

<i>Palaeontographia Italica</i>	89	2002	3-36	tavv.	Pisa, 2004
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Recent Advances on Multidisciplinary Research at Rudabánya, Late Miocene (MN9), Hungary: a compendium

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KEY WORDS – Mammal Faunas, Biogeography, Palaeoecology, Late Vallesian, Late Miocene, Rudabánya, Hungary

ABSTRACT – Rudabánya is a rich late Miocene fossil locality first exploited for its vertebrate remains by Pethő in 1902. The first fossil primate was discovered by the local Chief Mining Geologist, Gabor Hernyák. Professor Miklos Kretzoi made Rudabánya famous in 1969 by publishing a manuscript on the new hominoid primate, *Rudapithecus hungaricus*, recognized herein as *Dryopithecus brancai*. 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 radioisotopic 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 Astaracian (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 correlative 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 archaic late early and middle Miocene European faunas. Vallesian localities in Greece and Turkey document an entirely different and progressive "proto-Pikermian" mega-fauna 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.

RIASSUNTO – [Lo stato dell'arte sui risultati delle ricerche multidisciplinari a Rudabánya, Miocene superiore (MN9), Ungheria] - Rudabánya è una miniera di lignite i cui depositi, investigati per la prima volta da Pethö nel 1902, hanno restituito una associazione faunistica a vertebrati del Miocene superiore. La prima segnalazione di un primate nell'associazione di Rudabánya si deve a Gabor Hernyák, geologo responsabile della miniera. La notorietà di Rudabánya è invece legata al nome del Prof. Miklos Kretzoi, il quale nel 1969 istituì la nuova specie di primate ominoide, *Rudapithecus hungaricus* (qui riconosciuto come sinonimo di *Dryopithecus brancai*). Un importante progetto di ricerca internazionale su Rudabánya, che ha visto nuovi scavi ed uno studio dettagliato della associazione faunistica, è iniziato nel 1991, coordinato da L. Kordos e R.L. Bernor. Il presente lavoro (cui contribuiscono 36 autori) rappresenta una prima sintesi di questi undici anni di ricerche, e sarà seguito dalla realizzazione di un volume monografico. L'associazione faunistica di Rudabánya è costituita da 112 specie di vertebrati fossili, delle quali 69 sono mammiferi. La fauna proviene da almeno sette differenti affioramenti, tutti nell'area della miniera, e tutti correlabili ad uno stesso intervallo cronologico. Pur non essendo possibile effettuare una datazione radiometrica diretta per i sedimenti fossiliferi di Rudabánya è tuttavia disponibile, da una vulcanite sottostante i livelli fossiliferi, una età radiometrica (ottenuta con il metodo Ar/Ar su cristallo singolo) di 11.4 m.y. ± 0.1 my. che costituisce un vincolo post quem. Questa data è in accordo con la caratterizzazione bio-cronologica della fauna indicante una età a mammiferi tardo MN 9 (circa 10-9.7 Ma). Da un punto di vista paleogeografico Rudabánya si colloca sulle sponde settentrionali dell'esteso lago Pannonico, in un momento caratterizzato da un clima caldo e subtropicale. Da un punto di vista zoogeografico, la fauna di Rudabánya è più vicina alle località Spagnole dell' Astaraciano superiore (MN8) o del Vallesiano inferiore (MN9), ed in particolar modo alla fauna di Can Llobateres (che si colloca al passaggio tra MN9 e MN10). Si osserva un forte contrasto nella struttura delle comunità che caratterizzano questo complesso di località dell'Europa centrale ed occidentale, in rapporto alle località coeve del Mediterraneo orientale e del vicino oriente. In particolare, sia a Rudabánya che a Can Llobateres si mantengono varie linee di mammiferi di piccola e media taglia che sono state dominanti nelle associazioni Europee del Miocene inferiore finale e medio. Le località Vallesiane della Grecia e della Turchia registrano invece associazioni faunistiche completamente diverse, con faune a grandi mammiferi di tipo "proto-Pikermiano" caratterizzate dalla presenza di forme nuove soprattutto per quanto riguarda carnivori ed ungulati. Di particolare importanza è il forte incremento nella percentuale di ungulati ipsodonti che si osserva nelle associazioni del Mediterraneo orientale e del Sud-Est asiatico. Nella discussione finale vengono utilizzate le evidenze zoogeografiche e paleoecologiche per confrontare le ipotesi oggi in discussione riguardo all'origine "Europea" vs. "Africana" del clado comprendente Antropomorfe africane e uomo.

