Recent Advances on Multidisciplinary Research at Rudabánya, Late Miocene (MN9), Hungary: a compendium

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ABSTRACT – Rudabánya is a rich late Miocene fossil locality first exploited for its vertebrate remains by Pető in 1902. The first fossil primate was discovered by the local chief Mining Geologist, Gabor Hervayák. Professor Miklós Kretzoi made Rudabánya famous in 1969 by publishing a monograph on the new hominoid primate, Rudapithecus hungaricus, recognized herein as Dryopithecus brancoi. In 1991 L. Kordos and R. L. Bernor initiated a project to undertake new excavations and a detailed systematic study of the vertebrate fauna. This 37 author contribution represents a compendium initial report on these studies. A detailed edited volume will follow this publication. We find that there are 112 vertebrate taxa recorded from Rudabánya, 69 of which are fossil mammals. The Rudabánya fauna outcrops at no less than seven different localities, all believed to be essentially synchronous in age. There are no direct radiometric dates from Rudabánya, the lower age is constrained by a single crystal argon date of 11.4 m.y. ± 0.1 m.y., and biochronologic correlations support a latest MN 9 age of ca. 10-9.7 Ma. Paleogeographically, the Rudabánya fauna developed on the edge of the extensive Pannonian lake, which supported a warm, equable subtropical climate. Zoogeographically, Rudabánya is most closely allied with the late Asturian (MN8)-early Vallesian (MN9) Spanish vertebrate localities, and particularly Can Llobateres (straddling the MN9/MN10 boundary). These central and western European localities contrast strikingly with correlated eastern Mediterranean-Southwest Asian localities in their community structure. In particular, Rudabánya and

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Can Llobateres supported diverse lineages of small and medium sized mammals that were dominated by more arctic late early and middle Miocene European faunas. Vallesian localities in Greece and Turkey document an entirely different and progressive "proto-Pikermian" megafauna rich with advanced carnivore and ungulate assemblages. Of particular note is the sharp increase in hypsodont ungulates seen in the eastern Mediterranean-southwest Asian region. Finally, we briefly utilize these zoogeographic and paleoecological observations to contrast current competing hypotheses on "European versus African" ancestry of the African ape-human clade.


I) INTRODUCTION

(L. Kordos and R.L. Bernor)

Rudabánya is a very old settlement in NE Hungary. It has a long mining history extending back to the Age of Copper (5000-4000 BP). From the end of the 18th Century, several open-air pits and an underground shaft were excavated in order to mine iron. During the 1950’s extensive mining activity was pursued and uncovered the soft late Miocene fossiliferous sediments that cover the Triassic iron-bearing basement rock. The Rudabánya mining quarry was closed in the middle of the 1980’s (Text-fig. 1).

Discovery of the late Miocene lignitic sediments at Rudabánya occurred in the last century. The first known vertebrate find from Rudabánya, "Mastodon longirostris", was collected by Gy. Pethő in 1902. Later, Schrétér (1929) described more material, including "Hipparion", which was recognized as being important for the biochronologic determination of the deposits. After some sporadic late Miocene vertebrate finds from Rudabánya, the first primate fossils were found by the mine’s Chief Geologist, G. Herynay in the middle of the 1960s. Herynay brought these specimens via A. Tasnadi-Kubacska to Professor M. Kretzoi in Budapest (Geological Institute of Hungary). Kretzoi (in Anonymous, 1967) immediately named this specimen Rudapithecus hungaricus in a Hungarian daily newspaper, the Magyar Nemzet. This specimen was later figured for the first time in a popular Hungarian science publication (Tasnadi-Kubacska, A., 1967). Later in 1967, Kretzoi gave a lecture on the Rudabánya specimen at a symposium on human evolution (Budapest). In 1969, Kretzoi published a brief description of this same specimen, again under the nomen of Rudapithecus hungaricus.
Later in 1969, Hernyák found yet another *Rudapithecus* mandible from the same locality (Locality 1), and the Geological Institute of Hungary quickly organized and initiated an excavation at the locality.

Regular excavations were organized by Kretzoi at Locality 1 (“Mastodon Wall”) in 1971, and a second locality (Locality 2 or “Gibraltar”) was discovered in 1972. Locality 1 was mostly lost by slope collapse in 1973, but the excavation team collected further vertebrate and plant fossils from Locality 3 (“The Great Wall”) in 1974. During the last three years of field campaign led by Kretzoi, a number of significant accomplishments were realized. In 1976 a protective roof was built over Locality 2. Further fossil material was collected at this locality and localities 4, 5, 6 and 7 were discovered. In 1977, Rudabánya localities 1 and 2 were declared a natural protected area by the Hungarian government. In 1978, Kretzoi collected the last 8 of a total of 74 primate remains found up to that point-in-time. Kretzoi (1974), listed three primate taxa from Rudabánya. In addition to *Rudapithecus hungaricus*, two new taxa, *Pliopithecus* (Anatapithecus) *hernyaki*, and *Bodvapithecus altipalatus* were recognized by Kretzoi in the Rudabánya primate fauna. Finally, Kretzoi (1984) described a new subgenus and species from Rudabánya, *Rangwapithecus* (*Australopithecus*) *serus* based on the RUD-71 specimen. Later in the same paper, he recognized a second new taxon from Rudabánya, described only as Hominoidea indet., based on a single lower molar (RUD-19). In 1976, Kretzoi concluded that *Rudapithecus*’ phylogenetic relationships were as follows: “the australopithecines are representing a separate evolutionary line from the Asian *Rudapithecus-Pithecanthropus-Homo* lineage”.

Kretzoi (1975) and Kretzoi et al. (1976) published the first results on Rudabánya pollen, macroflora, ostracods, molluscs and vertebrates from all localities collected between 1967 and 1974. These studies concluded that the age of all Rudabánya localities was “Lower Pliocene” (= now early late Miocene), and established a new terrestrial mammal age, the “Bodvailum”, intermediate between the older “Monacium” and younger “Eppelsheimium”, which is correlated with MN9 (Kordos 1987b). Between 1979 and 1984, short excavation seasons were led by L. Kordos. In 1985 Kordos wrote a popular science book on the Rudabánya localities. In 1984, Kretzoi placed hominoid materials collected under his direction in the Geological Institute of Hungary. These collections remain closed to all other investigators. Only casts made by Alan Mann (University of Pennsylvania, Philadelphia) are currently available for study. At the same time, oversight of the Rudabánya localities was transferred from the local museum to the Geological Institute of Hungary (Budapest) where they are currently curated and conserved.

Gabor Hernyák discovered an important female skull, RUD-77, at locality 2 in 1985. This was only the fourth Miocene hominoid skull known at the time, the others being the early Miocene *Proconsul africanus* skull (Kenya), the late Miocene *Oreopithecus* skull (Baccinello, Italy), the late Miocene *Sivapithecus* skull (Pakistan) and the late Miocene *Lufungpithecus* skull (China). The Rudabánya skull was initially described by Kordos (1987a), and later revised by Kordos & Begun (1997). Kordos continued excavation at Localities 2 and 3 between 1986 and 1989. At Locality 2, the excavation was mostly in the gray marl, which was found to underlie the upper lignite, black clay and black mud where *Anapithecus* was found. *Anapithecus* material found included molar teeth, and in 1988 a partial cranium, RUD-83. At Locality 3 more lignite and conglutinated layers were excavated, and mostly large mammal bones were found. Kordos shifted his emphasis at Rudabánya, by concentrating his excavations at Localities 2 and 7 from 1989 through 1991. During this period, Kordos discovered that the Locality 7 paleokarst horizon was deposited on the Rudabánya paleovalley floor, and that the lignite deposits were deposited on top of the paleokarst. This period of the excavation witnessed major socio-political changes in Hungary, and difficulty in accessing funds from local sources.

In the summer of 1991, Kordos invited R.L. Bernor (Washington D.C.) to engage in a multidisciplinary research project at Rudabánya Locality 2. With funding from the L.S.B. Leakey Foundation and the National Geographic Society, excavations were continued by Kordos and Bernor, with M. Armour-Chelu (London) pursuing collection of taphonomic data both in the field, and the museum in 1992. Peter Andrews (London) led the taphonomic excavations at Rudabánya 2 in 1993 and 1994, while Kordos and Bernor focussed their efforts on the systematics of the Rudabánya vertebrate faunas. This review has been undertaken in collaboration with a number of specialists whose contributions follow in the chapters that follow. While the emphasis is on all of the Rudabánya Locality 2 fauna, several specialists looked at the vertebrate remains from all the Rudabánya localities as well as the late Miocene Hungarian faunal succession (re: Bernor et al., 1999). An edited volume with detailed descriptions of the fauna, its paleoecologic and taphonomic aspects will follow this contribution in the near future (Bernor & Kordos, Eds.).

Alongside these efforts, L. Kordos and D.R. Begun have made a focussed analysis of the Rudabánya primate fauna. In addition, Begun and Kordos have conducted three summer field seasons (1997-1999) under the aegis of the “Rudabánya Field School” offered to college students by the University of Toronto and the Geological Institute of Hungary.

II) GEOLOGICAL BACKGROUND

**GEOLOGY (L. Kordos and G. Hernyák)**

The Rudabánya hominoid localities are located on the western flank of the northern Carpathian mountains. Locally, the exposed basement rock includes the Slovakian Karst, the Aggtelek Karst, and the Rudabánya Hill Range. From a structural and historical viewpoint, the Slovakian and the...
Aggtelek Karst separated from the NW Carpathian range prior to the Oligocene. The Rudabánya Hill Range separated from the other two formations during the Oligo-Miocene, by the NE direction compression of the neighbouring Bükk and Szendrő Mountains. By this event, the Rudabánya Hill moved from the southern foreland to the eastern margin of the Aggtelek Karst.

The tectonic and sedimentologic history of the area has been extensively reevaluated during the last two decades (Balogh, 1982; Grill, 1989; Grill et al., 1984; Szentpétery, 1988; Less, 1998). The original Mesozoic sediments were mostly calcareous, deposited in three different environmental facies during the Triassic and Jurassic periods, namely from N to S: Szilice, Melléte and Torna facies. The Szilice and Torna facies were deposited on the continental plate, while the Melléte facies was deposited in the mobile continental self of the Tethys Vardar Ocean. The Szilice facies is Upper Permian to Late Jurassic age. These formations formed the Szilice Nappe system as their uppermost structural unit. The Melléte facies was deposited during the middle - late Triassic, and early Jurassic. Deposition was followed by regional metamorphism. The Torna facies contains only Triassic sediments with later epizonal regional metamorphism.

The oldest exposed sediments in the Rudabánya region are of latest Permian age. The underlying middle Permian landscape was covered by evaporites during the late Permian and early Triassic. At the beginning of the early Triassic, there is a major transgression, with three developed facies. The middle Triassic carbonate-platform type limestone was divided during the Ladinian into three units: the Szilice facies deposited on the northern continental base, the Melléte facies deposited on the thin continental and oceanic plates, the Torna facies deposited on the continental base to the south. Because the subsidence of this area continued during the middle Triassic and in the early Jurassic, sediments were deposited in a deep-sea environment. Subduction of the Melléte facies commenced in the middle Jurassic, and formed a series of nappe systems. Due to subduction, most of the sediments of the Melléte facies melted and formed granitic and rhyolitic magmatic rocks. This volcanic activity is responsible for the metasomatic type of mineralization typical of the Szilice facies sediments in the Rudabánya Hill Range. The original nappe system of the Aggtelek-Rudabánya range was strongly deformed and reduced in space after this event. During the Cretaceous, sediments of the three nappe systems again became deformed.

From the second half of the Cretaceous, the Mesozoic series became elevated and formed a karstic peneplain, and until the end of the Oligocene, produced bauxite type soils. The third and latest important tectonic event was during the latest Oligocene and earliest Miocene when a horizontal fault produced the compressed range known today as the Rudabánya Hills. This tectonic event was part of a larger tectonic mobilism that involved the Bükk and Szendrő Mountains, themselves part of an ancient microplate, which moved in a southwest to northeast trend to their present location due to encroachment by the African Plate.

Late Miocene Paleogeography of Rudabánya

The Rudabánya Range was formed in the middle Miocene as a peninsula of the Aggtelek Karst (Kordos, 1982). The late Miocene Pannonian Basin developed in an extensional basin behind the compressional arch of the Carpathians (Text-fig. 1). Subsidence began during the middle Miocene, forming deep, pelagic basins, separated by reef-bearing ridges. 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 surrounded by the Carpathians, Alps and Dinarids. The uplift of the Carpathian Mountains between 12-11 Ma ago established the Pannonian Lake system, separating it from the Eastern Paratethys. The Pannonian lake was completely filled in by the terminal Miocene or earliest Pliocene, ca. 5 Ma.

Magyar et al. (1999) have recently reconstructed the paleogeographic evolution of the Pannonian lake recognizing three distinct intervals of development: an initial, regressive stage that resulted in its isolation from the Eastern Paratethys; a second interval of gradual transgression, and a long third interval of protracted regression, sedimentary infilling and progradation.

During the early Sarmatian, the Rudabánya Range was 7-8 km in length and 1-2 km wide. It was connected to the Aggtelek Karst at its northernmost limit. At this time, it was likely covered by Sarmatian marine sediments. The Pannonian lake first formed circa 12.0 Ma, a time marked by the onset of a regression. This relative sea level drop resulted in isolation of the intra-Carpathian waters (Magyar et al., 1999). Unconformities between the marine Sarmatian and overlying Pannonian lacustrine environments are common, and especially in the Borsod Basin adjacent to the Rudabánya peninsula. At this time, the Rudabánya Range was eroded by fluvial activity, and tropical-subtropical karst surfaces formed on the base and on the slopes of the valleys. At the base of the interpeninsular valley-system, terrestrial variegated clay was deposited without any apparent fossil remains. After the separation of the Pannonian lake, the water table gradually increased, and circa 10.8 Ma penetrated the northern part of the Borsod Basin, flooding the Rudabánya Range and adjacent valleys. Between 11 and 10 Ma, the valley system was exposed to a variety of lacustrine and peri-lacustrine environments including: lake, swamp, wetland and paleosoil. Rudabánya's sediments include cyclic layers of gray marl, clay and lignite, totalling 8-12 meters in thickness. These sediments, include rich fossiliferous levels that contain plant impressions, seeds, molluscs, vertebrate remains and, of special note, catarrhine primates.

The Pannonian lake probably reached its greatest areal extension circa 10-9.7 Ma. The maximum transgression is likely marked by the uppermost elevation of the lacustrine-swampy sedimentation in the valleys of Rudabánya Peninsula. One oscillation of the water level probably precipitated the resedimentation of Locality 7. Because this sediment was hydraulically resorted, the bone matrix is...
rich and very broken. After its resorting, another transgressive lake cycle inundated and buried the Locality 7 bone breccia. According Magyar et al.’s (1999) reconstruction at the ca. 9.0 Ma Congeria praerhomboidea Biochron, the Pannonian lake suddenly reduced its areal extent and the lacustrine–swampy sedimentation regime ceased to occur. These sediment types were replaced by fluviatile sands which appear at the top of the Rudabánya Range succession covering all local depressions and forming a plateau that is elevated above the lake sediments.

