelanthropus*) to the Northwest, and Middle Awash (*Ardipithecus*) to the Northeast (larger squares).

CATARRHINI

PLIOPITHECOIDEA			
Pliopithecidae			
<i>Pliopithecus platyodon</i>	Göriach		Austria
<i>Pliopithecus</i> cf. <i>P. antiquus</i>	Děvínská Nová Ves Sd.		Slovakia
<i>Epipliopithecus vindobonensis</i>	Děvínská Nová Ves Sp.		Slovakia
Crouzelidae			
<i>Anapithecus</i> sp.	Götzendorf)		Austria
<i>Anapithecus hernyaki</i>	Rudabánya		Hungary
Crouzelidae gen. et sp. indet.	Taut		Romania
Pliopithecoida gen. et sp. indet.	Rudabánya, Felsőtárkány		Hungary
HOMINOIDEA			
Hominidae			
<i>Dryopithecus fontani</i>	St. Stefan		Austria
<i>Dryopithecus brancoi</i>	Rudabánya, Mariatal		Austria, Hungary
Griphopithecidae			
<i>Griphopithecus darwini</i>	Děvínská Nová Ves Sd.		Slovakia
cf <i>Griphopithecus darwini</i>	Klein Hadersdorf		Austria
CERCOPITHECOIDEA			
Cercopithecidae			
<i>Mesopithecus</i> sp.	Hatvan, Baltavár, Polgárdi		Hungary

Table 1: Primates from the Miocene of the Pannonian Basin. Here we follow most recent authors in including all great apes and humans in the Hominidae and African apes and humans in the Homininae. The classification here follows BEGUN (2002a,b).

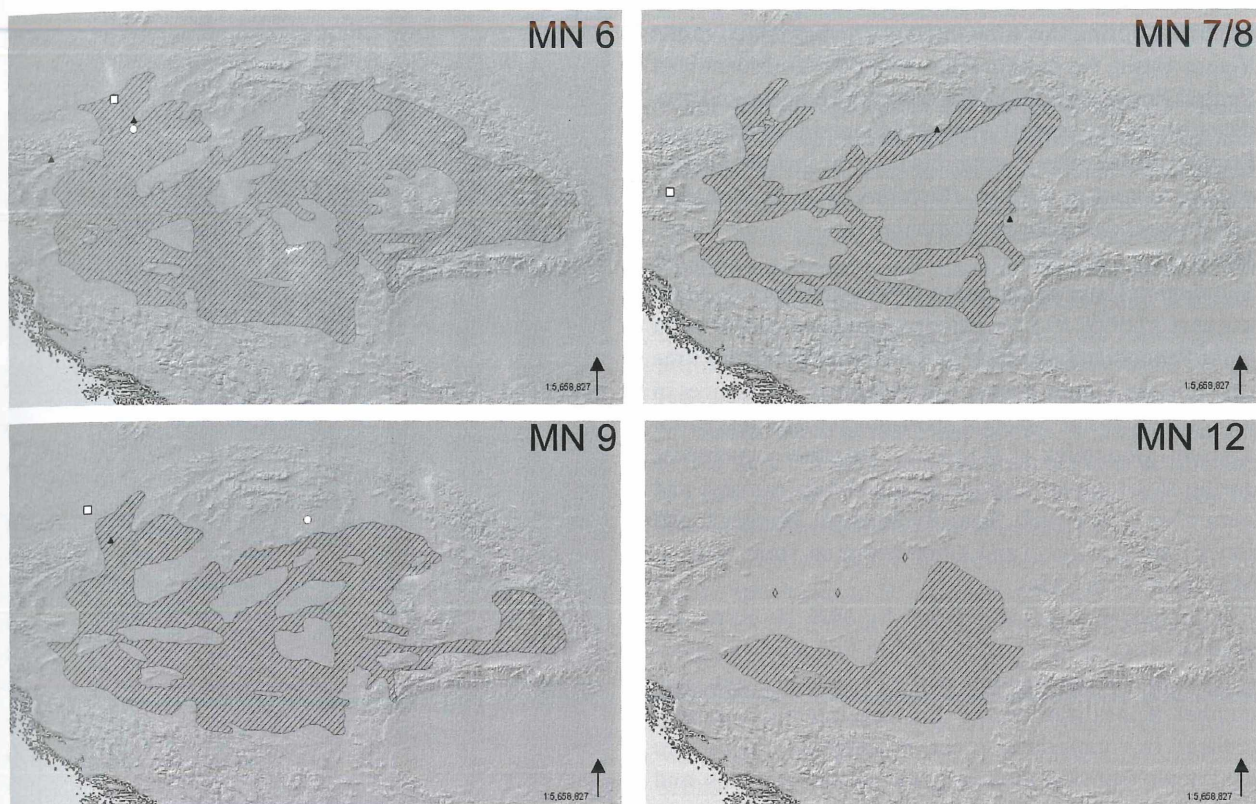


Figure 2: Changes in the shoreline and primate locality distribution over time in the Pannonian Basin. MN 6-localities are confined to the Vienna Basin, probably in nearshore environments. MN 7/8-localities are more widespread but fewer in number and less rich. They are also associated with the lake shore. MN 9-localities remain in association with the lake margins but include the rich locality of Rudabánya. MN 13-The lake is much smaller and the basin is occupied only by cercopithecoid primates that do not live in proximity to the lake, but in more open ecological settings. See text for discussion.

