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**SYMPOSIUM**

# New results of Hominoid research in the Carpathian Basin

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**ABSTRACT** Within the dynamic tectonic realm of the Carpathian Basin five succesive primate first appearance events has documented: *Griphopithecus darwini* and Pliopithecus (ca. 15 M years), *Dryopithecus carinthiacus* (ca. 12.5 M years), *Dryopithecus brancoi* (= *Rudapithecus hungaricus*) and *Anapithecus hernyaki* (ca. 10 M years), *Mesopithecus pentelici* (between 8 and 5.5 M years), and *Dolicopithecus sp.*(terminal Miocene and middle Pliocene). In 1998 an associated femoral remains of adult Anapithecus were discovered at Rudabánya. RUD-184 has a large and almost perfectly spherical head, a very long, antero-posteriorly compressed neck and a robust, curved shaft with a pronounced gluteal line. A new cranium of Rudapithecus (= *Dryopithecus brancoi*), RUD-200 ("Gabi") were found in 1999 at Rudabánya. RUD-200 is the first Dryopithecus cranial specimen preserving large portions of the face and neurocranium with direct bone to bone contact. It shares the same great ape characters found in other Dryopithecus from Rudabánya and elsewhere in Europe (dental proportions, labiolingually thick incisors, compressed canines, elongated postcanines, no cingula, reduced premolar cusp heteromorphy, large brain, high root of zygomatic, no subarcuate fossa). It also shares African ape characters seen in other Dryopithecus specimens (laterally facing malar surface, stepped subnasal floor, mildly elongated subnasal clivus, elongated cranium, prominent entoglenoid, fused articular and tympanic temporal, subtle but distinct supraorbital torus, supratoral sulcus, projecting glabella, small but inferiorly placed frontal sinus widest at or below nasion in ethmoidal region and thin enamel with high dentine penetrance).
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**KEY WORDS**

Dryopithecus
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## Current state of neogene primate research in the Carpathian Basin

The Carpathian Basin is a closed subsidence area with an unique Middle and Late Miocene paleogeographical history, containing some 50 terrestrial vertebrate reference localities including catarrhine primate assemblages (Neudorf-Sandberg, Neudorf-Spalte, Götzendorf, Felsőtárkány, Rudabánya, Alsótelekes) and some more in the surrounded areas (Klein Hadersdorf, Göriach, St. Stephan from Austria).

Within this dynamic tectonic realm documented five successive primate first appearence events has documented: *Griphopithecus darwini* and Pliopithecus (ca. 15 M years), *Dryopithecus carinthiacus* (ca. 12.5 M years), *Dryopithecus brancoi* (= *Rudapithecus hungaricus*) and *Anapithecus hernyaki* (ca. 10 M years), *Mesopithecus pentelici* (between 8 and 5.5 M years) and *Dolicopithecus sp.* (terminal Miocene and middle Pliocene).

### The *Griphopithecus darwini* - Pliopithecus event

The first primates, represented by the genera Griphopithecus and Pliopithecus migrated from Africa to Europe in the Middle Miocene (Badenian, MN5 and MN6 Zones).

Molars of Griphopithecus are thick-enamelled, and in combination with the extremely robust jaws it would appear that this primate was adapted for a hard fruit diet. The closest morphologically related African taxon to Griphopithecus is the Kenyapithecus (Kenyapithecines), which are medium sized semiterrestrial quadrupeds. The European Griphopithecus's phalanges indicate a mixture of terrestrial and arboreal adaptive features.

The first European hominoid (Griphopithecus) known from southeastern and central Europe only (Köhler et al. 1999) during the middle Badenian (ca. 15 M years). The earliest Griphopithecus found at Engelswies, southern Germany, MN5 Zone (Heizmann 1992), and the younger specimens from MN6 Zone at Klein Hadersdorf, Austria (Ehrensberg 1938), and from Neudorf-Sandberg, Slovakia (Abel 1902; Steininger 1967), recently named as *Griphopithecus darwini* (Andrews et al. 1996; Köhler et al. 1999). Another species of this genus known from Pasalar (Turkey) as *Griphopithecus alpani* (Tekkaya 1974; Andrews et al. 1996).