**TAPHONOMY**
(P. Andrews, M. Armour-Chelu, D. Cameron)

The fossil assemblages from seven stratigraphic levels at Rudabánya 2 will be described on the basis of two collections of material. The main collection consists of fossils excavated in place (Text-fig. 2). These are analysed for vertical and horizontal distribution relative to sedimentological differences, examining their size distribution, directions of preferred orientation, angles of dip, bone breakage patterns and surface modifications.

The second collection consists of the screening residues. The fine residues from the screening process have only been sorted in part, but the coarse residues retained in the 0.8 mm screens have been sorted into the following constituents: wood, seeds, root, molluscs, large mammal bone, small mammal bone and amphibians. The relative abundances and distributions of these fractions have been analysed relative to the meter grid laid down over the site.

Results indicate several modes of animal bone accumulation at Rudabánya. Tree trunks and roots are present in their growth positions in lignites, black muds and massive marls, and the fossil animal bones present show a lack of disturbance. Water transport is indicated for reworked marls, with the animal bones showing evidence of preferred orientation in the direction of water flow. The accumulation of shelly layers and small mammal assemblages is associated with pond deposits accumulated on lake-shore flats. Little evidence of predation has been found in any level (nevertheless see Armour-Chelu & Viranta, 2000), but there is extensive post-depositional modification of the fossils from most levels due to highly acid environments. The exception to this is the assemblage from the pond deposits (the "black mud"), which although heavily blackened, shows little other evidence of post-depositional modification.

### III) INVERTEBRATE FAUNAS

**TERRESTRIAL AND FRESHWATER MOLLUSCS**
(E. Krolopp)

The molluscan work reported herein is based on shells collected at Rudabánya during the early excavation years. The mollusc collections are all housed by the Museum of the Hungarian Geological Institute. Pantó (1956: 271) has reported 15 mollusc species in his monograph on the geology of Rudabánya, but his specimens have since been lost.

The Rudabánya mollusc fauna consists of 44 taxa (Table 1). The majority of the species are terrestrial, but the specimen number of aquatic forms is significantly higher than that of the terrestrial ones.

Both bivalve species diversity as well as number of individuals for those species is very low in the aquatic fauna. Unionids are completely lacking. Given that larvae of these animals live in the skin of fish species for a time as parasites, their absence may be connected to the absence of fish in the environment. The mud was rich in organic material, thus depleted of oxygen, and this may be the reason for the rarity and few specimen of the small sized Sphaeriidae. All sphaeriid specimens originate from a yellowish clay interdigitated between two lignitic horizons. The low organic content of this layer is suggestive of a well aerated environment. Similarly, the stagnant water and low oxygen level in other Rudabánya environments may explain the low number of Prosobranchiata species. Most specimens of this group originate also from the above mentioned yellowish clay.

The number of species and specimens of...
Table 1 - Rudabánya Terrestrial and Freshwater Mollusc Faunal List

<table>
<thead>
<tr>
<th>Species</th>
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<tbody>
<tr>
<td>Sphaerium aff. cornearum (L.)</td>
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<tr>
<td>Pomatias sp. indet.</td>
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<tr>
<td>Acticula cf. edulaueri Schlíkum</td>
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<tr>
<td>Bulimina cf. jurtinici Brusina</td>
</tr>
<tr>
<td>Viviparus sp. indet.</td>
</tr>
<tr>
<td>Brota escheri Bronngiart</td>
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<tr>
<td>Carychiopsis berltsae (Halaváts)</td>
</tr>
<tr>
<td>Carychiopsis sp. indet.</td>
</tr>
<tr>
<td>Lymnaea cf. palistriformis (Gottsch.)</td>
</tr>
<tr>
<td>Lymnaea cf. socialis (Gottsch.)</td>
</tr>
<tr>
<td>Planorbiorus aff. corneas (L.)</td>
</tr>
<tr>
<td>Antius conicus Süss</td>
</tr>
<tr>
<td>Antius cf. septiargyraiformis (Gottsch.)</td>
</tr>
<tr>
<td>Segmentina cf. filoccina (Sandberger)</td>
</tr>
<tr>
<td>Succinea sp. indet.</td>
</tr>
<tr>
<td>Granaria cf. sueberli (Klein)</td>
</tr>
<tr>
<td>Vertigo callossa (Reuss)</td>
</tr>
<tr>
<td>Vertigo angustior oceensis (Halaváts)</td>
</tr>
<tr>
<td>Vertigo cf. moedlingensis Wenz &amp; Edlauer</td>
</tr>
<tr>
<td>Vertigo sp. indet.</td>
</tr>
<tr>
<td>Argya oppoeliensa (Andrussow)</td>
</tr>
<tr>
<td>Gastrocopta acuminata (Klein)</td>
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<tr>
<td>Gastrocopta fissidens schenziatica Wenz</td>
</tr>
<tr>
<td>Gastrocopta cf. noulitiana (Dupuy)</td>
</tr>
<tr>
<td>Gastrocopta edulaueri (Wenz)</td>
</tr>
<tr>
<td>Gastrocopta aff. jurenes (Sandberger)</td>
</tr>
<tr>
<td>Azca cf. tridentiformis (Gottscheck)</td>
</tr>
<tr>
<td>Acanthina cf. anthonini (Michelin)</td>
</tr>
<tr>
<td>Vallonia sp. indet.</td>
</tr>
<tr>
<td>Strobilus sp. indet.</td>
</tr>
<tr>
<td>Helicodiscus sp. indet.</td>
</tr>
<tr>
<td>Discus cf. plehradus (Bourg.)</td>
</tr>
<tr>
<td>Trypitsia sp. indet.</td>
</tr>
<tr>
<td>Nordbeckia fischeri pontica Lueger</td>
</tr>
<tr>
<td>Serrulella sp. indet.</td>
</tr>
<tr>
<td>Vitrea sp. indet.</td>
</tr>
<tr>
<td>Limacidae indet. I</td>
</tr>
<tr>
<td>Limacidae indet. II</td>
</tr>
<tr>
<td>Triclia sp. indet.</td>
</tr>
<tr>
<td>Helicocyca sp. indet.</td>
</tr>
<tr>
<td>Tropidophalus cf. doderleini (Brusina)</td>
</tr>
</tbody>
</table>

Basommatophora is significantly higher than that of the prosobranchiates. Members of this group live mostly on seaweed and may repeatedly climb up to the water surface to breathe atmospheric air. Consequently, they are only moderately influenced by the decomposing organic rich mud and by the oxygen depleted water above it.

The most abundant forms of terrestrial gastropods lived on plants that set their roots in water, or on trees adjacent to the shoreline. These forms all require high humidity and live near waterbodies (Carychiurn and Succinea species). Carychiurn species are especially abundant. Besides these, Zonitidae, Limacidae and Helicidae, which also require an elevated level of humidity, lived farther from the shores, on areas of open vegetation or on gently overgrown ones (wet meadows and forests). Some forms, having modern relatives living on drier land, also were found (Pupillacea).

IV) VERTEBRATE FAUNA

AMPHIBIANS (Z. Roček)

Rudabánya’s amphibian fauna includes taxa that were common in Europe from pre-Oligocene times (such as Chelotriton, Discoglossidae, Pelobatidae, if the forms recorded are Eopelobates, Palaeobatrachus, Peltotes and Rana). These taxa also include forms that first appeared after the Grande Coupure (Eocene/Oligocene boundary) and became widely distributed throughout Europe during the Neogene (e.g. Latonia, Discoglossus), while others appeared only in the early Miocene and were widely distributed in eastern Europe, rarely reaching the western region of the continent (e.g. Mioproteus).

Tailed amphibians are represented by Mioproteus caucasicus (Family Proteidae). Mioproteus is the most abundant tailed amphibian at Rudabánya, and this is quite unusual if compared with its other known occurrences. Salamandridae are represented by two types of Chelotriton different in their morphology; both are morphologically similar to the late Oligocene articulated skeletons of Chelotriton from Rott and Enspel (Germany), but the Rudabánya forms differ in some significant anatomical features (e.g. morphology of the maxilla). Since these same morphological differences are seen in the Chelotriton from Gritsev (late Miocene, Ukraine [MN9]), they are believed to be of taxonomic importance. Another Rudabánya salamandrid is represented by fragmentary maxillae and praemaxillae recalling extant Salamandra, but larger, having tooth crowns with black tips and processes between tooth bases. This form was not yet formally described, and the same form has also been found at Gritsev. Tiny vertebrae may suggest the presence of still another salamandrid belonging to the Brachyphaxanus-Triturus complex. However, precise taxonomic assignment of this form can only be made on cranial elements that are not normally found because these bones break during screen washing. Vertebrae and other postcranial elements are relatively uniform in this group.

The most common Rudabánya anurans were discoglossids belonging to the genus Latonia (L. gigantea). In addition, there are several elements that also suggest the presence of Bombin, as well as Discoglossus. Another dominant anuran was a palaeobatrachid, here assigned only to Palaeobatrachus, although extreme differences in size, associated with some morphological differences, may indicate more than a single species. Rudabánya is one of few fossil sites in which Latonia is found together with palaeobatrachids. Besides Latonia and Palaeobatrachus which were dominant, there were also Pelobatidae (difficult to distinguish on the postcranial material only whether Eopelobates or Pelobates), Pelodytes, Hyla and Rana. Rudabánya’s Hyla appears to be the earliest record of this genus in Europe.

Size differences of ranid ilia may suggest that there were at least two forms of Rana at Rudabánya. A rather surprising aspect of the Rudabánya herpetofauna is the poor fossil repre-
sentation of the pelobatid frogs, known only from several ilia, and absence of the Bufonidae, although the earliest record of *Bufo* in Europe is from MN4 of Spain.

**SNAKES (Z. Szyndlar)**

The fossil snake material from Rudabánya described in this short report consists of nearly 500, mostly badly damaged, vertebrae belonging to four or five ophidian taxa. All but one of these vertebrae represent the trunk portion of the column.

A single vertebra, characterized by very small absolute dimensions (the centrum length less than 2 mm) and simplified morphology (lacking neural spine and haemal keel, with undivided paradiapophyses), is clearly referable to the Infaerodr Scolecophidia. The scolecophidian from Rudabánya is tentatively considered to be a member of the family Typhlopidae, the only representative of the family Typhlopidae known in Europe and adjacent areas. It should be qualified here however that the identification of scolecophidian vertebrae is unreliable even to the familial level. On the other hand, a possible presence of the other scolecophidian family Leptotyphlopidae, with the genus Leptotyphlops being found today very distant from Central Europe, is not highly likely.

There are forty-nine vertebrae that are clearly referable to natricine colubrids. These vertebrae are all characterized as having sigmoids shaped hypapophyses throughout the trunk portion of the column, long centra and with parapophyseal processes projecting anteriorly. Projecting structures are missing in most vertebrae. However, relatively high neural spines retained in several of the bones suggest a referral to the extant genus *Natrix*.

The informal term "Colubrinae" refers to colubrids devoid of hypapophyses in most of their trunk vertebrae. An overwhelming portion of the Rudabánya snake material, i.e. approximately 200 vertebrae, is referred to a single specifically unidentified form, named here Colubrinae A. The vertebrae belonged to relatively large snakes, the centrum length of the largest one being 8 mm. This snake most likely belonged to the living genus *Coluber*, although not resembling extant European members of the genus. In some aspects the Rudabánya colubrine trunk vertebrae are similar to those of the extinct species *C. hungaricus* from Polgárdi (re: Venczel, 1994). Six vertebrae, are referred to a different Colubrinae (Colubrinae B). They are minute and elongate, having strongly flattened haemal keels. It cannot be excluded that they actually represent the posteriormost trunk portion of the column of Colubrinae A. Approximately 200 vertebral fragments were too greatly damaged to be determined with any degree of accuracy. They are most likely referable to Colubrinae A.

Fossil remains of the Family Colubridae (s.l.), the most common and diverse snake group in Europe since at least the middle Miocene, are not very informative unless they can be identified to the specific level. This is also the case for Rudabánya's colubrid ophidians. Perhaps the Rudabánya Colubridae included the same or similar forms known from other late Miocene localities in the region: *Coluber hungaricus* and *Natrix longivertebra* (cf. Bachmayer & Szyndlar, 1985; Szyndlar & Zerova, 1992; Venczel, 1994).

The occurrence of *Naja romani* (Family Elapidae) was recognized mainly on the basis of a single, but perfectly preserved relatively large vertebra; the centrum length is 7.8 mm. Vertebral column of the genus *Naja* can be easily differentiated from those of other snakes. They represent a morphological pattern observed in large colubrines but, contrary to the latter, they are provided with hypapophyses throughout the trunk portion of the column. The Rudabánya vertebra displays a set of features characteristic of *Naja romani* (cf. Szyndlar, 1991b), the only extinct cobra known from the late Miocene of Central Europe (Szyndlar & Zerova, 1990). The referral of four other vertebral fragments to *Naja* cannot be fully corroborated.

As in most coeval localities in Europe, the Rudabánya fauna contained remains of two members of the genus *Vipera*; the poor state of preservation of these fossils, however, does not enable their identification to the specific level. Members of the Viperidae can be easily distinguished from other snakes bearing hypapophysess throughout their vertebral column (natricine colubrids and elapids) on the basis of posteriorly depressed neural arches, ventrally directed parapophyseal processes, and straight hypapophyses. Three viperid fragmentary trunk vertebrae found in Rudabánya are referred to *Vipera* sp. ("aspis" complex) based largely on their relatively small size. A single fragmentary trunk vertebra of *Vipera*, despite its strong damage, is clearly referable to *Vipera* sp. ("Oriental viper" group), based on its relatively large absolute dimensions.

The most characteristic elements of the ophidian assemblage from Rudabánya are the scolecophidian *Typhlops* and the elapids *Naja*. The present European range of the genus *Typhlops* is restricted to the Balkan Peninsula. The occurrence of these minute burrowing snakes, present in the region since at least the early Miocene (Szyndlar, 1991a), was also reported from the Ukrainian late Miocene (Szyndlar & Zerova, 1990, 1992). Before the end of the Miocene however, scolecophidians disappeared from the area of Central Europe. The fossil elapid from Rudabánya was classified as the extinct species *N. romani*. Perfectly preserved remains of this fossil cobra are known from several European countries from the period between the early (MN4) through late (MN11) Miocene (Szyndlar & Rage, 1990). In the vicinity of Rudabánya it was reported from Kohfulisch and Gritsev (Bachmayer & Szyndlar, 1985; Szyndlar & Zerova, 1990). As did *Typhlops*, *Naja* also disappeared from the Central Paratethys region before the end of the Miocene.

The European fossil record suggests that the geographic range of several snake taxa diminished during the latest phase of the Miocene. It seems that even before the Messinian Crisis the European distribution of at least *Typhlops, Erxys* (Boidae), *Naja* and large *Vipera* ("Oriental viper" group, Viperidae) became restricted to the peri-Mediterranean coastline, and to a lesser degree, the Black Sea. Then,
during the course of the Pliocene, all of these taxa disappeared entirely from the western Mediterranean. The extinction of the scolecophidian and elapid snakes in Hungary prior to the end of the Miocene confirms this supposition. During the terminal Miocene (MN 13), the snake fauna characteristic of Rudabánya was replaced in Hungary by the extant assemblage which was in place by the time represented by Polgárdi (Venczel, 1994).