dispersal events. *Dryopithecus* may also be closely related to the later occurring *Ouranopithecus* from Greece (BEGUN, 2002a; BEGUN & KORDOS, 1997) (see below). On the other hand, the record of *Griphopithecus* in the Pannonian region is very poor, and it is unclear how the taxon represented by the five isolated teeth from Děvínská Nová Ves in Slovakia is related to earlier occurrences of *Griphopithecus* from Turkey and cf. *Griphopithecus* from Germany (HEIZMANN & BEGUN, 2001; BEGUN et al., 2003; KELLEY, 2002).

2. Materials and Methods

Localities were identified using standard survey techniques including surface transects, existing geologic maps and remote sensing (e.g. landsat imagery). The GSP coordinates of all newly discovered localities were recorded and compared to existing geological and topographic maps. In instances where intensive sampling was warranted, site grids were laid out and sediment was processed using standard archeological techniques, with provenience data recorded in three axes, along with details of sedimentology and taphonomy. Details of the methods used can be found in a number of publications (BEGUN, 1992; BEGUN, 1993; BEGUN & KORDOS, 1993; KORDOS & BEGUN, 1997; KORDOS & BEGUN, 2001). GIS and geological data analysis methods are outlined in NARGOLWALLA et al. (2007).

3. Results

Figure 1 shows the distribution of primate localities in Europe and Western Asia between MN 5 and MN 13. Also included are two Afro-Arabian localities, Kalodirr in Kenya and Ad Dabtiyah in Saudi Arabia. These localities contain fossil hominoids that may be broadly ancestral to the earliest Eurasian hominoids (see below).

3.1. Paleogeography

MN 6 (15.2 – 12.5 Ma)

The temporal interval defined by MN 6 coincides with the MAGYAR et al.'s (1999) 13.5 Ma paleogeographic reconstruction of the intra-Carpathian extension of the Paratethys (Fig. 2). Localities within this temporal interval are clustered in the Vienna Basin, with occurrences also in the eastern Alps, the northern Apuseni Mountains in Romania, and the northeastern Dinarides in Serbia. Primates occurring during this interval include *Griphopithecus darwini*, *Pliopithecus* cf. *P. antiquus*, *Pliopithecus platyodon* and *Epipliopithecus vindobonensis*, all in the Vienna Basin.

MN 7/8 (12.5 – 11.2 Ma)

The temporal interval defined by MN 7/8 coincides with MAGYAR et al.'s (1999) 12.0 Ma paleogeographic reconstruction of the Pannonian Lake (Fig. 2). Localities

occurring during this time interval are distributed in the Vienna Basin, the eastern Alps, along the Transdanubian Central Range and Bükk Mountains of Hungary and also the northern and central Apuseni Mountains of Romania. Primate occurrences during this interval include *Dryopithecus fontani* in Austria, *Pliopithecus* sp. in Hungary, and Crouzelidae indet. in Romania.

MN 9 (11.2 – 9.7 Ma)

The temporal interval defined by MN9 coincides with MAGYAR et al.'s (1999) 10.8 Ma paleogeographic reconstruction of the Pannonian Lake (Fig. 2). Localities during this time cluster in the Vienna Basin, with additional occurrences in the Carpathians of Slovakia and Hungary and the central Apuseni Mountains of Romania. Primate occurrences during this interval include *Dryopithecus branchoi* and *Anapithecus hernyaki* from Rudabánya, Hungary, and *Dryopithecus branchoi* and *Anapithecus* sp. from Austria.

MN 10 (9.7 – 8.7 Ma)

The temporal interval defined by MN 10 coincides with MAGYAR et al.'s (1999) 9.5 Ma and 9.0 Ma paleogeographic reconstructions of the Pannonian Lake. The number of localities during this time interval is greatly reduced in comparison to earlier intervals. Localities are known from the Vienna Basin and eastern Alps, and in proximity to the Transdanubian Central Range in Hungary. With the contracting Pannonian Lake during this and subsequent time intervals, the distribution of localities begins to shift away from the basin margins for the first time and towards the interior of the Basin system. No primates are known in the Pannonian Basin from this time interval.

MN 11 (8.7 – 8 Ma) and MN 12 (8 – 6.6 Ma)

The temporal intervals defined by both MN 11 and MN 12 coincide with the 8.0 Ma paleogeographic reconstruction of the Pannonian Lake by MAGYAR et al. (1999). During this time intervals the number of localities continues to decline. Our localities are distributed in the Vienna Basin of Austria and Slovakia and in proximity to the Transdanubian Central Range (Hungary) in MN 11, while MN 12 localities again remain in proximity to the Transdanubian Central Range, with one other locality occurring more centrally.