The first Pliopithecus migrated to Europe during the early Middle Miocene (MN5 Zone). The pliopithecids are a conservative group of catarrhines that had a small to medium body size, and originated in Africa probably sometime during

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the Oligocene (Andrews 1996). These forms include *P. platyodon* from Elgg, Switzerland, dated as MN5. The other occurrence from Göriach, Austria, already belongs in zone MN6. A series of MN5 occurrences are reported for *P. antiquus* from France. The third species, *P. vindobonensis*, belongs to the uppermost MN5 known from Neudorf-Spalte (= Dévényújfalu, = Devinska Nova Ves) close to Bratislava (=Pozsony) (Rögl 1999).

### The *Dryopithecus carinthiacus* event

During the Sarmatian (MN7-8 Zones, 13-11 M years) the Paratethys isolated from the open oceans and formed a see with reduced salinity. Anatolia connected the Mediterranean and the Eastern Paratethys. The MN8 Zone is the appearence of the hominoid Dryopithecus in Europe (Rögl, 1999). The type specimen of Dryopithecus (*D. fontani*) comes from latest middle Miocene (MN8) deposits in Saint Gaudens, France. A single mandible from Seu d'Urgell (Lleida, Spain) is attributed to the same species (Köhler et al. 1999). The evolutionary pattern of Dryopithecus suggests that there was an early MN8 separation of the Spanish dryopithecines from other Western and Central European species. This suggests a possible MN7+8 dispersal of a primitive member of Dryopithecus. *Dryopithecus carinthiacus* from the western margin of the Carpathian Basin (Mottl 1957) is recognized as a clade distinct from Spanish and French taxa (Andrews et al. 1996).

### The *Dryopithecus brancoi - Anapithecus hernyaki* event

At the end of the Middle Miocene a series of smaller or greater depressions are associated with the Alpine chain along the southern margin of the European plate, and the largest of these is the Pannonian Basin, which is sorrounded by the Carpathians, Alps and Dinarids. The uplift of the Carpathians between 12-11 M years ago established the Pannonian Lake system, separating it from the rest of Paratethys. Time duration of the Pannonian lake is 7-8 million years because it was completely filled with sediment by the end of Miocene or Early Pliocene (Magyar et al. 1999).

Late Miocene primates in the Carpathian Basin occurred during the first phase and are largely preserved in swampy (Rudabánya, Felsőtárkány, Alsótelekes) or fluviatile (Götzendorf) environments between 10.5 and 9.5 M years, when the Pannonian Lake was at its greatest extent.

*Dryopithecus brancoi* (= *Rudapithecus hungaricus* from Rudabánya) known from German localities, other Dryopithecus species (*D. laietanus, D. crusafonti*) appeared in Spain at the same time. First appearence of Anapithecus was also during the MN9 Zone, not only from NE Hungary (Rudabánya, Alsótelekes, probably Felsőtárkány) but from the western part of the Carpathian Basin (Götzendorf), from Salmendingen, Germany (Begun 1989) and Priay, France (Welcomme et al. 1991).