**AVES (D. Janossy)**

The systematic excavations at Rudabánya have yielded bone fragments representing 12 bird species. This material is particularly valuable because Rudabánya's age has been established as being late Miocene (MN 9; re: Correlation below). It is valuable to compare the Rudabánya ornithofauna with the recently analysed one from Polgárdi (MN 13). The Rudabánya galliforms are completely different from galliforms at Polgárdi. Also, Polgárdi's only owl is the Barn Owl (Tyto), while that at Rudabánya is Strix.

I provide here a short evaluation of both older (reported by Jánossy, 1976, 1977 and by Kretzoi in Kretzoi et al., 1976) and newer material collected at Rudabánya. Although a great deal of the Rudabánya avian material is too fragmentary to identify beyond the incertae sedis level, several taxa can be identified within the avian assemblage.

**Family: Anatidae**

Milne-Edwards (1871) described Anas velox from the middle Miocene (MN 6) French locality of Sansan. In his revision of the group, Cheneval (1987) mentioned this small form from Germany (Steinheim am Albuch), Bohemia (Dolnice) and Roumanian Dobrjua (Credinta). In spite of the fact that the Rudabánya material is fragmentary and of uncertain determination, it seems distinctly possible that this Anas is well referred to A. aff. velox. There likely is also a larger duck of the genus Anas at Rudabánya; because of the extremely fragmentary condition of the remains the determination cannot be more accurate than Anas sp. (size of acuta-querquedula).

**Family: Phasianidae**

Bochenski (1987) revised Miophasianus medius from Przeworno (Peniborn), which is the same size as the Rudabánya form. However, Przeworno is much younger in age (MN 17) and I thus prefer to maintain Miophasianus cf. medius for the Rudabánya pheasant. Palaearctyx aff. grivensis is a small Galliform bird known from La Grive (France) and Gargano (Italy) (Ballman, 1969a, 1976), Rudabánya, Tardosbánaya and Sámeg (Hungary) and Malusteni (Roumania) (Kessler, 1984; Jánossy, 1991). Given that the relevant Rudabánya material is so fragmentary, I am only able to establish that there is another pheasant taxon intermediate in size between the smaller Palaearctyx aff. grivensis and the larger Miophasianus. This intermediate sized taxon is approximately the size of Palaearctyx phasianoides and/or Palaearctyx intermedius.

**Family: Rallidae**

Milne-Edwards (1871) described Miorallus major from the middle Miocene (MN 6) locality of Sansan. The Rudabánya form agrees well with this taxon in its size and according to Lambrecht (1953) it agrees in size with Pollica atri. Ballmann (1969b) has noted the occurrence of a rail, "Rallidarium gen. et. sp. indet." from La Grive (MN 7+8) which is chronologically closer in age to Rudabánya than is Sansan. He claims that this taxon is a rail the size of Gallinula chloropus. Given the fragmentary nature of the relevant material, little more can be said about this rail, whose attribution is maintained as Miorallus sp.

**Family: Strigidae**

Ballmann (1969a) described a tawny owl, Strix intermedia, from Wintershof-West (MN3) which is morphologically quite similar to the extant tawny owl, Strix aluco. The Rudabánya striiform bone fragments are referable to Strix aff. brevis (Jánossy, 1977). The tarsometatarsus and the length of a well-preserved phalanx 2 digiti 2 support this assignment. There is yet a smaller owl at Rudabánya which I refer to Athene sp.

**Family: Sylviidae**

There is a Passeriforme bird (Acrocephalus sp.) at Rudabánya that is the size category and has the morphology of the Great Reed Warbler, Acrocephalus arundinaceus. Of particular morphological importance is the Rudabánya taxon's processus extensorius (proc. metacarpalis I) and the trochlea carpalis, as well as the reduction of the processus alularis. The morphology is not sufficient for a specific determination. The Rudabánya material includes an acrocoracoideum that agrees most closely in its morphology to those of the grasshopper warblers and its allies (Genus Locustella). The Rudabánya material appears to be smaller than the savis grasshopper warbler (Locustelle fascioides).

**Family: Corvidae**

The presence of corvids at Rudabánya is supported by a suite of terminal phalanges (claws). The claws in question are characterized as being the size of corvids. They also have grooves on the side of the claws that have the length and flatness seen in corvids. Cranes and geese have similar grooves, but the shape of their bones is much more robust. Yet, the Rudabánya material is too fragmentary to identify this taxon beyond the nomen Corvus sp.

Kretzoi (in Kretzoi et al., 1976) characterized the Rudabánya avifauna as being indicative of a swamp-forest environment. The modest song-bird fauna composition suggests an environment covered with reeds. A comparison with the avifauna of Polgárdi (MN13; Jánossy, 1991) exhibits a number of similarities. The most readily comparable forms are the galliforms, including the small galliform, Palaearctyx cf. grivensis , the intermediate sized P. aff. phasianoides and the somewhat larger Miophasianus cf. medius. Polgárdi has similar small and large species. However, the Rudabánya
and Polgárdi owl faunas are completely different from one another: Strix at Rudabánya versus Tyto at Polgárdi.

**INSECTIVORA (R. Ziegler and L. Meszaros)**

The Rudabánya insectivore fauna includes species belonging to the families Erinaceidae, Metacodontidae, Soricidae, Dimylidae and Talpidae.

The erinaceids include three species: *Lanthanootherium sanmigueli*, *Galferix* sp. and *Postpalerinaceus* sp. The remains referred to *L. sanmigueli* compare closely in their morphology to the type mandible of Viladecaballs and the more informative specimen of Can Llobateres, the reference locality of MN 9, with which the Rudabánya fauna correlates. They also are of the same size as the teeth from Montredon, referred to *L. sanmigueli*. The remains of *L. cf. sanmigueli* from Dorn-Dürkheim and Eichkogel roughly fit the present ones in their size. A small *Galferix* species is represented by an M1 trigonid. The referral of this specimen to *Schizogalerix* cannot be excluded. Medium-sized erinaceine dental remains can be referred to a new species of *Postpalerinaceus*, somewhat smaller and differing in some morphological details from the type species *Postpalerinaceus vireri*.

Family Metacodontidae is represented by dental remains referred to *Plesiosorex*. These compare most closely to *Plesiosorex styriacus*. Given the metric deviation from the type material it will be referred to *Plesiosorex aff. styriacus*. The Rudabánya *Plesiosorex* is the latest occurrence of the genus known to date.

Including four taxa, the soricids are the most diverse insectivore family in the Rudabánya fauna. The *Dinosorex* remains are, in overall size, robustness of the mandibular corpus, and in some other features, indicative of a close relationship to *Dinosorex pachygnathus*, the youngest known species of the genus. Some conspicuous morphological differences make the description of a new species necessary. Most of the Rudabánya soricids are referable to *Crusafontina*. They are closely related to *Crusafontina endemic* from Can Llobateres, representing an early member of the evolutionary lineage Rudabánya - Can Llobateres - Kohfidisch. The specimens are referred to *Crusafontina aff. endemic*. They are the biostatigraphically most important soricid from Rudabánya. One tiny mandibular fragment with three molars in situ is referred to *Puaenelmmoceus aff. repenningi*, in large part because of its biostatigraphic and geographic proximity to the type locality of Kohfidisch, Austria. *Puaenelmmoceus crouzeli* from Sansan is markedly earlier in time and smaller in size but would fit well morphologically. One lower jaw fragment bearing M3, can only be allocated to Soricinae gen. et sp. indet. due to the lack of a sufficient number of diagnostic characters.

There are also some fossil remains of the family Dimylidae. There are dental remains referable to *Metacordylodon schlosseri* from Opole that compare well in their degree of amblyodonty and exoelessodonty, in the strong fusion of the trigonid cusps of M1, and in the reduction of the M3 talonid. However, because of some differences with the type specimen, we refer the Rudabánya remains to *Metacordylodon aff. schlosseri*. They represent the latest occurrence of this species currently known. The teeth and mandibular fragments referred to *Plesiodinomys chantrei* compare closely with *Pl. chantrei* from the type locality La Grive. This species is known for its long biostatigraphic range (MN 3/4 to MN 11). A mandibular fragment with an open symphysis is referred to *Dimylidae gen. et sp. indet.* Perhaps it represents an anatrophic element in the *Metacordylodon* sample. Together with *Crusafontina*, the talpid remains referred to a new species of *“Archaeodesmansana”*, represent the dominant insectivores in the Rudabánya fauna. However, the most diagnostic element, the H1 with a bifid apex, is not preserved, allowing no more precise referral than genus *Archaeodesmansana*. *Talpa* sp. is represented by some humeri and a jaw fragment. The humeri differ in size and/or morphology from known *Talpa* species that are either slightly older or younger than the Rudabánya sample.

The diverse insectivore fauna indicates a paleoenvironment that had abundant water and forests. The galericines, represented by numerous *Lanthanootherium* and by one specimen of *Galferix*, compare with extant S.E. Asian faunas that have humid forest biotopes with thick undergrowth, often close to water bodies. *Crusafontina aff. endemic* is morphologically comparable to the extant species *Anuaroosorex squamipes*, living in the mountainous forests of SE-Asia. The extremely specialized dentition of the extinct dimylids, especially of *Metacordylodon*, suggests a conchivorous diet. Some dimylids are believed to have been semi-aquatic in their behavior. The desman *Archaeodesmansana*, like extant desmans, certainly had a semi-aquatic mode of life.

**CHIROPTERA (G. Topal)**

The Rudabánya bat assemblage includes the following species: *Eptesicus campanensis*, *Eptesicus* sp. nov.; cf. *Miostrellus risgoviensis*. Up to now, all of the Rudabánya localities sample open-air habitats where bats occur occasionally. Rudabánya's bats are indicative of tropical marshy woods where they lived under tree bark, in the holes of trees, or in the cracks of mountain walls. Their occurrence in the pond and marsh environments would have been the coincidence of their falling into those habitats. It is worthwhile noting that Rudabánya's bat fauna lacks "true" tropical forms such as hipposiderids. However, bones of a few species of the generally distributed vespertilionids have been found. Some of them have been found to be related to the North American fauna. Engesser (1979) has established this same biogeographic connection for Miocene insectivores and rodents, while Topal (1989a, b) has demonstrated it for plecotine bats.
**PRIMATES**

_Pliopithecidae_ or _Incertae sedis_ (L. Kords)

_Anapithecus hernyaki_ was initially reported from Rudabánya (Hungary, late Miocene, MN9 Zone) by Kretzoi (1974) as _Pliopithecus hernyaki_. Kretzoi (1975) then nominated a new subgenus, _Pliopithecus (Anapithecus) hernyaki_, which he distinguished from other European pliopithecines including the well-known genera _Pliopithecus_ sensu stricto, _Epipithecus_ and _Plesiopithecus_. Ginsburg & Mein (1980) raised _Anapithecus_ to genus rank and referred it to the Subfamily Crouzelinae (of the Pliopithecidae) (also see: Ginsburg, 1964, 1986; Harrison, 1987). Dental characters of _Anapithecus_ have been analysed and reported since by Begun (1989, 1991), discussed and compared further by Harrison (Harrison et al. 1991; Harrison in Andrews et al., 1996).

The Rudabánya _Anapithecus hernyaki_ teeth are morphologically identical to those from Götzdorf (Austria; Zapfe, 1989a; Andrews et al., 1996), Salmendingen (Germany; Begun, 1989) and Priay (France; = _Pliopithecus priay_; Welcomme et al., 1991, formally attributed here to _Anapithecus hernyaki_).

Harrison et al. (1991) gave an emended diagnosis for the genus _Pliopithecus_, and later Harrison (in Andrews et al., 1996) listed some key characters of the lower dentition that he erected to distinguish species of Crouzelinae and Pliopithecinae. He further described a number of dental characters that are significant for the Pliopithecidae, placing them in a monophyletic group.

Up until this time, it has never been questioned whether _Anapithecus hernyaki_ belongs to the Pliopithecidae. However, a detailed morphological analysis (Kords, in progress) reveals that _Anapithecus hernyaki_ differs from _Pliopithecus antiquus_ (the type of the Pliopithecidae) in many critical morphological characters of the dentition. The other pliopithecine taxa (_Pl. platyodon_ and _Pl. vindobonensis_) also exhibit significant differences with _Anapithecus hernyaki_ in their tooth morphology, while _"Pliopithecus priay"_ is almost identical in all characters to _Anapithecus hernyaki_.

The crouzelines are taxonomically more diverse than the pliopithecines. They differ from the latter in their greater development of cheek tooth shearing crests (Köhler et al., 1999). According to Kords' observations on the Rudabánya assemblage, _Anapithecus hernyaki_ lower dentition differs significantly from both the pliopithecines and crouzelines, and is phylogenetically distinct from the Pliopithecidae. This result is supported by the recently discovered _Anapithecus hernyaki_ femur at Rudabánya that differs significantly from the _Pliopithecus vindobonensis_ "Eppelsheim femur" (Kords & Begun, 1999).

_Hominioidea_ (D. Begun)

Begun & Kords (1993) have assigned the Rudabánya _Dryopithecus_ to the species _D. brancoi_. The conclusions that _D. brancoi_ is represented at both Salmendingen and Rudabánya, and that the _St. Stephan_ and _St. Gaudens_ samples are both _D. fontani_, have interesting paleobiogeographic implications (Begun, 2001). Other probable localities for _D. brancoi_ are Mariathal in Austria and Ebingen, Troughtelfingen, Wissberg, and Melchingen in Germany. Most of the datable localities with _D. brancoi_ are MN 9 in age (Mein, 1986, 1990; Steininger, 1986; Steininger et al., 1990; de Brujin, et al., 1992; Rogl, et al., 1993; Andrews, et al., 1996).

Only Salmendingen is younger and probably attributable to MN 10 (Mein, 1986; 1990; Sen, 1996). This is broadly contemporaneous with _D. laietanus_ and _D. crusafonti_ (Spain). The MN 8 taxon _D. fontani_ has the greatest geographic range, extending from southwestern France to southeastern Austria. MN 9-10 taxa are more geographically restricted, with two species known only from northeastern Spain, and a third ranging from the Hessen Rhine to the Pannonian Basin.

_Dryopithecus fontani_ is the oldest and most primitive species (Begun, 1992). The Vallesian species _D. crusafonti, D. laietanus_ and _D. brancoi_ have more elongated molars and premolars, labiolingually thicker upper incisors, buccolingually compressed canines, and little or no expression of molar cingula. The mandibles of Spanish _Dryopithecus_ tend to be more robust relative to depth and to dental dimensions, and have broad extra molar sulci (Begun, 1992). The Vallesian species of _Dryopithecus_ probably represents the sister clade to _D. fontani_.