MN 13 (6.6 – 4.9 Ma)

The temporal interval defined by MN13 coincides with MAGYAR et al.'s (1999) 6.5 Ma paleogeographic reconstruction of the Pannonian Lake (Fig. 2). Localities occurring during this time interval are again located in proximity to the Transdanubian Central Range (Hungary) and southeast of the Eastern Alps. Importantly, this MN unit marks the reemergence of primates in the Pannonian Basin, represented by the cercopithecoid *Mesopithecus pentelicus*. Later, in the Pliocene, *Dolicopithecus* and *Macaca* appear.

3.2. *Dryopithecus* Alphataxonomy

In order to explore details of origins and dispersal, it is essential to agree on the alphataxonomy of the primates under analysis. Two samples are currently the subject of

discussion regarding details of taxonomy. The results of our analysis of these samples are presented below.

3.2.1. St. Stefan

As noted above, there are differences of opinion as to the most appropriate nomen for the specimens from St. Stefan. The job of attributing this specimen to a taxon is made more difficult by the fact that only male mandibles of *Dryopithecus fontani* are known, and the St. Stefan specimen is a female, as indicated by the lower canines. ANDREWS et al. (1996) attribute this specimen to the same species of *Dryopithecus* present at Rudabánya, which they refer to *Dryopithecus carinthiacus*. In order to resolve this issue, we examined the morphological data in more detail.

The mandible and dentition from St. Stefan (Fig. 3) are similar to St. Gaudens (*Dryopithecus fontani*) and different from Rudabánya (*D. branchoi*) in a number of features. A digitized morphometric analysis of the m1 crowns of these specimens reveals relatively large protoconids and reduced hypoconids on the m1 of St. Stefan and St. Gaudens (ZYLSTRA, unpublished). At St. Stefan the hypoconulid is quite large, occupying 17% of the crown area, well above the range of any other *Dryopithecus* sample. In contrast, the relative entoconid size is well below the range of variation at Rudabánya and St. Gaudens (ZYLSTRA, unpublished). More traditional morphological observations are also informative. Both metaconids on the St. Stefan first molars are notched, separating the cusp apices from the postmetacristids. This also occurs on all St. Gaudens specimens but not on females from Rudabánya. The postmetacristids are straight and separated from the lateral protocristids on the St. Stefan and St. Gaudens molars, whereas they curve buccally to meet the lateral protocristids at the metaconid apex on the Rudabánya first molars. A partial cingulum between the protoconid and hypoconid is also present on the St. Stefan and St. Gaudens molars but not at Rudabánya. Finally, the buccal cusps on the St. Stefan and St. Gaudens specimens are broader transversely and fill the talonid, whereas in the Rudabánya sample they tend to be more marginalized and bucco-lingually compressed.

As noted by ANDREWS et al. (1996), the p4 is long relative to breadth compared to the Rudabánya sample. Like *D. fontani* the p4 talonid is low relative to the trigonid, and the buccal crown surface is more strongly flared, whereas at Rudabánya and in other *Dryopithecus* the mesial and distal halves of the crowns are close to the same height and the buccal surface is more vertical. The p3 is also elongated relative to breadth, again most like *D. fontani*. The mesial beak is not well developed, as in most *D. fontani*, and unlike the Spanish and Hungarian samples, which have well developed mesial beaks. The p3 also has a relatively large metaconid, as in *D. fontani*.

The canine is similar to but slightly smaller than female canines from Rudabánya. The distal slope of the female canines from Rudabánya is more inclined and ends in a more prominent disto-buccal bulge than is the case on the St. Stefan specimen. There are no female lower

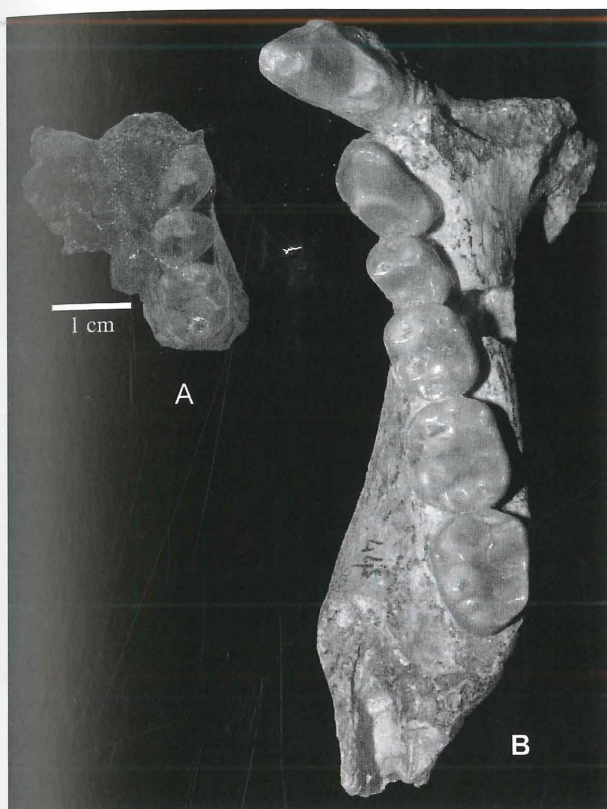


Figure 3: Comparison of the St. Stefan (left) female *Dryopithecus fontani* and St. Gaudens (right) male *D. fontani*. See text for discussion.

central incisors of *Dryopithecus* from Rudabánya, but the central incisors of the male RUD 14 are more flared toward the incisive edge, and have much more prominent lingual pillars. The root of the one complete i1 of RUD 14 is bilaterally compressed, unlike the thicker root on the incisor from St. Stefan.