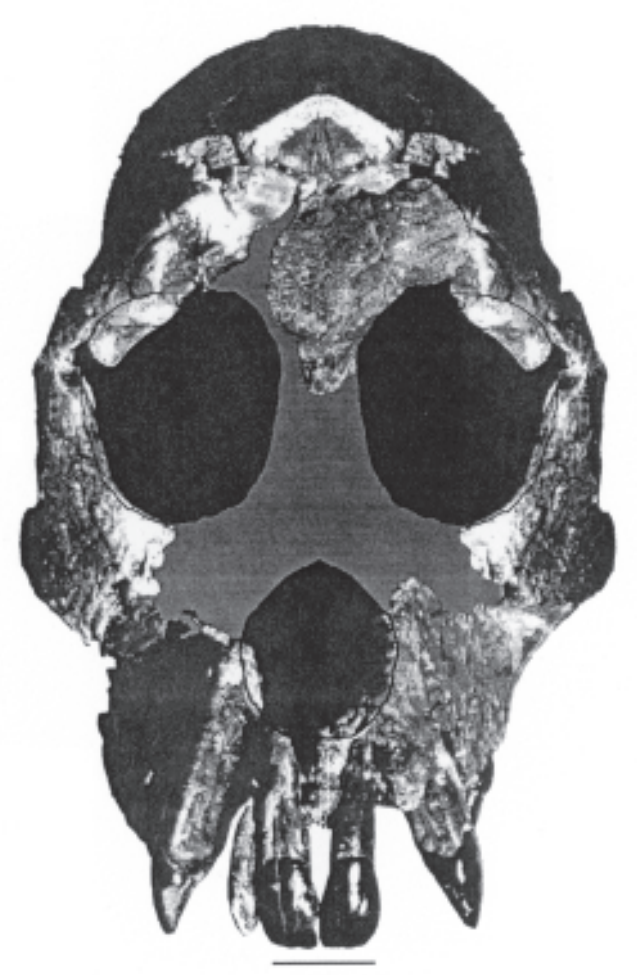

**Figure 1.** Female *Dryopithecus brancoi* (= *Rudapithecus hungaricus*), RUD-200 cranium in frontal view from Rudabánya found in 1999 (photo: Begun DR). Scale = 1 cm.

### The *Mesopithecus pentelici* event

The hominoids disappeared from Europe during the early MN10 Zone (ca. 9.5 M years), and as a new immigrant appeared the colobine Mesopithecus. It is known from Central Europe across to southwest Asia. *Mesopithecus pentelicus* is the most geographically widespread primate in the European Miocene. It has been described as a relatively terrestrial form (Köhler et al. 1999). From the Carpathian Basin *Mesopithecus pentelicus* known only from the Latest Miocene (MN13 Zone, 7.1-5.3 M years), from Polgárdi, Baltavar and Hatvan localities.

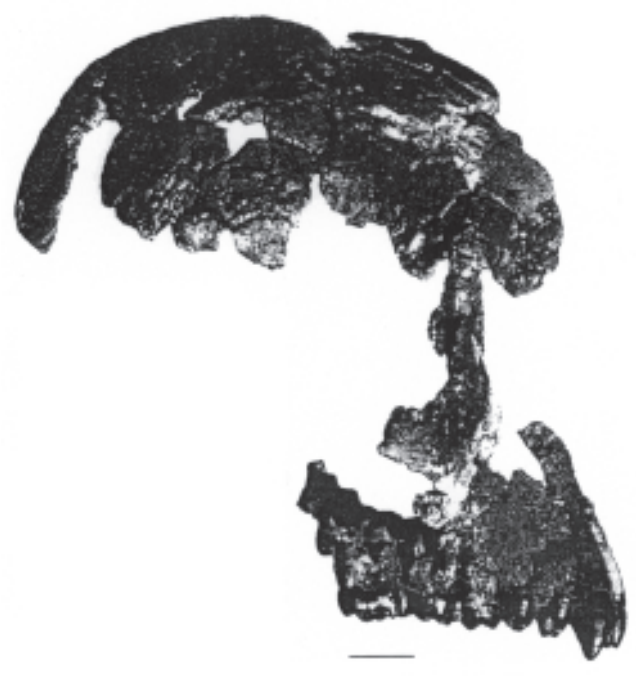

**Figure 2.** RUD-200 in lateral view. Scale = l cm.

### The Dolicopithecus event

A new colobine lineage, Dolicopithecus, also was thought to first appear in MN13 before coming even more widespread in the Pliocene (Western, Central and Southeastern Europe, MN14-16/17), with an apparent congener in Northeastern Asia. Most probably *Mesopithecus pentelicus* ancestry of Dolicopithecus because of apparent polarity reversal of some pedal traits. The widespread occurrence of *D. ruscinensis* in the more forested early Pliocene suggest that environmental changes at the end of the Miocene was significant (Andrews 1996).