_Dryopithecus_ is cladistically a stem great ape (hominid), but there is disagreement on the relationship of _Dryopithecus_ to other hominids. Andrews (1992) and Andrews et al. (1996) consider _Dryopithecus_ to be stem great ape. However, several researchers including Andrews et al. (1996), have presented evidence of shared derived characters of specific great apes and _Dryopithecus_. One hypothesis is that _Dryopithecus_ is a member of a _Sivapithecus/Pongo_ clade (Moya-Sola & Köhler, 1993). An alternative hypothesis is that _Dryopithecus_ is in the clade of the African apes and humans (Begun, 1994, 1995; Begun & Kords, 1997). _Dryopithecus_ shares with African great apes and _Australopithecus_ a continuous supraorbital torus, a shallow sulcus supratoralis, a prominent glabella, an increase in the anterior-posterior development of the frontal bone in the temporal fossa, increased neurocranial length relative to breadth, fused tympanic and articular portions of the temporal bone, a deep glenoid fossa, a small articular tubercle, a broad, projecting entoglenoid process, a broad, flat nasal aperture base, a stepped sub-nasal floor, a biconvex nasoalveolar clivus, and an ethmoidal frontal sinus. There are no derived characters shared between _Dryopithecus_ and any one member of the African ape/human clade, suggesting that _Dryopithecus_ is the sister clade to the African apes and humans as a group. _Ouranopithecus_ shares many of these characters as well, and is probably closely related to _Dryopithecus_ (Begun, 1995; Begun & Kords, 1997).

_Dryopithecus_ probably evolved _in situ_ in Europe after the divergence of the _Sivapithecus/Pongo_ clade. The oldest species, _D. fontani_, split to form two allopatric clades, one in Spain with two species, and the other in Germany and Central Europe with one species. This pattern of species
distribution along with independent evidence of ecological changes and the apparent extinction of *D. fontani*, suggests a vicariant mode of speciation.

While there is no clear evidence of hominids in Africa before about 6 Ma (Hill & Ward, 1988; Leakey et al., 1996), hominids are numerous and varied in Eurasia until about this time. This suggests the hypothesis that one Eurasian form, probably closely related to the *Dryopithecus/Otaropithecus* clade, migrated to Africa and radiated into the known lineages of African apes and humans (Begun, 1997).

**Sexual dimorphism in *Dryopithecus brancoi* (D. Cameron)**

The range of metric and non-metric variability seen in the Rudabánya dryopithecine sample is best attributable to sexual dimorphism and does not support the assertion of two dryopithecine species at the site. While in some morphological characters this sample is demonstrated to have ranges beyond that of extant hominids, overall morphologic variability is consistent with the occurrence of a single extant hominid species at Rudabánya. Furthermore, *Dryopithecus* male and female specimens are shown to closely resemble the size and range seen in *Pan*. The overall faciodental size of *Dryopithecus* male specimen RUD 44 is similar to *Pan troglodytes verus*, and probably had a body weight similar to it (averaging around 47 kgs), while the female specimen RUD 77 is similar in faciodental size to females of *Pan paniscus* (averaging around 34 kgs).

Two data sets were used to test whether the range of variability within the Rudabánya hominid sample can be attributed to sexual dimorphism, or whether two species should be recognized. The first examined metric data using principal components analysis (PCA), while the second examined morphologic characters using a correspondence analysis (CA). Inferences of male and female dryopithecine body weights were also estimated by examining the size component of a PCA generated using sexed specimens of *D. brancoi*, *P. paniscus*, *P. troglodytes* and *G. gorilla*. The programs used here are included within the MV-NUTSHELL computer package (Wright, 1994).

Cameron (1995, 1997) has identified a number of sexually distinctive features in the extant hominid faciodental complex that are suitable for sexing fossil hominid specimens. Using these same sexually distinctive characters, RUD 7 and RUD 44 are considered to be males, while RUD 12 and RUD 77 are likely females. It is also clear that these hominids have distinct male and female patterns compared to extant hominids.

The PCA scores calculated for this sample did not contradict the morphometric data: there is one species of dryopithecine at Rudabánya. All fossil specimens were shown to be within extant hominid ranges of variability. The major factor affecting these analyses was size. There apparently is a real difference between fossil and extant hominids in shape. Thus from these analyses much of the non-size variance is based on the “similar” extant morphometric patterns seen in *P. paniscus*, *P. troglodytes*, *G. gorilla* and *P. pygmaeus*, as opposed to the more distinctive morphometric pattern seen in the Hungarian fossil hominids.

The correspondence analysis suggests that with the exception of male specimen RUD 7, and female specimen RUD 77, all ranges of fossil phenetic variability were within the extant species range. Indeed, it was difficult to identify likely male and/or female features from the correspondence analyses as male and female dryopithecine specimens tend to cluster together. This test shows that RUD 7 and RUD 77 exhibit a P4 and M1 morphological variability that is greater than that observed in extant hominids. However, this analysis alone cannot refute the single species hypothesis, rather it infers that these Miocene fossil hominids exhibit a pattern of sexual dimorphism different from extant hominids.

While it is common to estimate body weights from molar dimensions, the correlation of extant species body weight and molar dimensions has been subject to recent scrutiny (Smith 1985, Conroy 1987, Jungers 1988; Rafferty *et al.*, 1995). Rudabánya dryopithecine male and female body
weight was estimated using a principal components analysis (PCA). The use of a PCA was deemed appropriate as it examines the size of a number of variables within the one analysis (in this case 15 variables were analysed including upper facial, palate and dental morphometrics), rather than examining variables individually. Text-fig. 3 is a histogram of the first component (size) of a PCA including Pan and Pongo as well as the most complete fossil specimens RUD 44 (male) and RUD 77 (female). Pan troglodytes specimens were divided into subspecies, so that a greater resolution of body weights could be achieved for the fossil specimens. Those specimens that could not be allocated to a subspecies were removed from the data set. From this analysis it is shown that RUD 44 is similar in size to specimens of P. t. versus, while RUD 77 is similar to males and females of P. paniscus. From the correlation with fossil and extant hominid faciodental size, male D. brancoi specimens are estimated to have had an average weight of 47 kg, while the female specimen is estimated to have a weight of 34 kg.

Rudabánya fossil primate paleodiet (P. Ungar)

At least two ape-like primates are known from late Miocene deposits in western and central Europe. Both primitive catarrhines called pliopithecids and the hominoid Dryopithecus have been reported from deposits ranging from Castell de Barbera, Spain to Salmendingen, Germany, to Rudabánya, Hungary (e.g., Begun, 1989; Kretzoi, 1975; Mová-Solá et al., 1990). While it is difficult to determine whether these primates coexisted in both space and time, it has been argued that they show adaptations indicating that they partitioned their niches to allow “noncompetitive sympathy”. Following this line of reasoning, Szalay & Delson (1979) suggested that the pliopithecids as a group were probably folivores, whereas Dryopithecus species were more likely frugivorous. Ginsburg & Mein (1980) further argued that among the pliopithecids, the crouzelines were more folivorous than the pliopithecines. This latter scenario can be considered consistent with the concept of diet-related niche separation, as those pliopithecids found at the Dryopithecus-bearing localities at Rudabánya, Salmendingen, and Castell de Barbera may all be crouzelines (re: Begun, 1989; Ginsburg, 1986).

I attempt here to reconstruct the diets of Anapithecus hernyaki and Dryopithecus brancoi from Rudabánya, through the quantitative studies of molar tooth shearing crest development and antemortem microscopic tooth wear (i.e., microwear). These approaches allow comparisons of the diets of these primates to one another and to those of other fossil and extant catarrhines. This in turn can provide new insights into the paleoecology (and perhaps even paleosynecology) of these catarrhines. The present results provide no evidence for broad trophic differences or concomitant niche separation between Anapithecus and Dryopithecus from Rudabánya. Evidence from the microwear and shearing crest length data both suggest that these primates had diets dominated by soft fruits.

All second molars (M2s) of Rudabánya primates examined come from collections at the Magyar Geologai Szolgalaat and Naturhistorisches Museum Wien. High-resolution replicas were prepared following conventional procedures (re: Ungar, 1996). Only unworn or nearly unworn mandibular second molars (M2’s) were examined for the shearing crest length study (following Kay, 1978). While no available Dryopithecus brancoi specimens met this criterion, eight Anapithecus hernyaki teeth could be included in this analysis (see Table 2). The lengths of shearing crests 1-8 and mesiodistal occlusal lengths of these specimens were measured and log-transformed (re: Ungar & Kay, 1995). Shearing quotients (SQs) were computed as deviations from a least-squares line regressing summed shearing crest length over mesiodistal occlusal length for a variety of extant frugivorous hominoids (Text-fig. 4). Positive SQ values indicate longer crests than expected for an extant frugivorous ape, whereas negative SQ values indicate shorter crests.

Table 2 - Shearing Crest and Microwear Pit Percentage Data for Available Primate specimens from Rudabánya.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>M2 Length (mm)</th>
<th>Shearing crests</th>
<th>Microwear Study Pit percentages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anapithecus hernyaki</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RUD 76</td>
<td>~</td>
<td>~</td>
<td>37.3</td>
</tr>
<tr>
<td>RUD 89</td>
<td>8.5</td>
<td>19.9</td>
<td>43.8</td>
</tr>
<tr>
<td>RUD 90</td>
<td>~</td>
<td>~</td>
<td>29.9</td>
</tr>
<tr>
<td>RUD 91</td>
<td>8.6</td>
<td>19.6</td>
<td>~</td>
</tr>
<tr>
<td>RUD 98</td>
<td>8.7</td>
<td>18.3</td>
<td>~</td>
</tr>
<tr>
<td>RUD 100</td>
<td>9.4</td>
<td>19.6</td>
<td>~</td>
</tr>
<tr>
<td>RUD 106</td>
<td>8.8</td>
<td>19.5</td>
<td>29.3</td>
</tr>
<tr>
<td>RUD 108</td>
<td>8.6</td>
<td>20.0</td>
<td>37.5</td>
</tr>
<tr>
<td>RUD 122</td>
<td>8.8</td>
<td>19.8</td>
<td>~</td>
</tr>
<tr>
<td>RUD 128</td>
<td>8.2</td>
<td>19.3</td>
<td>~</td>
</tr>
<tr>
<td>Dryopithecus brancoi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RUD 77</td>
<td>~</td>
<td>~</td>
<td>43.0</td>
</tr>
<tr>
<td>RUD 141</td>
<td>~</td>
<td>~</td>
<td>36.6</td>
</tr>
</tbody>
</table>

Tshear is the summed lengths of shearing crests 1-8.

Replicas of all worn M2’s were examined in secondary mode by scanning electron microscopy (SEM). Five specimens of Anapithecus hernyaki and two Dryopithecus brancoi individuals (see Table 2) preserved antemortem microwear unobscured by taphonomic or casting artifacts (re: Teaford 1988a). Polaroid photomicrographs of Phase II facets of these specimens were taken at 500x magnification and scanned to computer image files. Dental microwear features were identified using Micware 2.1, and pit percentages (percentages of all features with length-to-width ratios less than 4:1) were computed for each specimen. Microwear data were then compared between the Rudabánya primates, and results were put in the context of studies of extant primates and other fossil forms from the late Miocene of Europe (Text-fig. 4).

Results for both the shearing crest and microwear studies indicate that Anapithecus hernyaki had a mean SQ value of 0.60, nearly at the center of the range for extant frugivorous apes. This value falls closest to those for Hylobates agilis.
and *Hylobates lar*. This SQ value also falls within the range of *Dryopithecus* specimens from other localities (i.e., *D. fontani* from St. Gaudens, France, and *D. laietanus* from Can Llobateres and La Tarumba, Spain). An examination of worn *D. branconi* specimens suggests that unworn M2's of this species would have also had similar shear potential. This is consistent with a Rudabánya primate diet dominated by soft fruits. SQ values for *Anapithecus* fall intermediate between those of the inferred hard-object feeder *Ouranopithecus* and the inferred folivore *Oreopithecus* (Ungar, 1996).

As for the microwear data, *Dryopithecus branconi* pit percentage values fell within the *Anapithecus hernyaki* range. Statistical comparisons of *A. hernyaki* and a combined sample of *Dryopithecus* specimens from Spain and Hungary (Ungar, 1996) evinced no significant differences. Both *Anapithecus* and *Dryopithecus* had microwear pit percentages comparable to those of extant frugivores (Teaford, 1988b). These values also fell intermediate between those of the inferred hard-object feeder *Ouranopithecus* and the inferred folivore *Oreopithecus*.

Both the shearing crest and microwear data presented here (Text-fig. 4) suggest that *Anapithecus hernyaki* was predominantly a soft-fruit eater. Further, the microwear evidence indicates that *Dryopithecus branconi* was also a soft-fruit eater. Therefore, the Rudabánya primates probably had broadly similar diets. These results are not consistent with previous notions of broad trophic differences between pliopithecids and *Dryopithecus* to facilitate "noncompetitive sympatry". These results are also inconsistent with the suggestion that the crouzelines (as represented here by *Anapithecus*) were necessarily more folivorous.

The principle of competitive exclusion states that no two species can occupy the same ecological niche (Gause, 1934). Theory dictates that where two ecologically similar species overlap in space, differences between them are likely to become accentuated (Brown & Wilson, 1956). These notions are well-entrenched in paleoanthropological literature, particularly with respect to Plio-Pleistocene hominids (Grine, 1985 for a review).

Does this mean that *Anapithecus* and *Dryopithecus* from Rudabánya could not have both had diets dominated by soft fruits? Absolutely not! First, it remains to be demonstrated that these primates were actually sympatric and synchronous. Furthermore, even if they did live together in space and time, examples of extant, sympatric anthropoids with broadly similar diets abound in the primatological literature. For example, sympatric platyrrhines in Peru (Terborgh, 1983) and sympatric cercopithecines in Uganda (Cords, 1987) exhibit broadly similar diets dominated by soft-fruits. Sympatric primates may partition their niches in subtle ways — ways perhaps too subtle to be distinguished on the basis of shearing crest development or microwear, especially on such small samples of fossil primates.

Text-fig. 4 - A) Lower second molar shearing quotients for a variety of extant hominoids and European Miocene catarrhines. Data from Ungar & Kay (1995). B) M2 Phase II pit percentage data comparisons. Vertical bars indicate mean values and horizontal lines denote 2 standard deviations except where marked by an asterix, where ranges (n=2) are presented.
LAGOMORPHA (S. Sen)

At Rudabánya lagomorphs are represented only by the Ochotonidae Eurolagus sp.. This genus had a geographical distribution typically limited to central and western Europe. Eurolagus first occurs at Rothenstein 1 (MN 5, Germany) and persists, although as a relatively rare element, until the early Late Miocene. With only one species recognized, Eurolagus fontomnesi, its last occurrence is reported in the Spanish locality of Terrassa (MN 10).

RODENTIA

Cricetidae, Sciuridae, Gliridae and Eomyidae

(R. L. Bernor - L. Kordos - L. Rook)

At Rudabánya rodents belonging to the families Cricetidae, Sciuridae, Gliridae and Eomyidae include: Cricetidae - Spermophilus bredai, Blackia miocaenica, Hylotepes sp., Miopetaurista sp., Albanenstia grimmni; Cricetidae - Eumynarion aff. latior, Democricetodon sp., Kowalskiia cf. schaubii, Microtocrictetus molassicus; Gliridae - Paraglirulus werenfelsi, Glis aff. minor, Myoglis ucrauincis, Muscardinus hispanicus, Muscardinus aff. vallesiensis, Glirius lissiensis. Eomyidae -Eomypops catalaunicus.