In overall size the St. Stefan specimen conforms to the expected size of a female of *Dryopithecus fontani*, if the level of sexual dimorphism in that species was similar to that seen at Rudabánya and other rich localities, such as Can Llobateres. It is slightly smaller than females from Rudabánya, whereas males from Rudabánya tend to be slightly larger than those from St. Gaudens. Overall, the differences between St. Stefan and Rudabánya are not overwhelming, but in most instances St. Stefan resembles St. Gaudens more closely than it does Rudabánya. The balance of the morphological evidence suggests that Mottl's original attribution of this specimen to *D. fontani* was correct. There is much less evidence linking this specimen to the sample from Rudabánya.

3.2.2. Rudabánya

While there is agreement that the great ape from Rudabánya is *Dryopithecus*, there is a difference of opinion concerning the species to which it should be assigned. Three possibilities are most likely. BEGUN & KORDOS (1993) have argued that *Dryopithecus* from Rudabánya should be assigned to the taxon *D. brancoi*, based on the type specimen from Salmendingen in Germany. ANDREWS et al. (1996) argue that the great ape from Rudabánya is attributable to *Dryopithecus carinthiacus*, based on the type specimen of *Dryopithecus fontani carinthiacus* from St. Stefan (MOTTL, 1957) (see above). A third possibility is that the *Dryopithecus* from Rudabánya is attributable to a new species, *Dryopithecus hungaricus*, based on the type of *Rudapithecus hungaricus*, RUD 1.

As noted above, there is good evidence to attribute the St. Stefan specimens to *Dryopithecus fontani*. Another species of *Dryopithecus* is identified at both Rudabánya and Mariatal. This is either the same species identified at Salmendingen or a new species. The presence of this species at other localities (Ebingen, Melchingen, Trochtelfingen, Wissberg, and Udabno), while not definitively established at this time, is likely (see below). The question of the nomen at Rudabánya boils down to the issue of the true affinities of the type of *D. brancoi* from Salmendingen.

BRANCO (1898) described an isolated tooth from Salmendingen, which he called a deciduous molar of *Dryopithecus*. This and other isolated teeth of fossil hominoids from Germany were reviewed by SCHLOSSER (1901), who named a new taxon, *Anthropodus brancoi*, for Branco's deciduous tooth, describing it instead as a permanent molar. Abel noted that the nomen *Anthropodus* was unavailable because it is previously occupied by *Anthropodus rouvillei*, and proposed instead the nomen *Neopithecus* (ABEL, 1902). Subsequent taxonomic revisions have for the most part placed these isolated teeth in *Dryopithecus* (HRDLICKA, 1924; GREGORY & HELLMAN, 1926; SIMONS & PILBEAM, 1965; SZALAY & DELSON, 1979; KELLEY & PILBEAM, 1986;

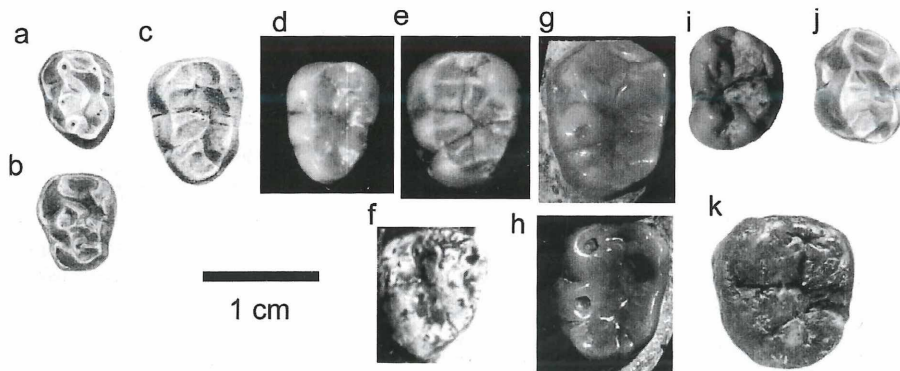


Figure 4: Comparison of lower molar specimens discussed in the text. **m3:** a) *Pliopithecus piveteaui*; b) *Pliopithecus platyodon*; c-d) *Dryopithecus brancoi* type from Salmendingen; e) *Dryopithecus brancoi* from Trochtelfingen; f) *Dryopithecus brancoi* from Rudabánya; g-h) two specimens of *Dryopithecus fontani* from St. Gaudens; k) *Griphopithecus darwini* type from the Děvinská Nová Ves sands; **Other lower molars:** i) a *Dryopithecus* dp4 from Wissberg; j) m2 of *Anapithecus* from Salmendingen. a-c modified from HÜRZELER (1954); j modified from HÜRZELER (1951); k modified from ABEL (1902).