## New results of Hominoid research at Rudabánya

### Femora of Anapithecus from Rudabánya

The 1998 excavation of the late Miocene locality of Rudabánya led to the discovery of numerous primate fossils including the associated femoral remains of an adult Anapithecus. The left femur is nearly complete, lacking only the distal end, while the right side specimen preserves the proximal end and about 5 cm of shaft. Anapithecus is well known from Rudabánya, being represented by over 200 teeth and a small number of phalanges. These femora are the first long bones to have been recovered for this catarrhine. Though demaged, both specimens reveal numerous details of the femoral anatomy of this taxon. RUD-184 is similar in overall lenght to the femur of *Epipliopithecus vindobonensis* from Slovakia. However, in contrast to the femur of Epipliopithecus, RUD-184 has a large and almost perfectely spherical head, a very long, antero-posteriorly compressed neck and a robust, curved shaft with a pronounced gluteal line. RUD-184 is also much smaller and morphologically distinct from the catarrhine femur from Eppelsheim, Germany. This specimen is morphologically very similar to Epipliopithecus but from a much larger individual. The morphology of RUD-184 and RUD-183, the more fragmentary specimen, reveal much new information on the positional behavior of Anapithecus, and have taxonomic and phylogenetic implications as well. Their overall size suggest an individual larger than Epipliopithecus, which is consistent with the Anapithecus dental remains. The functional anatomy suggests more strongly developed suspensory positional behavior to Epipliopithecus, and the amount of morphological distinctivness calls into serious question previous suggestion of the pliopithecid status of Anapithecus (Kordos and Begun 1999).

### RUD-200, a new cranium of Rudapithecus from Rudabánya

RUD-200 ("Gabi"), discovered during the 1999 field season at the late Miocene locality of Rudabánya, is the most complete cranial specimen ever recovered of the fossil great ape Dryopithecus (incl. Rudapithecus). Dryopithecus has been known since 1856, and its evolutionary relationship to other apes has been hotly debated since that time. RUD-200 for the first time reveals details of the cranial anatomy of Dryopithecus that allies this taxon phylogenetically with the African apes and humans. The combination of RUD-200 and other specimens of Dryopithecus from Hungary, France and Spain provides evidence of an African great ape morphology of the palate, mid-face, orbital region, neurocranium and craniofacial hafting, lending substantial support to the hypothesis of European origin of the African ape and human clade.

RUD-200 is the first Dryopithecus cranial specimen preserving large portions of the face and neurocranium with direct bone to bone contact. It shares the same great ape characters found in other Dryopithecus from Rudabánya and elsewhere in Europe (dental proportions, labiolingually thick incisors, compressed canines, elongated postcanines, no cingula, reduced premolar cusp heteromorphy, large brain, high root of the zygomatic, no subarcuate fossa). It also shares African ape characters seen in other Dryopithecus specimens (laterally facing malar surface, stepped subnasal floor, mildly elongated subnasal clivus, elongated cranium, prominent entoglenoid, fused articular and tympanic temporal, subtle but distinct supraorbital torus, supratoral sulcus, projecting glabella, small but inferiorly placed frontal sinus widest at or below nasion in ethmoidal region and thin

enamel with high dentine penetrance). RUD-200 is most similar to RUD-77 but much smaller, both dentally and cranially. RUD-77 appears to have slightly broader premolars and a less strongly tapered M3, but the same dental size proportions. RUD-200 differs more from other females from Rudabánya, such as RU-12 and RUD-15, which have more robust canines, relatively longer incisors compared to labiolingual breadth, lower crowned molars, shallower palates, more vertically implanted canines in frontal and lateral views, and deeper canine fossae. The males RUD-7 and RUD-44/47/144, are more similar to RUD-200 in maxillary and dental morphology. Currently we view the diversity in this sample as within the expected range of variationof one species. The RUD-200 and RUD-121 I1 specimens are the smallest from Rudabánya, while RUD-82 is the largest. The RUD-200 M3 specimens are also the smallest from the site, while RUD-85 is the largest. In both cases, the range of variation of I1 and M2 falls within, though at the high end, of the ranges of variation observed within large samples of living hominoids.

Previous, less complete specimens of Dryopithecus from Hungary and Spain have provided some evidence of a link between European late Miocene hominoids and African apes and humans, but much has been based on heavily reconstructed specimens. RUD-200 reveals without such reconstruction the basic African ape character of the cranium of Dryopithecus, and lends strong support to previous interpretations based on less direct evidence. If this interpretation is correct, then it supports the view that the African ape and human clade originated in Eurasia in the late Miocene, and that the common ancestor of this clade migrated to Africa to establish the African ape/human clade sometime during the late Miocene. This is likely to have occurred at a time close to the extinction of hominoids from Europe (Kordos and Begun 2000).

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