This portion of the rodent fauna of Rudabánya is characterized by a early Vallesian (MN9) association with: 1) mainly middle Miocene rodents with 2) some late Miocene first appearing taxa and 3) the lack of murids and some other rodents known to first occur regionally in MN10.

Among cricetids Eumynarion latior, is known to occur in Central Europe during the middle and late Miocene, while Microtocrictetus molassicus is known to occur only in early late Miocene horizons (MN 9-10) of western, central and eastern Europe (Welcomme et al., 1991; Fahlbusch & Mayer, 1975; Kowalski, 1993; Daxner-Höck, 1996; Topachevskii & Scorik, 1992).

Among the Rudabánya flying squirrels and sciurids, Albanenstia grimmni dominates the rodent assemblage in its abundant and well preserved teeth. This species is mainly recorded in central Europe in MN 9 but rarely occurs in MN 10 (Daxner-Höck, 1996). Miopetaurista is thus far very rare in the late Miocene and is represented in Rudabánya by a more progressive form related to Miopetaurista crusafonti from Can Llobateres (MN9). Blackia miocaenica is a species with a very long stratigraphic duration, and as such is of limited biostratigraphic use. An advanced species of Hylotepes was not known from Rudabánya before now, but is known from elsewhere to range at least from MN4 to present. Spermophilinus bredai is a very abundant sciurid in middle Miocene faunas, and as a rule is replaced by Spermophilinus tur- olenis in the late Miocene. The Rudabánya form is one of a few rare occurrences of Spermophilinus bredai known from the late Miocene.

Glirids are documented from Rudabánya, in some cases by relative meagre material. There are a few teeth referable to Paraglirulus werenfelsi, Muscardinus hispanicus, Muscardinus aff. vallesiensis and Glirius lissiensis, and better quality material of Myoglis ucrauinics and Glis aff. minor.

Although descending from early Miocene glirid lineages, four species (M. vallesiensis, M. hispanicus, M. ucrauinics and G. minor intermedius) first occurred in MN9. The eomyid Eomypops catalaunicus is known to occur only in the Vallesian.

Anomalomyidae (L. Kordos)

Two species of anomalomyids were reported in the first faunal list of Rudabánya (Kretzoi et al., 1976): Anomalomys cf. guillaudi and Prospalax petteri. This material was subsequently studied by Fejfar and later published by Rabeder (1985) as Anomalomys gaudryi. On the basis of material collected between 1977 and 1987, Kordos (1989) described a new species, Anomalomys rudabanyensis in place of the two previous taxa, reviewed by Bolliger (1996) and Kowalski (1994). A detailed study of central and eastern European Neogene Anomalomyidae is important from both a phylogenetic and biostratigraphic point-of-view. Along with cricetids and murids, the anomalomyids are one of the most abundantly represented families in the late Miocene of the Carpathian Basin. The Rudabánya Anomalomyidae belongs to the Anomalomys gaudryi - rudabanyensis - petteri lineage. The genus Anomalomys may be derived from a small species of Eumynarion. Early Miocene members of primitive Anomalomys, A. aliveriensis and A. minor, are early derivatives of the group (de Bruijn & Sarac, 1991). The occurrence of A. cf. rudabanyensis has been reported from outside the Carpathian Basin at Hilleniche, in Germany (MN 9; Bolliger, 1996). Some newly discovered and partly unpublished Vallesian samples of Anomalomys have been recovered from Gritsev (Ukraine; possibly MN 9) and Götzendorf (Austria; MN 9), and exhibit a transitional morphology between Anomalomys rudabanyensis and Allospalax ("Prospalax" or "Allospalax") petteri (Kordos, unpublished). Consequently, the Allospalax species should be synonymized with Anomalomys.

Castoridae (L. Kordos)

The lacustrine and swampy sediments of Rudabánya contain a large sample of a single beaver species, Trogontherium minutum. Trogontherium minutum is smaller in size than Trogontherium rheananum from Dorn Dürkheim (Germany; Franzen & Storch, 1975), and is well known in the Carpathian Basin between MN9 and MN13. Trogontherium minutum is first recorded from Oellingen (MN 3), Germany, and was frequent in Europe from MN4 to MN11, becoming rare during MN12 and MN13.

CARNIVORA (L. Werdelin)

Carnivora are taxonomically well represented at Rudabánya, although most of the material is fragmentary in nature and no large samples are available for statistical analysis. Most of the taxa identified herein are known from other deposits that are similar in age to Rudabánya, but there may be some new taxa represented among the Amphicynoidae and Mustelidae. All in all, a minimum of 17 species-level taxa have been identified, representing 8 carnivoran families: Ursidae,
Procyonidae, Amphicyonidae, Mustelidae, Viverridae, Nimravidae, Felidae, and Hyaenidae.

As is usual in European deposits of Astaracian and Vallesian age (Werdelin, 1996), the Mustelidae are by far the most diverse family, with a minimum of 7 species-level taxa. This taxa represent a diversity of adaptational types, including small, omnivorous Melinae and Mephitinae (*Taxodon* cf. *T. sansaniensis*, Melinae gen et sp. indet., *Propotiorius*) and small hypercarnivorous Mustelinae (*e.g.*, *Martes* cf. *M. filboli*, cf. *Troechictis* sp.). The most abundant mustelid is, however, the semi-aquatic Lutrinae *Paralutra jaegeri*. At Rudabánya, this species is accompanied by rare remains of another, larger species of *Paralutra*, previously unknown.

The Ursidae are represented by two species, *Ursus primaeus* and *U. brevihirminus*. This association is interesting in itself, as it is otherwise reported only at Can Llobateres (Spain, MN 9), although this may in part be an artefact of the relative rarity of both of these taxa.

A unique association for Rudabánya is between the two Procyonidae *Alopecocyon* sp. and *Simoecyon diaphorus*. Of these, the former is generally a middle Miocene taxon and the latter exclusively a late Miocene one (Werdelin, 1996).

Some of the few remains of large carnivores can be attributed to a large sized amphicyonid. This family is relatively rare in European late Miocene deposits (Viranta, 1996) and the morphological characteristics of the available material from Rudabánya indicates the presence of a new taxon with more omnivorous adaptations than *Amphicyon* sp.

Another large carnivore represented at Rudabánya is the nimravid *Sansanosmilus journansi*, of which only a single definitely referred fragment has been identified. Felid sabertooths are, however, conspicuously absent at Rudabánya, unlike in some other penecontemporaneous localities such as Can Llobateres (Spain) and *Paralutra* sp. The posttrites have 1-3 internal conelets and undeveloped conules. In some cases the secondary trefoil is visible. Cement is lacking.

Material referred to *Tetralophodon longirostris* is abundant and includes lower and upper tusks, lower and upper molars, as well as deciduous dentition. The crown morphology is typical of tetralophodont gomphotheres. The intermediate molars have four loph(id)s, the last ones (*M*3 and *M*) have five transverse crests. The development of the talon(id)s is variable. The pretrite halfcrests exhibit a trefoil pattern, and on the posterior aspect the conules are less developed or missing. The postribs have 1-3 internal conelets and undeveloped conules. In some cases the secondary trefoil is visible. Cement is lacking.

Material referred to *Stegotetrabelodon gigantorosiris* includes four upper tusks, lower and upper molars, as well as deciduous dentition. This taxon is distinguished from *Tetralophodon longirostris* by its larger size and some small differences in the molar crown morphology. The incisors have a large diameter. On the molar crowns the conules are slightly more developed than in the case of *T. longirostris*. The holl loph(id)s show an incipient anancoidy. This is not a true anancoidy because the main cones (conids) are approximately in line with one another, but the pretrite conules are well developed (the posterior conules on the lower molars and the anterior ones on the uppers) hence it seems that the halfcrests are in slight alter-

**PROBOSCIDEA** (M. Gasparik)

Four proboscidean taxa are known from the late Vallesian (MN 9) vertebrate fauna of Rudabánya: *Deinotherium giganteum*, *Tetralophodon longirostris*, *Tetralophodon cf. longirostris* and *Stegotetrabelodon gigantorosiris*. These species are typical proboscideans for the European Vallesian. *Deinotherium giganteum* is represented by a dp4 and another milk molar fragment in that the deinotheria cheek tooth morphology is rather uniform between later Miocene species (Gasparik, 1993). Up until recently, *Deinotherium* was not known from Rudabánya. These new finds are very important because the *D. giganteum* and *T. longirostris* have been found together from other European Vallesian localities, such as the “Dinotheriensande” in Germany and from Kobáná in Hungary.

*Tetralophodon cf. longirostris* has been identified on the basis of two lower tusk fragments and some upper and lower molars. Tobien (1986) referred all of the Rudabánya *Tetralophodon* to this taxon. It seems however that with the material at hand, one can separate some *Tetralophodon* remains from the typical *T. longirostris*, but it is not certain whether they can be segregated into a different species or subspecies, or if they fall within a single population's range of variability.

Material referred to *Tetralophodon longirostris* is abundant and includes lower and upper tusks, lower and upper molars, as well as deciduous dentition. The crown morphology is typical of tetralophodont gomphotheres. The intermediate molars have four loph(id)s, the last ones (*M* and *M*) have five transverse crests. The development of the talon(id)s is variable. The pretrite halfcrests exhibit a trefoil pattern, and on the posterior aspect the conules are less developed or missing. The postribs have 1-3 internal conelets and undeveloped conules. In some cases the secondary trefoil is visible. Cement is lacking.

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**RECENT ADVANCES ON MULTIDISCIPLINARY RESEARCH AT RUDABÁNYA**

The most surprising aspect of the carnivoran assemblage of Rudabánya lies in the dearth of hyaenas. Only some fragmentary specimens tentatively assigned to *Thalassictis montadai* are present, in contrast to contemporaneous localities, which generally include relatively abundant material of one or two species of hyaenid (*Werdelin & Solounias*, 1996). The explanation for this relative lack of Hyaenidae must lie in local environmental conditions at Rudabánya.

The carnivoran diversity at Rudabánya is matched among MN 9 localities only by Can Llobateres in Spain, which records 24 species-level taxa (*Petter*, 1963, 1967; *Crusafont Pairó* & *Kurtén*, 1976). The carnivoran assemblages of these two localities are very similar, both in species content and in trophic structure. The few differences can be accounted for by the more isolated geographic location of Can Llobateres, leading to greater endemism, and a somewhat greater environmental heterogeneity, leading to the presence of derived species characteristic of somewhat more open environments than were apparently present at Rudabánya.
Austria) hipparion assemblage, Bernor lineage at Rudabánya. In a subsequent comparison Hippotherium primigenium MN 9 time, or Pannonian F equivalent, the occlusal morphology to the Götzendorf and Sümeg Prottes would appear to be very similar in its molar 10 localities in the Vienna Basin, material from III. While there are few fossil hipparion from MN 11 hipparions to the west. The small Sümeg hipparion is suggestive of a Pannonian F correlation for Rudabánya. A recent analysis of the Dorn Dürkheim (Germany, MN 11) hipparion assemblage by Bernor & Franzen (1997), the Sümeg (Hungary, MN 10) assemblage by Bernor et al. (1999), and a study of the entire Rudabánya hipparion assemblage collected between 1977 and 1994, have led us to new interpretations of this assemblage's systematics, ecological preferences and biogeographic relationships (Bernor et al., in press).

We still recognize Hippotherium intrans as being a valid taxon and being the predominate hipparion at Rudabánya. We also recognize that there is a rarer, smaller hipparion morph that has been found in the Upper Lignite levels of Rudabánya II, the youngest stratigraphic bed in this particular Rudabánya section. Because of the rarity of this smaller hipparion, we have chosen not to recognize a formal species name for it.

Rudabánya Hippotherium intrans is distinct from German and Austrian populations of Hippotherium primigenium in its longer metatarsal III. While there are few fossil hipparion from MN 10 localities in the Vienna Basin, material from Prottes would appear to be very similar in its molar occlusal morphology to the Götzendorf and Sümeg species. These observations suggest that by latest MN 9 time, or Pannonian F equivalent, the Pannonian Basin hipparions diverged from Hippotherium primigenium. Bernor & Franzen's (1997) study of the early Turolian (MN 11) hipparion assemblage from Dorn Dürkheim (Germany) showed that this population retained conservative characters that ally it closely with older MN 9 hipparion from Eppelsheim and Höwenegg, Germany. Given the current state of knowledge, the Pannonian late MN 9 (= Pannonian F) hipparion assemblagles would appear to have become vicariantly separated from the German late MN 9 – MN 11 hipparions to the west. The small Sumeg hipparion appears to be most closely related to the small Greek MN 10 form Cremothippus macdonicus, and would if that attribution were to prove to be true, be an indication of an opening biogeographic connection between the central Paratethys and Macedonia (Bernor et al., in press).

In Kaiser's recent analysis of Hippotherium intrans mesowear (Bernor et al., in press), he found that this predominant Rudabánya hipparion had a mixed diet including grass and less abrasive browse components. This is observed as a deep grooving across the middle of the maxillary cheek (axis being along the protocone-mesostyle plane) teeth flanked by sharp peaks with the axis running labio-lingually across the central point of the prefosette and postfossette.

We have used a series of statistical tests to characterize Hippotherium intrans postcranial functional anatomy and ecomorphology. This includes bivariate plots, logarithmic ratio diagrams and principal components analysis (Bernor et al., in press). We have found that Hippotherium intrans had relatively longer metapodials than the Höwenegg sample and as such was adapted for more cursorial behavior. Its closest relatives in this regard are the larger horses from the Vienna Basin locality of Gols (MN 10, Austria) and specimens from Csákvr (MN 11, Hungary). The estimated body mass for Hippotherium intrans based on MAFIV12038 (= 242 kg) is the same as for the Höwenegg MTIII sample (=242 kg). The smaller and rarer horse at Rudabánya, Hipparion sp., may be related to a smaller MCIII, MAFIV12039, which has an estimated body mass of 194 kg.

The Rudabánya hipparions have proven useful for finer correlations: Rudabánya 2 correlates with the latest part of MN 9. This is based on the observation that Hippotherium intrans is advanced over Vienna Basin Pannonian D-E populations of Hippotherium primigenium, while not being so advanced as the Götzendorf hipparion. Rögl et al. (1993) argued for a latest MN 9 (= Pannonian Stage F) age for Götzendorf based on the absence of murids there. Bernor et al. (1999) have recently studied the equids from Sümeg identifying two taxa in this fauna: a larger species, Hippotherium sumegense, and a smaller species, "Hipparion" sp. small. Of these two, Hippotherium sumegense compares closely to the Götzendorf hipparion in its distinct mandibular premolar morphology. Biochronologic correlations based on Sümeg's small mammals strongly support the fauna's MN 10 age. Therefore, we can either accept the latest MN 9 attribution for Götzendorf based on the absence of murids, or accept the occurrence of Eozapus and Hippotherium aff. sumegense at Götzendorf as evidence of its MN 10 age. In either case, Rudabánya's hipparion is suggestive of a Pannonian F correlation and late MN 9 attribution, ca. 10.0 – 9.7 Ma (Rögl & Daxner-Hock, 1996; Steininger et al., 1996; Bernor et al., 1999). By the same argument, Götzendorf and Sümeg are most plausibly correlated with Pannonian G, circa 9.7 – 9.0 Ma (sensu Rögl & Daxner-Hock, 1996).