BEGUN, 1987; BEGUN & KORDOS, 1993), though there have been occasional suggestions that the type of *Neopithecus* more closely resembles *Pliopithecus* than *Dryopithecus*, and that the *Neopithecus* nomen should be retained as a pliopithecine-like form (VON KOENIGSWALD, 1956; HÜRZELER, 1954; ANDREWS et al., 1996).

The type specimen of *Dryopithecus brancoi* is a left lower third molar (Fig. 4). The specimen has been described and figured by BRANCO (1898), SCHLOSSER (1901), HRDLICKA (1924), GREGORY & HELLMAN (1926), HÜRZELER (1954), SZALAY & DELSON (1979), KORDOS (1990) and BEGUN & KORDOS (1993). BEGUN & KORDOS (1993) found a quantitative similarity between the Salmendingen specimen and the sample from Rudabánya in the degree of distal tapering, as measured by length relative to talonid breadth (BEGUN & KORDOS, 1993: fig. 3). Additional qualitative morphological similarities between the two samples include long, curved postmetacristids, large, broad anterior fovea, well-defined hypoconulid cristids and a relatively large, distally positioned, hypoconulids (BEGUN & KORDOS, 1993).

In a separate analysis, KORDOS (1990) coded m3 morphotypes based on the following characters: a) cingulum present (1), or absent (2); b) fovea anterior absent (1), single (2), or double (3); c) accessory cusp between the metaconid and entoconid present (1), or absent (2); d) accessory cusp between the entoconid and hypoconulid present (1), or absent (2); e) continuous cristid between the hypoconulid and hypoconid present (1), or absent (2). Within the sample of *Dryopithecus* the morphotype of the type of *Dryopithecus brancoi* was found to be very close to all the specimens from Rudabánya, and more distinct from other *Dryopithecus*, especially *D. fontani* (KORDOS, 1990).

Although ANDREWS et al. (1996) do not comment specifically on the merits of the comparisons summarized above, they note that because they as a group cannot decide if the Salmendingen specimen is pliopithecine or hominoid the nomen should be designated as *incertae sedis*. As noted above, there are a number of specific resemblances of this specimen to the Rudabánya sample of *Dryopithecus* (see also KELLEY & PILBEAM, 1986). There are also many clear distinctions from all pliopithecoids, both pliopithecids and crouzelids (see below).

ANDREWS et al. (1996) consider that the type of *Dryopithecus brancoi* may be pliopithecoid, citing HÜRZELER (1954). It is useful to recall Hürzeler's careful consideration of this specimen. He notes that it is much larger than any pliopithecine. The type of *D. brancoi* is actually about 27% larger than the largest m3 of *Anapithecus*, 11% larger than the largest *Pliopithecus* m3, that of *Pliopithecus zhanxiangi* from China (HARRISON et al., 1991), and 25% larger than the largest *Pliopithecus* from Europe, *Pliopithecus platyodon* (HÜRZELER, 1954; ANDREWS et al., 1996). HÜRZELER (1954) speculates that the large size of this specimen may be related to its later occurrence in the geological record, evoking COPE's rule. He is cautious, however, and notes that there are important morphological differences from pliopithecids, including a broad talonid basin with marginalized cusps and the absence of a buccal cingulum, all of which cause him to regard his hypothesis as tentative.

The type of *D. brancoi* also lacks a pliopithecine triangle. In fact, it is these very characters that distinguish pliopithecine m3's from those of *Dryopithecus*. HÜRZELER (1954) himself was not completely convinced that the type of *D. brancoi* was attributable to a pliopithecoid, and he recognized that his argument relied completely on a scenario of increasing dental size in pliopithecids. As an indication of his uncertainty, consider his concluding remarks on the subject: "I therefore dare to try to classify the tooth from Salmendingen as ?*Pliopithecus brancoi*" (translation DB) (HÜRZELER, 1954:54). Given the similarities to the fossil material from Rudabánya, which was not known when HÜRZELER (1954) struggled with the type of *D. brancoi*, there is no evidence that this specimen is a pliopithecoid and not *Dryopithecus*. It is even less likely that the type of *D. brancoi* can be attributed to a crouzeline, as it lacks all the diagnostic characters of this taxon (GINSBURG & MEIN, 1980; ANDREWS et al., 1996). In sum, there is no evidence for attributing the type of *Dryopithecus brancoi* to the Pliopithecoidae and much evidence against it. The detailed similarities between the Rudabánya sample and the type of *D. brancoi* justify including both in the same species until new specimens from Salmendingen or elsewhere indicate otherwise.

4. Discussion and Conclusion

The paleobiogeographic evolution of primates in the Pannonian Basin is complex and unique. The earliest primates from the Pannonian Basin are confined to the northwestern margins of the region, the Vienna Basin (Fig. 2). It seems most probable that primates entered the region from the northwest, via a lowland corridor north of the eastern Alps. Earlier occurring and more primitive pliopithecoids and hominoids are both known from these more westerly areas. The oldest occurrence of *Pliopithecus platyodon* is the MN 5 locality of Elgg, in Switzerland, but the majority of the specimens come from MN 6 Vienna Basin locality of Göriach (Fig. 2) (BEGUN, 2002b; HÜRZELER, 1954). The oldest occurrence of a hominoid in Europe, in fact in all of Eurasia, is cf. *Griphopithecus* from Engelswies (MN 5) (HEIZMANN & BEGUN, 2001). *Griphopithecus* is thought to have evolved from an African *Afropithecus*-like ancestor, with which it shares thickly enameled molars and robust jaws. *Griphopithecus darwini* appears later in the Vienna Basin in MN 6 at Děvinská Nová Ves Sandberg and Klein Hadersdorf (Fig. 2). On the other hand, *Griphopithecus* is also known from MN 5 localities in Turkey (Çandır and Paşalar), to the southeast, and pliopithecids are represented by the genus *Dionysopithecus* from 16-18 Ma localities in China and Thailand (HARRISON & YUMIN, 1999). Thus, a southeastern route for *Griphopithecus*, through the Balkans, and a northeastern route for *Pliopithecus*, north of the Parathethys, are possible. However, given the distances involved and the consistent presence of marine facies in the south, we think the northwestern route is the most likely. While we favor a northwest passage for *Griphopithecus* into the Pannonian Basin, it is worth noting that there is

evidence of dispersals among thickly enameled hominoids between Eurasia and Africa in the Middle Miocene as well. *Griphopithecus* and *Kenyapithecus* from Turkey are older than *Kenyapithecus* from Fort Ternan (Kenya) and *Equatorius* (Maboko, Kipsarimon and other localities in Kenya), the latter taxon sharing many characters with *Griphopithecus* (BEGUN, 2000; BEGUN et al., 2003; KELLEY, 2002; WARD et al., 1999). While there is disagreement on the relations among these taxa (e.g. WARD et al., 1999; BEGUN, 2000; BENEFIT & MCCROSSIN, 2000) it is clear that there were at least two dispersals between Eurasia and Africa involving Middle Miocene thickly enameled hominoids. Hominoids and pliopithecoids, along with other land mammals, may have been prevented from entering the Pannonian Basin until MN 6 given possible marine connections between the Fore-Carpathian Basin to the north and east, and the Vienna Basin to the west and south. The pre-MN 6 connection between the Pannonian Basin and the Mediterranean would have prevented dispersals from the south.

Like most mammals, primates are poorly represented in MN 7/8 sediments in the Pannonian Basin. This may simply be a sampling artifact, as there are relatively fewer land mammal localities of this time period in the basin. There are relatively few lowland facies that might have been associated with subtropical forested conditions suitable for primates. Where primates are known, they appear to be associated with lake shore environments in St. Stefan, south of Vienna, Felsőtárkány, east of Budapest, and Taut, in the Transylvanian Basin (Fig. 2). As noted above, the St. Stefan specimens are attributable to *Dryopithecus fontani*. The Felsőtárkány and Taut specimens are pliopithecoid (see below).

Paleogeographic origins of *Dryopithecus fontani*

Dryopithecus fontani is also known from MN 7/8 localities in France, and possibly from sites in Spain of similar age. It is not known where the taxon originated, but it most likely evolved from European *Griphopithecus*. European *Griphopithecus* is known from MN 5-6 from Germany to Slovakia, and *Dryopithecus fontani* appears in MN 7/8 more or less at both extremes of that range. Other taxa that share morphological attributes with *Griphopithecus darwini* include *G. alpani* from Turkey, and *Equatorius*, *Nacholapithecus*, and *Kenyapithecus*, all from Kenya. All of these taxa share thickly enameled molars and retain primitive attributes of the teeth while *Dryopithecus* has thin enamel, a more modern hominid dentition, and modern hominid postcrania (BEGUN, 2002a). Proximity then is the main factor in favor of a European origin. However, the recent discovery of *Pierolapithecus* strengthens this argument by possibly representing another case of a widely distributed, centrally occurring taxon that may be ancestral to more peripheral descendants.

MOYÀ-SOLÀ et al. (2004) describe a new genus of Middle Miocene hominid of MN 7/8 age, *Peirolapithecus catalaunicus*, from northeastern Spain. They suggest that *Pierolapithecus* is a primitive member of the clade that includes *Dryopithecus* and *Pongo*, among others.

BEGUN & WARD (2005) agree that *Peirolapithecus* is more primitive than later occurring MN 9 *Dryopithecus*, but put both taxa in the hominine (African ape and human) clade. The differences in subfamily attribution notwithstanding, both groups of researchers agree that the most primitive member of the *Peirolapithecus*/*Dryopithecus* clade is in Western Europe. It is unclear whether *Peirolapithecus* is distinct from *Dryopithecus fontani*, because very few directly comparable parts are preserved. The La Grive upper teeth usually attributed to *Dryopithecus fontani* do closely resemble those of *Peirolapithecus*, and if both taxa are the same, *D. fontani* would be confirmed as a significantly more primitive member of the genus with a range from Spain to Austria (BEGUN et al., 2006). From this widely distributed species the more derived members of the genus (*D. brancoi*, *D. laietanus*, and *D. crusafonti*) may all have diverged vicariantly. At least one species *D. brancoi*, may have subsequently spread into the range previously occupied by *Griphopithecus*, accounting for its presence in Germany (see below). A more complete analysis of *D. fontani* or *Peirolapithecus* is needed to address this hypothesis.