Tapiroidea (R.L. Bernor)

The tapiridae consist of a single fragmentary lower molar tooth and a fragmentary phalanx from Rudabánya 2. The molar tooth fragment includes the posterior lophid and distal tooth margin. It was originally referred to the suid, Listriodon. This specimen compares well with other Vallesian samples of Tapirus priscus known from MN 9 of Central and Western Europe. This species is associated with warm moist forested environments.
**Clasticotheriidae** (L. de Bonis, R.L. Bernor and J. Franzen)

The Rudabánya fauna contains the relatively rare occurrence of the claticotheres, *Chalicotherium aff. goldfussi*. This taxon is common in MN 9 of Central and Western Europe and like the tapir, is indicative of warm moist forested environments. This claticotherium is known to occur at both Rudabánya localities 2 and 3, and includes good diagnostic maxillary and mandibular cheek tooth material. The most complete specimen is an associated partial upper and lower dentition. Our study of this material has provisionally revealed some unique features of the anterior cheek tooth dentition that may or may not prove to distinguish it from other members of *Chalicotherium goldfussi*. *Chalicotherium goldfussi* is well known from Eppelsheim and Höwenegg, Germany (Zapfe, 1989b). Of the two localities, Eppelsheim (ca. 10.5 Ma.) is believed to be slightly older than Höwenegg (10.3 Ma; Woodburne et al., 1996); which, in turn, is believed to be older than Rudabánya (ca. 10-9.7 Ma; Bernor et al., 1993).

Biogeographically, Rudabánya's claticotherium would appear to be a central European form and may prove to be distinct from western European Vallesian claticotheres.

**Rhinocerotidae** (K. Heissig)

There are three species of rhinoceroses in the Rudabánya fauna. Two of them belong to the tribe *Aceratherini* (*Hoploaceratherium belvederense* and *Aceratherium incisivum*) and one to the *Rhinocerotini* (*Lartetotherium sansaniense*).

The medium sized, primitive dicerorhine (*Rhinocerotinii*) species cannot be related to one of the known *Dicerorhinus* species of the Miocene. It shows more similarities to the small, middle Miocene *Dicerorhinus steinheimiensis* than to the well known large species *Dicerorhinus schleiermaecke* from the Vallesian of central and western Europe. Its dimensions are intermediate between both of these species, and similar to the middle Miocene species *Lartetotherium sansaniense*. The observed differences indicate some phylogenetic trends within the species which suggest their separation from the typical *L. sansaniense* as *Lartetotherium aff. sansaniense*. No postcranial remains have been assigned to this species.

The skeletal elements of the two *Aceratherini* species are easily distinguished by their size difference and several very specific characters. The Rudabánya fauna is the first record of the larger species, *Hoploaceraetherium belvederense* in the late Vallesian. The other one, the well known *Aceratherium incisivum*, is smaller and less frequent. Both have very large, high crowned male lower incisors in contrast to smaller female ones (not represented in this collection). Strongly curved incisors with rather distinct wear surfaces are ascribed to *Aceratherium incisivum*, less curved incisors with diffuse wear may represent *Hoploaceraetherium*.

All three rhinoceroses had low crowned teeth indicative of browsing, and all three are believed to have inhabited a wooded or bush habitat. Whereas *Hoploaceraetherium* is known from the middle Miocene, there is no record of *Aceratherium incisivum* earlier than lower Vallesian. The last occurrence of both aceratherini is not sufficiently known. These taxa add no specific information about the stratigraphic correlation of the site other to say that Rudabánya is the youngest known locality with *Lartetotherium*.

**Artiodactyla**

*Suinae* (M. Fortelius, R.L. Bernor, N. Fessaha and M. Armour-Chelu)

The Rudabánya suid fauna has been collected over 18 years time and two taxa are currently recognized from the Rudabánya locality: *Propotamochoerus palaeochoerus* an early suine which is the most abundant artiodactyl at the site, and a rarer form, a previously unrecognized species of the primitive tetracodont, *Parachleuastochoerus* sp. nov.

Kretzoi (in Kretzoi et al., 1976) listed the following suid taxa from Rudabánya: *Korynochoerus palaeochoerus*, *Conohyus ferreus* (n. sp.) and *Listiriodon splendens*. We have found no evidence of *Listiriodon* in the MAFI collections. The suid material is mostly dental but there are some important postcranial remains probably referable to both species.

The *Propotamochoerus* sample includes over 400 specimens allowing some reconstruction of the sequence of tooth eruption and replacement in this taxon. Our analysis of this sample shows that the Rudabánya population of *Propotamochoerus palaeochoerus* compares most closely with the type specimen of the species from Eppelsheim, Germany.

*Parachleuastochoerus* is possibly represented by two morphs, a larger form with relatively broad cheek teeth and a smaller one with relatively narrow ones. Both morphs are larger than the Spanish species *Parachleuastochoerus crusafontii* (which also appears to show a high degree of interpopulation variability), and appears to have thinner enamel, at least on the first molars. We do not recognize Kretzoi's nomen *Conohyus ferreus* for this material because no type specimen was designated and there remains uncertainty as to which specimen specimens would constitute a valid lectotype. Rather, we will erect a new species, *Parachleuastochoerus* n. sp. (to be named in an edited volume to follow), provisionally restricted to the larger morph represented by a virtually complete upper and lower dentition. We do not formally recognize the smaller morph as a taxon and defer this decision until a larger sample becomes available.

The Rudabánya suid fauna may suggest a biogeographic disjunction between Spain and Hungary sometime during MN 9. The Rudabánya suids are not particularly informative about palaeoecology. Suines are notoriously broad in their habitat tolerance, and the rather pecary-like *Parachleuastochoerus* persisted in western Europe (at least) into the drier world that followed the mid-Vallesian crisis. However, the extremely high local abundance of *Propotamochoerus* is difficult to reconcile with arid and open habitats.
Ruminants (A. Gentry)
The Rudabánya ruminants are represented by five species and four families including one Tragulidae (*Dorcatotherium naui*), one Cervidae (*Lucentia aff. pierensis*), one Moschidae (*Micromeryx* *flourensianus*) and two Bovidae (*Miotragocerus* sp. and *Bovidae*, smaller sp.).

A Rudabánya right upper molar in early wear (1973/15), agrees with *Dorcatotherium naui*, first described from Eppelsheim, Germany. It is more advanced than upper molars of middle Miocene *Dorcatotherium* (Fahrbusch, 1985; pl. 2) in that its lingual cusps are more fully crescentic, the outer walls more nearly vertical, the labial rib of the metacone reduced, the enamel thinner, the mesostyle more prominent, the parastyle projecting less forwards, and the cingula weaker and smoother surfaced. A tragulid left astragalus (1988/50), could be conspecific with the upper molar.

*Lucentia aff. pierensis* is the most common ruminant at Rudabánya, with over 100 identified specimens. Antlers are about the size of the modern European *Capreolus capreolus*, although the teeth are perhaps bigger. The pedicle is long and set at a low angle above the horizontal plane. The pedicle and antler diverge a little from their partner of the other side, and the antler then curves slightly upwards and forwards in side view and eventually inwards again. The first tine is short and small, inserted quite high above the rose and often only slightly angled on the distal beam. There is no additional tine above the first tine. The cheek teeth are low crowned and have rugose enamel. Upper teeth have lingual cingula. Upper molars have basal pillars (entostyles), the styles are quite bulky, the posterior crest of the protocone is absent. The posterior crest of the protocone is bifurcated. On most lower molars there is a central fossette. On P 4 the lingual end of the metacone is rounded off and the anterior keel is just visible at the base of the fragment. The termination of the anterior keel is somewhat below the tip of the horn core creates a demarcation between the main proximal part of the horn core and a distal part often of markedly smaller antero-posterior diameter. This condition allows 1992/66 to be identified as a boselaphine. Most probably this boselaphine is *Miotragocerus pannoniae*, but for the present it is better to label it only as *Miotragocerus* sp.

Fourteenth tooth specimens belong to a Bovidae species smaller than the middle Miocene taxon *Tethytragus koehleri* of Pašalar or *Eotragus clavatus* (Gervais 1850 - in Gervais 1848-1852) of western Europe. The teeth are slightly hypsodont.

With a tragulid, two cervids and two boids, the ruminant fauna has a composition familiar in central European localities of late middle or late Miocene age. No giraffid material has yet been discovered at Rudabánya. The strength of the cervid representation and the presence of *Dorcatotherium* must indicate a less open, more moist or more temperate habitat than in the classical Turolian faunas further to the south and east in Europe and neighbouring parts of Asia. Compared with present-day *Muntiacus*, *Micromeryx* had longer legs and longer distal elements in relation to humerus and femur, but it might still have lived in habitats with thickets if the African neotragine antelope *Neotragus moschatus* (also with longer legs and relatively longer distal elements than *Muntiacus*) were a satisfactory modern analogue (Kingdon, 1982:194). Kohler (1993:51) suggested closed rather than open habitats for *Micromeryx*.

The teeth of the small bovid agree with late Miocene species of *Gazella*, but their generalised morphology and degree of hypsodonty do not allow a safe attribution even to the Antilopini. This diminishes any need to infer an open habitat.

Every clue given by the ruminants about the temporal correlation of Rudabánya suggests an early late Miocene and even an early Vallesian date. The *Dorcatotherium* supports a late Miocene age. The *Lucentia* has antlers with long pedicles and only one bifurcation. It is rare to find fossil antlers with preserved second bifurcations before MN12, although earlier incomplete antlers may have been referred to species or genera known to have second bifurcations at later time levels. Species lacking a second bifurcation persisted into the Pliocene, although pedicles did become shorter. *Micromeryx* *flourensianus* mainly occurs in the middle Miocene, but is known to have survived into the Vallesian of Spain. On what is known of it, the *Miotragocerus* would fit a pre-Turolian date.
V) AGE AND ZOOGEOGRAPHY

FAUNAL LIST AND CORRELATIONS (R.L. Bernor, L. Kordos, P. Müller and P. Renne)

Rudabánya II has yielded an extraordinarily diverse vertebrate fauna: 112 species (re: Table 3) including 1 species of fish, 18 species of amphibians, 13 species of reptiles, 11 species of birds and 69 species of mammals. Our attempts to directly date the locality using magnetostratigraphy failed to yield a discernable magnetic signal. Yet, we can constrain the lower limit using the stratigraphically distantly underlying radioisotopic determination of the "Upper Sarmatian Tuff" which has been dated by the potassium-argon method as being 11.5 Ma ± 0.5 Ma (Balogh, 1984) and 11.4 Ma ± 0.1 m.y. by single crystal argon (P.Renne, unpublished).

Rudabánya's age depends on biochronologic correlations. The fauna includes an interesting mixture of archaic holdover taxa alongside MN 9 immigrants. The retention of archaic taxa in the fauna is clearly due to the subtropical forest conditions nurtured by warm equable lakeside climates. The fish, amphibian, reptile and avian faunas are of little use for correlation. The exceptions are the protodont amphibian Miopterus sp. which first occurs in Central Europe during the late Miocene (Rudabánya likely being an early occurrence), Typhlops sp. that last occurs in MN 12?, and Naja urcauminus which last occurs in MN 11.

The insectivore taxa include Galerix sp., Plesiosorex aff. styriacus and Talpa sp. which are archaic and have very long chronologic ranges. Lanthanotherium samminguei, Postpalerinaeus sp., Crassafonita aff. endemica and Archeomedusa n. sp. are advanced forms that support an MN 9 correlation. The erinaceid Postpalerinaeus n. sp. does not otherwise have a first occurrence earlier than MN 10, and suggests the possibility of a later MN 9 correlation.

The rodents include a number of taxa that support an MN 9 age, including: Democricetodon n. sp., Microtoreticactus molassicus, Kowalskia cf. schauba, Albanensia grimmi, Miopetaristta sp., Eomys catalausicus, Trogonotherium minutum and Anomalomys rudabanyensis and Myoglis ucrainicus. The rodents further biochronologically characterize the Rudabánya fauna as follows: 1) mainly middle Miocene rodents (Eumamirion laitor, Spermophilus bredai, Paraglirulus werenfelsi, Myoglis meinii) associated with 2) late Miocene first appearing taxa (Microtoreticetus molassicus, Albanensia grimmi, Gliurinus lissiensis, Muscardinus aff. vallesiensis, Myoglis ucrainicus, Kowalskia cf. schauba) but without 3) Progonomys, Parapodemus, modern Kowalskia-species and Pliopetarista. The assemblage is characteristic for an early Vallesian (MN9) age. It should be further remarked that the lack of Megacricetodon in this assemblage further supports Rudabánya's MN 9 age. The most significant change in Central Paratethys rodent faunas took place in MN 10, a period when middle Miocene species were almost completely replaced (Daxzer-Hock, 1996: 6-7).

The carnivore fauna has many taxa that first occur in the early and middle Miocene of Central and Western Europe. Taxa that would appear to be limited to a MN 9 distribution include the viverrid Semigenetta grandis and the large new species of Amphiacyon. Many of these archaic taxa carry over into the Turonian making them useless for correlation.

The cooccurrence of Deinotherium giganteum and Tetruloaphodon cf. longirostris is characteristic for MN 9 in Central Europe. The equid, Hippotherium intrans Kretzoi is an advanced member of the Hippotherium lineage (re: Bernor et al., 1993a; Bernor et al., 1996; Bernor & Armour-Chelu, 1999) correlates with Pannonian F, upper MN 9, ca. 10-9.7 Ma. Hippotherium intrans is perhaps the most biochronologically discriminating species in the assemblage. The rare occurrence of Hippotherium small sp. from the Upper Lignite zone may herald a younger age for that horizon than the remainder of the Rudabánya II fauna. The tapir, Taipus cf. priscus, and chalicothere, Chalicothere aff. goldfussi, are a characteristic association for MN 9.

The rhinoceroses Hoploaceratherium belvederense and Aceratherium incisivum are also MN 9 biochrons. Aceratherium incisivum is an MN 9 immigrant into Central Europe. Lartetotherium aff. sansaniensis is an archaic form and its occurrence at Rudabánya is believed to be the latest known in Europe.

Of the Artiodactyla, the suids are the most useful for biochronologic correlations. The suine, Propotamochoerus palaeochoerus, occurs in Central Europe during MN 8 and MN 9; it has a very late (and very rare) occurrence at Maramena Greece during MN13/14 (Hellund, 1995). The tetraconodont Parachlesastochoeerus n. sp. is known only from Rudabánya, and its closest related forms are from MN 8 and MN 9 of Spain. The ruminants mostly have extended geochronologic ranges. The cervid Loxentia aff. pierrensis has its earliest known occurrence at Rudabánya, and the bovid Miotragocerus sp. (similar to M. pannoniae) is typical for MN 9 in the Central Paratethys.

A synthesis of the biochronologic bases for Rudabánya II's age strongly supports a late MN 9, Pannonian F correlation, ca. 10-9.7 Ma.

PALAEOZOO GEOGRAPHY OF THE RUDABÁNYA FAUNA (R.L. Bernor and L. Rook)

The Rudabánya fauna accumulated in late MN 9, near the shoreline of the Pannonian lake. The fauna is now known to have a unique combination of primitive early and middle Miocene vertebrates mixed with relatively few first occurring MN 9 taxa.

Text-fig. 5 is a Genus Faunal Resemblance Index (GFRIs) histogram between Rudabánya and 15 other European, west Asian and African late Middle Miocene – Late Miocene vertebrate localities. The dataset used for this study was derived from a data file downloaded from the NOW database (M. Fortelius, coordinator), available online at the website: www.helsinki.fi/science/now/. As in Bernor et al. (2001) we calculate both Dice and Simpson GFRIs. Dice's index is the one most commonly used (neo-zoological) faunal resemblance
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<td>MN 11</td>
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<tr>
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<td>MN 5</td>
<td>MN 10</td>
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<tr>
<td>Paraglirius aff. ferafelsi</td>
<td>MN 7/8</td>
<td>MN 9</td>
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<tr>
<td>Glis aff. (cf. minor Kowalski)</td>
<td>MN 9</td>
<td>MN 9</td>
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<tr>
<td>Myoglis aff. latior</td>
<td>MN 9</td>
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<tr>
<td>Muscardinus aff. hispanicus</td>
<td>MN 7/8</td>
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<tr>
<td>Muscardinus aff. vallesiensis</td>
<td>MN 9</td>
<td>MN 9</td>
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<tr>
<td>Glirurus aff. ferafelsi</td>
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<tr>
<td>Eomyops aff. latior</td>
<td>MN 9</td>
<td>MN 12</td>
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<td>Troglotherium aff. latior</td>
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<td>L. Plio.</td>
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<td>Eutremites aff. latior</td>
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<td>Carnivora</td>
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<td>Sunciasaff. aff. latior</td>
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<td>MN 9</td>
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<td>Melinae aff. latior</td>
<td>MN 5</td>
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<td>Martes aff. latior</td>
<td>MN 5</td>
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<td>cf. Trochites aff. latior</td>
<td>MN 5</td>
<td>MN 9</td>
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<td>Paralutra aff. latior</td>
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<td>Ursavus aff. latior</td>
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<td>MN 11</td>
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<tr>
<td>Ursavus brevivarius</td>
<td>MN 4</td>
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<td>Procyonidae</td>
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<td>Alopecocyon aff. latior</td>
<td>MN 4</td>
<td>MN 13</td>
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<tr>
<td>Simocyon aff. latior</td>
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<td>Amphicyonidae</td>
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<td>Amphicyon aff. latior</td>
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<td>Nimravidae</td>
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<tr>
<td>Sunciasaff. aff. latior</td>
<td>MN 6</td>
<td>MN 9</td>
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The Rudabánya fauna exhibits its strongest resemblance with the Spanish MN 9 localities of Can Llobateres and Can Ponsic I. Its next strongest resemblance is with the late MN 8 locality of Castell de Barberá (Spain), the MN 9 locality of Eppelsheim (Germany) and the MN 11 locality of Dorn Dürkheim (Germany). The strong resemblance of this suite of latest MN 8 – MN 11 western and central European localities suggests a strong provinciality for this geographic region (Bernor, 1978, 1983, 1984). In contrast, this set of central and western European faunas has relatively low resemblance to the remaining 10 localities. A striking contrast is revealed between Rudabánya and the Spanish and German MN 8-MN 9 localities on one hand, and the Sinap Hominid Zone (HZ) on the other. The Sinap Hominid Zone (Sinap HZ) fauna of Anatolia is closely similar in age to the Rudabánya fauna, but is 100% different from it at the genus level. The closely equivalent-aged Macedonian localities yielding the fossil Ape Ouranopithecus (Ouranopithecus Faunal Zone) (re: Greece below) are likewise strongly dissimilar to Rudabánya in its faunal content. The remainder of the faunal sample has little similarity at the genus level to Rudabánya: the Oreopithecus Fauna Zone (OFZ in Bernor et al., 2001) faunas were highly endemic during the MN11-12 interval; Baynunah, Lothagam, Sahabi, Venta del Moro and Italian MN 13 localities are substantially younger and the latter reflect the strong faunal turnover that occurred in Europe during the Turolian age, and most specifically the medial (MN12) and late (MN13) Turolian. Interestingly, Pikermi (MN 11/12) and Maramena (MN 13) have slightly elevated GFRI’s in comparison to Rudabánya, probably because of their more forested character.

Text-fig. 6 presents a pie-diagram of the mammalian family composition of the Rudabánya, Can Llobateres, Sinap HZ and Ouranopithecus Faunal Zone assemblages (Ouranopithecus FZ): the first three sites are late MN 9 age, while the last is MN 10 age. Rudabánya and Can Llobateres are similar in their higher diversity of mammalian families (Rudabánya with 34 families and Can Llobateres with 36 families), while the Sinap HZ (22 mammalian families) and Ouranopithecus FZ (13 families) have much reduced faunas. Faunal composition at Rudabánya and Can Llobateres suggests the presence of warm equable forested environments, and in respect to the presence of: Amphiiconydidae, Castoridae, Cervidae, Chalicotheriidae, Deinotheriidae, Erinaceidae, Eomyidae, Gliridae, Hominidae, diverse Mustelidae, ?Pliopithecidae (Anaptipithecus bernyaki at Rudabánya only), low crowned Rhinocerotidae, Sciridae, Soricidae, Felidae, Primates, etc.
Talpidae, Tapiridae, Tragulidae, primitive Ursidae and Viverridae. The Sinap HZ and Ouranopithecus FZ have an early "Pikermian type" open country woodland chronofauna (re: Bernor, 1983, 1984; Bernor et al., 1996; Solounias et al., 1999; Fortelius et al., in press), characterized by a strong reduction of Vallesian forest elements and enhancement of diverse Bovidae, Felidae, Giraffidae, Hyaenidae and Percrocutidae.

VI) PALAEOCLIMATE ESTIMATES FROM BIOTIC PROXIES

Quantitative reconstruction of past climatic conditions based on faunal and floral associations is still fairly imprecise under our current state of knowledge. However, it is possible to provide for Rudabánya independent estimates of mean annual precipitation from large mammals, small mammals, and fossil plant remains, respectively. Fossil floras also permit reconstruction of a wider range of climatic parameters. The estimates we are able to offer are consistent with each other and with the interpretation of forested subtropical habitats at Rudabánya. Note that the reconstructed rainfall values are estimates of the realized amount of moisture experienced by the plant and animal communities in one specific locality. Rudabánya probably represents an unusually wet local environment as a result of its physical setting, so these palaeoprecipitation estimates do not necessarily correspond to average regional values of true precipitation.

The mean value of ungulate herbivore tooth-crown height (hypsodonty) can be used to estimate mean annual precipitation (e.g. Fortelius et al., 2002), and gives a value for Rudabánya of 1190 mm/yr. Unfortunately, there is much scatter in the regression (95% confidence interval is 250–5070 mm). In addition, when virtually all species are brachydont (as at Rudabánya) the mean hypsodonty statistic is at a minimum and cannot further resolve differences in precipitation. An alternate method (PMH; Damuth et al., 2002) does not have this statistical limitation and shows a stronger relationship, but the PMH value depends upon both mean hypsodonty and species richness, which introduces a complication. Species richness for Miocene mammalian faunas of Rudabánya's age and older is often considerably higher than in modern faunas from comparable habitats (Janis et al., 2000, 2002); with 15 ungulate browsers Rudabánya is unusually rich. This currently poorly-understood phenomenon causes PMH to yield, for mid Miocene and earlier faunas in North America, unrealistic estimates that are about twice those that are estimated from contemporaneous fossil floras. PMH estimates rainfall for Rudabánya as

Text-fig. 5 - Genus Faunal Resemblance Index (GFRI's) between Rudabánya and 15 other European, West Asian and African late Middle Miocene – late Miocene vertebrate localities (re: Bernor et al., 2001 for further information on methods and dataset).
Using the North American data for a rough calibration, this would represent the expected approximate doubling of the proper estimate caused by the high species richness. Thus, the large-mammal data suggest a most probable range of 900–1200 mm in annual precipitation for Rudabánya, although there is still considerable uncertainty about this estimate.

A new method for estimating past rainfall levels on the basis of small mammal community structure has recently been developed and applied to the Neogene of Europe (van Dam, 2001; van Dam, to be submitted). The method involves a multiple regression equation based on recent small mammal communities using the proportions of arboreal and insectivorous species as independent variables. The size of the 95% confidence intervals for the predicted mean annual rainfall levels in the individual localities ranges between 350 and 400 mm/year (one-sided). In addition to mean levels, the amount of rainfall in the driest month could be best estimated using the proportion of arboreal species only. The confidence intervals around this estimate average about ±20 mm.

In Rudabánya both the percentages arboreal and insectivorous species are very high: 41% and 34%, respectively (12 and 10 out of 29, with aerial, aquatic, and semiaquatic forms excluded). This results in a mean annual precipitation 1235 mm/yr, which is the highest value for the entire data set of almost 250 Neogene small mammal faunas studied. The small mammal results support the existence of an important regional component in the Rudabánya precipitation regime, because time-equivalent small mammal faunas generally show high values as well: Götzendorf (Austria), Jujurieux (France), Grtsev (Ukraine), and Can Llobateres (NE Spain) all have levels between 1000 and 1200 mm/year. The estimated value for precipitation in the driest month is 84 mm. This value might be slightly too high, although the large numbers of arboreal small mammals certainly indicate the presence of forest and the absence of a significant dry season.

These results are supported by the analyses of the paleobotanical record (Kretzoi et al., 1974) using the coexistence approach (Mosbrugger and Utescher, 1997). The method employs tolerances of the Nearest Living Relatives known for a fossil flora with respect to various climate parameters to determine intervals in which most of the taxa can coexist. The significance of the results obtained highly depends on the taxa diversity of the flora analyzed. In case of Rudabánya, 30 extant plant taxa contribute with climate data. With maximum percentages of coexisting taxa between 86.7 and
includes many aquatic forms and is typical of a
before the end of the Miocene. The avian fauna
have a distinctly subtropical character highlighted
sistent wet conditions at Rudabánya. The snakes
marize further below.

As stated above, the Rudabánya flora most probably existed in a very wet habitat. This is also obvious from the floral composition. Approxi-
mately 60% of the extant reference taxa of the fos-
sil assemblage presently occur in the alluvial wet-
land vegetation, additionally, numerous water
plants have been recorded. Thus, precipitation
potentially was not as important as limiting factor
for the plant community, a fact that could bias the
reconstruction of precipitation data using the coex-
istence approach. However, the mean annual pre-
cipitation calculated for the Rudabánya flora is
obvious from the data. Additionally, wet climate conditions during the warm season are
indicated by mean precipitation rates of the
warmest month between 83 and 89 mm. Summarizing up these results, the Rudabánya flora
grew in a warm temperate, permanently humid cli-
mate with warm summers and mild winters (Cfa
Köppen-type climate; Köppen, 1931).

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consistent with data obtained from neighboring,
about time-equivalent localities. The precipitation

The Amphibia all suggest the existence of per-

The Rodentia fauna is characterized by a high
diversity of small rodents, including the primitive
 genre Archoedemus, which is considered to be
a typical Miocene rodent (Andrews et al., 1997).

The Carnivora include several lineages that con-
tinue from earlier Miocene times of central
and western Europe. The diverse sciruids, glirids
and eomyids suggest forested conditions. The cas-
toridae, Trogontotherium minutum was an obligatory
aquatic form.

The Carnivora include several lineages that con-
tinue from earlier Miocene times of central
and western Europe, and include: Semigenetta,
Propotomus, Ursavus (U. primaevus and U. brevith-
nis), Amphiocyon, Sansanosmius and Pseudalurus
(P. turuenensis and P. loreti). The high diversity of
mustelids, with which cooccur a viverrid, primitive
ursids, nimravid and felids are characteristic of sub-
tropical environments typical of western and
central European middle Miocene localities. The
diversity of smaller body size Carnivora, especially
mustelids, is also typical of extant tropical
environments. The low diversity of hyaenids is atypical for
late Miocene Eurasian faunas and is yet another
indication of the relatively closed forested condi-
tions that prevailed at Rudabánya.

The ungulates further support the interpretation
of subtropical forests at Rudabánya. The pro-
oscidean species were all browsers. Deinotherium
giganteum and Tetrabelodon cf. longirostris consti-
tute a characteristic proboscidean element for MN 9
of central Europe.

100% (mean: 92.2%) the resulting climate intervals
are considered as reliable. The climate data are
summarized in Table 4. The mean annual tempera-
ture ranges between 15.6 and 15.7°C, with a warm
month mean temperature of around 26°C, and a
cold month mean temperature of ca. 5°C. With
mean annual precipitation rates between 897 and
1297 mm and a mean annual range of precipitation
between 86 and 89 mm, a moderate seasonality in
precipitation is obvious from the data. Additionally,

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The analysis of Hippotherium primigenium verifies its mixed browse/graze dietary behavior. This taxon, along with the smaller hipparion and the hyaenid cf. Thalassictis montdai support the hypothesis that more open country mesopיחסic habitats were found distal to the lake margin such as has been characterized for MN 9 of the Vienna Basin (Bernor et al., 1988). The remaining perissodactyls - Tapirus cf. priscus, Chalicotherium aff. goldfussi, Hoploaceratherium belvederense, Acratherium incisivum and Lartetotherium aff. santamariae - all were brachydont browsers and are characteristic taxa of central European subtropical/warm temperate Miocene faunas.

The suids Propotamochoerus palaeocheirus and Parachelaustachoerus are also characteristic of central and western European MN 8-9 faunas; the former was an omnivore and the latter likely a mixed hard-object frugivore and omnivore. Neither of these suids have been found in the open country Pikermian faunas that characterize the later Miocene of Hungary.

The ruminants are not diverse, but include a species of tragulid, a cervid, a moschid and two bovids. All ruminant species were browsers and characteristically are found in central European subtropical forest settings.

The prevailing habitat type at Rudabánya was subtropical forest that prevailed under equable climatic conditions. If seasonality existed, it was mild and experienced summer rainfall. It is evident, however, that some taxa were adapted to more open country mixed woodland and grassland. Hippotherium intrans was a mixed feeder (grass and browse). The proboscideans, rhinos and hyaenid also probably inhabited more open woodlands distal to the lake margin forests.

Bernor et al. (2001) presented a simple contrast of several late middle Miocene – latest Miocene localities from the standpoint of ungulate crown height. In Text-fig. 7 we provide a contrast between Rudabánya, Can Llobateres, Sinap HZ and Ouranopithecus FZ ungulate crown heights. The 3-part subdivision: brachydont whereby M2 crown length is greater than its crown height; mesodont whereby M2 crown length is roughly the same as crown height; hypsodont whereby M2 crown height is 2X + that of crown length.