Pliopithecoids

The Taut and Felsőtárkány primates are difficult to identify due to their fragmentary nature. Taut is an isolated lower second deciduous molar (dp4). The dp4 is difficult to attribute to either a pliopithecoid or a hominoid because this tooth tends to be more similar among fossil catarrhines than are the adult counter parts. Detailed comparisons to the relatively large sample of dp4 specimens from Rudabánya and Göriach suggest the strongest affinities with *Anapithecus*. In particular, the specimen has a hypoconulid, which *Pliopithecus* lacks, and it has an obliquely oriented crista obliquid, giving the tooth a characteristic “waisted” appearance, as is common in *Anapithecus* but not in hominoids. The specimen is quite unlike the dp4 from Wissberg attributed to *Dryopithecus* (VON KOENIGSWALD, 1956) (Fig. 4). A more comprehensive analysis of the specimen, presenting the alternative interpretation that this specimen represents *Dryopithecus*, is underway (McNULTY et al., in prep.).

The Felsőtárkány specimen is a well-preserved intermediate phalanx that most closely resembles *Epipliopithecus vindobonensis* but with more strongly developed secondary shaft characters, in which it resembles *Anapithecus* (KORDOS & BEGUN, 2003). Thus, it is possible that the MN 7/8 pliopithecoids are early crouzelids, which, generally speaking are derived compared to pliopithecids. The question is, did these Pannonian crouzelids evolve *in situ* from local ancestral pliopithecoid populations, such as *Epipliopithecus* or *Pliopithecus platyodon*? Or, did they disperse into the basin from the west, as in MN 6?

The evidence for the latter scenario comes from the fact that the oldest known crouzelid is *Plesiopliopithecus austrianensis* from MN 6 Sansan (GINSBURG & MEIN, 1980; BEGUN, 2002b). Pliopithecids become rarer and crouzelids more common after MN 6. It is certainly possible that the Vienna Basin is the source of the earliest crouzelids. The

level of temporal resolution does not currently allow for a determination of the relative ages of Göriach, Děvínská Nová Ves and Sansan, all of which are attributed to MN 6, but it is not impossible that the Vienna Basin localities are older than Sansan. In fact, VAN DER MADE (1999) considers Göriach to be late MN 5, which would make it older than Sansan. A resolution to this issue will require the discovery of more complete MN 7/8 crouzelids in the Pannonian Basin. After MN 6, crouzelids appear to evolve vicariantly in Europe into a western clade represented by *Plesiopliopithecus* and an eastern clade represented by *Anapithecus*.

Dryopithecus brancoi

Among primate faunas, MN 9 is dominated by *Dryopithecus*. The largest samples of *Dryopithecus* occur in the Pannonian Basin and in the Vallés Penedés of north-eastern Spain. In the Pannonian Basin *Dryopithecus* is represented by *D. brancoi* from the MN 9 locality of Rudabánya (KORDOS & BEGUN, 2002). Interpretations of the evolutionary relations of *Dryopithecus* vary. MOYÀ-SOLÀ & KÖHLER (1993) interpret *Dryopithecus* to be related to *Pongo*, based in large part on their analysis of the fossils from Can Llobateres. PILBEAM & YOUNG (2004) suggest that *Dryopithecus* is a stem hominid with no direct relationship to extant hominids. BEGUN (2002a) interprets *Dryopithecus* to be a member of the African ape and human clade. This is based on analyses of the entire record and a comprehensive cladistic analysis including all well-known Miocene hominoids (BEGUN et al., 1997). The evidence for the hominine status of *Dryopithecus* is quite strong and is supported by the most recent discoveries of *Dryopithecus* and related taxa (KORDOS & BEGUN, 2001; BEGUN & WARD, 2005).

The conclusions that *D. brancoi* is represented at both Salmendingen and Rudabánya, and that the St. Stefan and St. Gaudens samples are probably the same species both have interesting paleobiogeographic implications. Salmendingen and Rudabánya are close in age and contain the same dental morphs (BEGUN & KORDOS, 1993). Rudabánya is MN 9 and Salmendingen is probably MN 10 (SEN, 1996; AGUSTÍ et al., 2001). There are only three primate specimens from Salmendingen, one that very closely resembles *Anapithecus*, a second that looks most like the m3 of female *D. brancoi* (see above), and a third the size and morphology of which is closest to the male mandibular specimen from Rudabánya, RUD 14 (BEGUN & KORDOS, 1993).