This analysis reveals that Rudabánya and Can Llobateres are similar in their predominance of brachydont forms and low percentage of hypsodont forms. In fact, the only hypsodont taxa at Rudabánya are the two hipparion species; a smaller form known from one or two specimens, and the remainder of the collection being referable to Hippotherium intrans. As demonstrated by Bernor et al. (in press), Hippotherium intrans was a mixed feeder with a substantial amount of browse in its diet. The Sinap HZ and Ouranopithecus FZ show a dramatic drop in the percentage of low-crowned ungulates. Both have a substantially larger percentage of hypsodont and mesodont forms at Sinap HZ and 51% forms in the Ouranopithecus FZ (Text-fig. 7).

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and bovines). Initially, this extinction event did not affect the occurrence of Dryopithecus. Rare, but well preserved finds of Dryopithecus still occur in fact at the beginning of the late Vallesian (MN 10), just after the Mid-Vallesian Crisis (Moya-Solá & Köhler, 1993, 1996; Agustí et al., 1996), but it is absent from younger deposits. The environmental change involved in the Mid-Vallesian Crisis seemed to strongly affect Dryopithecus, but after the exit of these hominoids, the pliopithecines, absent from the rich early Vallesian localities such as Can Ponsic 1 and Can Llobateres 1, reappeared again shortly before final extinction.

The hominid fossil record of Greece (L. de Bonis and G. Koufos)

There are very few Greek Vallesian macromammal faunas. An exception is the suite of macromammal localities in central Macedonia (Axios Valley and Chalkidiki), where the hominid Ouranopithecus macedoniensis is found. These faunas have a macromammal fauna very different from those of central and western Europe, and exhibited under more seasonal, open country environmental conditions. The localities of the lower Axios Valley are found in the Nea Messimvria Formation which includes the lower part of the late Miocene succession (Koufos, 1980; de Bonis et al., 1988, 1998; de Bonis & Koufos, 1999). Recent magnetostratigraphic studies of the Axios Valley deposits suggest an age of ~9.6 Ma for the Xirochori-1 fauna and ~9.3 Ma for faunas of Ravin de la Pluie and Ravin des Zouaves-1 (Sen et al., 2000). Ravin de la Pluie, Ravin des Zouaves-1, Xirochori-1 and Pentalophos-1 includes faunal elements different from those of the typical Vallesian of NW Europe, making biochronological comparisons difficult. Nevertheless, such fauna is best correlated with the late Vallesian. MN 10 (de Bonis et al., 1990; de Bonis & Koufos, 1999). A possibly younger locality is that of Nikiti 1, in the area of the Chalkidiki Peninsula (Koufos et al., 1991). This site has yielded remains of Ouranopithecus macedoniensis (Koufos, 1993, 1995) in association with a fauna showing similarities with those of Axios Valley, but with some taxa, namely Microstonyx erymanthius, believed to be a local first occurrence. Although Nikiti was originally attributed to the early Turolian (MN 11; Koufos, 1993), at present it is interpreted by us as representing a latest Vallesian assemblage (de Bonis & Koufos, 1999). Using all biochronological data for Nikiti-1, the comparison of that fauna with those of the Axios valley (Ravin de la Pluie and Ravin des Zouaves-5), and their known magnetostratigraphic ages, suggests a latest Vallesian age attribution or an age between about 9.3-8.7 Ma for Nikiti-1 (Sen et al., 2000; Koufos, 2000). Ouranopithecus macedoniensis appears to have out-survived western and central European Dryopithecus species. Ouranopithecus macedoniensis is currently understood not to have occurred in any Greek localities of Turolian
age, among which only the colobine Mesopithecus is found.

The hominid fossil record of Turkey (Sinap) (R.L. Bernor and M. Fortelius)

At Sinap (Turkey), recent field work has yielded a precise magnetostratigraphic framework for a critical interval of the late Miocene, which includes a dense chronologic and mammalian biostratigraphic record across the middle – late Miocene boundary (MN 8/ MN 9) and across the MN 9/ MN 10 boundary. Ankarapithecus metaei occurs within Vallesian age horizons and is roughly similar in age, or slightly younger than the Rudabánya 2 locality. Kappelman et al. (1996:92) have reported an age of 9.74 Ma for the Locality 12 occurrence of Ankarapithecus metaei. This age correlates closely then with ages projected for both the Can Llobateres and Rudabánya hominoid occurrences (see also Lunka et al., 1999). The associated Sinap mammalian fauna is, like the Ouranopithecus FZ, an open country fauna thought to be of the proto-Pikermi chronofauna type. An edited volume on the fauna, its geological and paleoecological contexts, will elaborate further on Sinap’s significance (Fortelius et al., in press).

The hominid fossil record of Italy (L. Rook)

Late Miocene paleogeography of the central Mediterranean area had a complex history that led to the development of endemic land mammal bio-provinces within Italy (Kotsakis et al., 1997). One of these, the Tusco-Sardinian paleobioprovince, is documented by the late Miocene Baccinello faunal succession made famous by the abundant sample of the enigmatic hominoid Oreopithecus bambolii (cf. Bernor et al., 2001). Biochronologic correlations of the Oreopithecus – bearing faunas has been problematic because of their endemic character. Recent geochronologic work has secured a single crystal argon date of 7.55 +/- 0.03 Ma for a horizon at the V1/V2 boundary (Rook et al., 2000). This has provided a basis for a more robust estimate of the Baccinello V0-V2 (Oreopithecus-bearing) horizons as ca. 9.5-6.5 Ma (Rook et al., 2000; Bernor et al., 2001).

The apparent extinction of Oreopithecus circa 6.5 Ma is significantly later than that of other European Miocene hominoids, all presumably extinct by the late Vallesian (Bernor et al., 1996; Agusti et al., 1996, 1999). Both Ouranopithecus macodontiensis and non-cercopithecid eucatarhines (such as Pliopithecus) occur rarely in localities post-dating the mid-Vallesian crisis (Andrews & Bernor, 1999; de Bonis et al., 1999). The distribution pattern of fossil reef-building z- corals (Esteban, 1996; Rosen, 1999) would suggest that the eastern Mediterranean (terrestrial) environments (and especially that of the north Tyrrenian) experienced warmer and possibly wetter conditions, and persisted longer than elsewhere in Europe. Terminal Miocene paleogeographic changes in the Tyrrenian area were a consequence of intensive Messinian tectonism which itself produced the Apennine mountain chain, and as well the termination of the Tusco-Sardinian paleobioprovince and, evidently, the consequent extinction of the Oreopithecus bambolii insular fauna.

ANCESTRY OF THE AFRICAN APE/HUMAN CLADE? (L. Rook and R.L. Bernor)

European-S.W. Asian hominoid primates of the later Miocene have a patchy distribution in time and space, but nevertheless show considerable evolutionary diversity. These hominoids have a varied repertoire of morphologies, locomotor and dietary adaptations, and an evolutionary history covering a time span of more than 6 million years. This diversity has led to a variety of hypotheses concerning their phylogenetic relationships and adaptations (re: Andrews and Bernor, 1999). We briefly discuss here some competing hypotheses concerning the origin of the African ape-human clade.

The European hominoid with the greatest temporal span and geographical range is Dryopithecus. It was a large-bodied arboreal primate with below branch arm swinging capability adapted for soft object frugivory (Moyá Solá & Köhler, 1996; Kay & Ungar, 1997). It is a stem great ape (hominid), but there is disagreement on the relationship of Dryopithecus to other hominids (Andrews, 1992; Andrews et al., 1996; Andrews & Bernor, 1999). Moyá Solá & Köhler (1993) have advanced the hypothesis that Dryopithecus is a member of the Sivapithecus/Pongo clade. Begun (1994, 1995, 2002) and Begun & Kordos (1997) have advanced the hypothesis that Dryopithecus is a member of the African ape/human clade. Köhler et al. (2001) have countered this hypothesis by arguing that there are no clear synapomorphies between Dryopithecus and the African ape-human clade. According to them, Dryopithecus is then a primitive, generalized, hominoid.

Oreopithecus bambolii is in many aspects a very peculiar hominoid with a typical hominoid postcranial skeleton, a very specialized dentition, and an unusual cranial morphology. Craniodental anatomy has always played a particularly important role in discussions of the phylogenetic relationships of this fossil primate (re: Alba et al., 2001, for an exhaustive review). Oreopithecus is currently broadly accepted as a hominoid belonging to the great ape and human clade (Hominidae s.l.) (Moyá Solá & Köhler, 1997; Harrison & Rook, 1997). Oreopithecus and Dryopithecus are uniquely similar Eurasian apes in their postcranial anatomy and intermembral proportions. This observation has led Moyá Solá & Köhler (1997), Harrison & Rook (1997), Andrews & Bernor (1999) and Alba et al. (2001) to suggest that they are sister taxa. The derived craniodental and postcranial structure of Oreopithecus developed under insular conditions (Moyá Solá & Köhler, 1997; Alba et al., 2001). The cheek tooth dentition has been found to be homoplasious with peccaries (Alba et al., 2001), while the lower limb is structurally convergent on hominids (s.s.) in having evolved a degree of habitual bipedalism (Köhler & Moyá Solá, 1997; Rook et al., 1999). The hand, with precision grip, is also like that of African hominids (s.s.) (Moyá Solá et al., 1999b).

The European faunal affinities of the Maremma region (Rook et al., 1996; Rook et al. 2000; Bernor et al. 2001) argue in favor of European origin for Oreopithecus. Supporting this evidence is the fact
that: a) Dryopithecus had a very broad geographic range (Spain to Georgia, Caucasus - Gabunia et al., 2001) and long temporal range (ca. 12 – 8 m.y.; Andrews et al., 1996; Andrews & Bernor, 1999); b) that possibly there is only an insignifi-
cient temporal gap between the last appearance of Dryopithecus in Can Llobateres (about 9.5 Ma; Agústí et al., 1996) and the first occurrence of insular faunas in the Maremma region (Bernor et al., 2001).

Ouranopithecus (= Graecopithecus of Andrews et al., 1996) is a large hominoid, the size of a female gorilla, adapted to extreme hard object frugivory, and known only from some late Vallesian localities (MN 10) of Greece. De Bonis & Koufos (1997, 1999) and de Bonis et al. (1998), have recently identiﬁed a set of craniodental characters in Ouranopithecus which they argue are synapomorphies with African hominins, Australopithecus and Homo. Further they suggest a direct phylogenetic relationship between Ouranopithecus and the Australopithecinae/Homo clade. On the contrary, Begun and Kordos (1997) have argued that Ouranopithecus is related most closely to Dryopithecus. However, critical postcranials are entirely unknown in Ouranopithecus. The relationship between these two taxa solely on the basis of craniodental adaptations is still ambiguous. In fact, Dryopithecus has been established as a soft object frugivore with below branch suspensory adaptations, while Ouranopithecus, whose locomotor character is unknown, was adapted to hard object frugivory (Andrews & Bernor, 1999).

Begun (1997) and Begun & Kordos (1997) have argued that the Dryopithecus / Ouranopithecus clade is effectively ancestral to the African ape-human clade, and thus a Eurasian origin for the latter. We are of the opinion that one cannot rule out that the cranio-dental morphology of Ouranopithecus is an example of convergent evolution. Both Ouranopithecus and Australopithecus were adapted to hard-object frugivory as a consequence to a likely increased terrestrial adaptation (Andrews & Bernor, 1999).

The adaptive radiation of Eurasian Miocene hominoid was the consequence of one or more dispersal events from Africa that took place sometime(s) during the middle Miocene (Andrews et al., 1996; Andrews & Bernor, 1999; Moya Solà et al., 1999a; but see Heizmann & Begun, 2001). There can be no doubt that habitats differed, even strikingly, between Dryopithecus and penecontemporaneous and slightly younger Ankarapithecus (Sinap HZ, Turkey) and slightly younger Ouranopithecus (Macedonia, Greece). The mammalian faunas of Rudabánya and Sinap are demonstrably 100% different from one another at least at the generic level. The Rudabánya fauna is associated with lakeside swampy subtropical environments whereas Sinap HZ, and the Ouranopithecus FZ are faunas of open country woodlands. Sinap, at the very least, was apparently even more open country than the Turolian fauna of Pikermi, Greece.

Does the available paleontological/paleoecological information support the dispersal of Dryopithecus from Europe into Africa? Do they support the dispersal of an Ouranopithecus-like form into Africa? Or does the available evidence support better an intra-African origin for the African ape-human clade? Which one of these several possibilities is the more probable? The “out of Europe” hypothesis is strongly favoured by some authors (Begun & Kordos, 1997; Begun, 1997, 2002; Stewart & Disotell, 1998) on the basis of a “hominoid vacuum” in Africa between 12.5 and 6 m.y. These authors further support this hypothesis with cladistic analyses that represent Dryopithecus and Ouranopithecus as sister-taxon of the African ape-human clade. In fact, the macromammal fossil record in Africa is still relatively poor for this time interval. Nevertheless, the absence of hominoid evidence within the relatively scant African fossil record is not necessarily demonstrative of their absence (Andrews & Bernor, 1999; Moyá Solà et al., 1999a).

Dryopithecus, with its dependence on equable, subtropical/warm temperate forests, below branch locomotion and soft-object frugivory, is not a very likely candidate for a biogeographic extension across the more open country (“Pikermian”) environments that existed in southwest Asia and North Africa during most of the late Miocene interval. Latest Miocene environments were probably even more seasonal and dry in these regions. Ouranopithecus also does not appear to be a likely candidate for ancestry of the African ape-human clade because its thick enamel and extreme adaptation to hard object frugivory is advanced compared to an Ethiopian bipedal hominid, Ardipithecus ramidus (White et al., 1994), that is known to have had thin enamel and lived within a forested context. In fact, the 9 m.y. old hominoid Ouranopithecus macedoniensis had a masticatory apparatus that is more closely comparable functionally to mid-Pliocene - early Pleistocene hominids than that of Ardipithecus. There is effectively a 5+ m.y. hiatus between the craniofacial morphology of Ouranopithecus and that of the australopithecines with which it is homoplasic.

IX) CONCLUSIONS

(R. L. Bernor and L. Kordos)

Rudabánya is a very diverse MN 9, ca. 10.-9.7 m.y., vertebrate fauna. It provides one of the most detailed “windows” into the evolution, biogeography and paleoecology of late Miocene terrestrial ecosystems in Europe. It is clear that the Rudabánya fauna from the mammalian faunas of the eastern Mediterranean and southwest Europe. Having some biogeographic connections to the eastern Mediterranean and southwest Europe. At the same time, there was a virtually complete disjunction of the Rudabánya fauna from the mammalian faunas of the eastern Mediterranean and southwest Asia. Rudabánya has, and will continue to stimulate a great deal of interest from the vertebrate paleontology community because of its extraordinary fossil primate collection. It will, of course, continue to be a pivotal fauna for testing the “out of Eurasia” versus the “within Africa” hypotheses for the origin of the African ape-human clade. We hope that the succeeding monographic treatment of the Rudabánya fauna will shed more light on these actively competing hypotheses.
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