Another probable *Dryopithecus brancoi* locality in the Pannonian Basin is Mariatal. The Mariatal specimen is worn but it does closely resemble Rudabánya female lower molars in size and morphology, and lacks the characters that distinguish both the Can Llobateres and St. Stefan specimens from Rudabánya. ZAPFE (1989) attributed two teeth from Götzendorf to *D. brancoi*, but subsequent examination of these specimens reveals them to be clearly attributable to *Anapithecus*. Outside the basin, in addition to its presence at Salmendingen, a number of isolated teeth from several German localities may also belong to *D. bran-*

coi, as well as two isolated teeth from Udabno, in Georgia (BEGUN, 1987). The P4 from Udabno, which along with an upper molar are the only specimens attributed to the taxon *Udabnopithecus*, is smaller than most from Rudabánya, though close in size to RUD 79. However, it is relatively short compared to breadth, and no more closely resembles Rudabánya than it does specimens from Can Llobateres, such as CLI 18000, which is attributed to *Dryopithecus laietanus*. The M1 is also smaller and shorter than most from Rudabánya, and is again not particularly diagnostic. The specimens from Udabno are thus most likely attributable to *Dryopithecus*, but they may represent yet another species of the genus (GABUNIA et al., 2001). In sum, *Dryopithecus brancoi* ranges at a minimum from Germany to Hungary, and possibly as far east as Georgia, but by far the richest locality is Rudabánya.

Most of the datable localities at which *Dryopithecus brancoi* can be identified (Rudabánya, Mariatal, Melchingen, and Wissberg) are considered to be MN 9 in age (MEIN, 1986, 1990; STEININGER, 1986; STEININGER et al., 1990; DE BRUIJN et al., 1992; RÖGL et al., 1993; ANDREWS et al., 1996). Only Salmendingen is younger and probably attributable to MN 10 (MEIN, 1986, 1990; SEN, 1996; AGUSTÍ et al., 2001). At two localities *D. brancoi* is found in association with *Anapithecus* (Rudabánya and Salmendingen). At other localities in the Pannonian Basin *Anapithecus* occurs without *Dryopithecus* (Götzendorf), or, *Dryopithecus* occurs without *Anapithecus* (Mariatal). Further work is needed at Götzendorf and Mariatal to determine if the absence of two catarrhines is a true indication of absence or a sampling issue. At any rate, though the paleoenvironment at Salmendingen is not known due to the incomplete nature of the fauna, the paleoenvironment at Rudabánya, Mariatal and Götzendorf was forested swamp/wetlands (THENIUS, 1982; ZAPFE, 1989; KORDOS & BEGUN, 2002; HARZHAUSER & TEMPFER, 2004). Both taxa are also known to have been frugivorous and highly arboreal, which is consistent with the paleoenvironmental association. However, if *D. brancoi* is really as widespread as suggested here, it was probably a more cosmopolitan taxon inhabiting a wider range of ecological settings. But, while *D. brancoi* and *Anapithecus* persist in Germany and *D. brancoi* possibly in Georgia into the late Vallesian, they did not survive in the Pannonian Basin. This follows the more typical pattern extinction of forest adapted faunas throughout Europe, which has been identified as the mid-Vallesian crisis (AGUSTÍ et al., 2003). In fact, primates disappear completely after MN 9 from the basin, only to return in the form of *Mesopithecus* in MN 13. By this time the extent of Lake Pannon was greatly reduced and the open ecological settings were much more prevalent (Fig. 2) (NARGOLWALLA et al., 2007).

One species of *Dryopithecus*, possibly *Dryopithecus brancoi*, may be ancestral to MN 10 *Ouranopithecus* from Greece. *Ouranopithecus* is the sister taxon to *Dryopithecus* (BEGUN & KORDOS, 1997; BEGUN et al., 1997), and both share numerous synapomorphies with extant hominines (BEGUN, 2002a). *Ouranopithecus* is also associated with more open settings, which begs the question as to why this taxon did not evolve or appear in the Pannonian Ba-

sin. More research on MN 10 localities in the Basin may reveal the presence of this taxon in the future, and serve to test the hypothesis of a phylogenetic connection between *Dryopithecus* and *Ouranopithecus*.

The return of primates to the Pannonian Basin in MN 13 is a testimony to the resilience and adaptability of Old World monkeys. The terrestrial and flexible feeding adaptations of *Mesopithecus* suited them well for the ecological changes in the region, to much more open conditions (JABLONSKI, 2002). *Mesopithecus* was widespread across the Mediterranean region and could quite easily have entered the basin from any number of access points, given the greatly reduced extent of the lake. The species present in the basin, *M. pentelicus*, found at three localities in Hungary, is known from numerous localities in Greece and Bulgaria, and is most likely to have arrived in Hungary from the south.

To conclude, the Pannonian Basin can fairly be called a major crossroads of primate dispersals during the Miocene. Turkey, often described as a crossroads during many time periods, boasts a couple of stem hominids (*Griphopithecus* and *Kenyapithecus*), a pongine (*Ankarapithecus*), and a third taxon with a possible hominine affiliation (SEVIM et al., 2001) in the Miocene. This is diverse, but not in comparison to the comparably sized Pannonian Basin, with its three superfamilies and eleven species of primates during the same time period.

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