1) 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. Pethö in 1902. Later, Schréter (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. Hernyák in the middle of the 1960's. Hernyák 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*.



Text-fig. 1 - Location map of Rudabánya in Hungary; the small box indicates the location of Rudabánya within a paleogeographic sketch of the Pannonian basin (modified from Kordos, 1982), and view of the old lignite mine.

Later in 1969, Hernyak 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 (Anapithecus) hernyaki*, and *Bodvapathecus altipalatus* were recognized by Kretzoi in the Rudabánya primate fauna. Finally, Kretzoi (1984) described a new subgenus and species from Rudabánya, *Rangwapithecus (Ataxopithecus) 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 “Bodvaium”, 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 National Museum 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 conglomerate 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. Hernyak)

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 shelf 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 metamorphosis.

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 and late 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 (L. Kordos)

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 top of 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 especial 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 *Conger* *praeirrhomboides* Biochron, the Pannonian lake suddenly reduced its areal extent and the lacustrine-swampy sedimentation regime ceased to occur. These sediment types were replaced by fluvial 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 specimens 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



Text-fig. 2 - The excavations at Rudabánya site II. Different views of 1993 excavation.

TABLE 1 - Rudabánya Terrestrial and Freshwater Mollusc Faunal List

<i>Sphaerium</i> aff. <i>corneum</i> (L.)
<i>Pisidium</i> sp. indet.
<i>Pomatias</i> sp. indet.
<i>Acicula</i> cf. <i>edlaueri</i> Schlikum
<i>Bithinia</i> cf. <i>jurinaci</i> Brusina
<i>Viviparus</i> sp. indet.
<i>Brotia escheri</i> Brongniart
<i>Carychiopsis berthae</i> (Halaváts)
<i>Carychium</i> sp. indet.
<i>Lymnaea</i> cf. <i>palustriformis</i> (Gottsch.)
<i>Lymnaea</i> cf. <i>socialis</i> (Gottsch.)
<i>Planorbarius</i> aff. <i>corneus</i> (L.)
<i>Anisus confusus</i> Soós
<i>Anisus</i> cf. <i>septemgyratiformis</i> (Gottsch.)
<i>Segmentina</i> cf. <i>filocincta</i> (Sandberger)
<i>Succinea</i> sp. indet.
<i>Granaria</i> cf. <i>suebleri</i> (Klein)
<i>Vertigo callosa</i> (Reuss)
<i>Vertigo angustior oecensis</i> (Halaváts)
<i>Vertigo</i> cf. <i>moedlingensis</i> Wenz & Edlauer
<i>Vertigo</i> sp. indet.
<i>Argna oppoliensis</i> (Andrusow)
<i>Gastrocopta acuminata</i> (Klein)
<i>Gastrocopta fissidens infrapontica</i> Wenz
<i>Gastrocopta</i> cf. <i>nouletiana</i> (Dupuy)
<i>Gastrocopta edlaueri</i> (Wenz)
<i>Gastrocopta</i> aff. <i>farciimen</i> (Sandberger)
<i>Azeca</i> cf. <i>tridentiformis</i> (Gottschieck)
<i>Acanthinula</i> cf. <i>anthonini</i> (Michelin)
<i>Vallonia</i> sp. indet.
<i>Strobilops</i> sp. indet.
<i>Helicodiscus</i> sp. indet.
<i>Discus</i> cf. <i>pleuradrus</i> (Bourg.)
<i>Tryptichia</i> sp. indet.
<i>Nordsieckia fischeri pontica</i> Lueger
<i>Serrulella</i> sp. indet.
<i>Vitrea</i> sp. indet.
Zonitidae indet.
Limacidae indet. I
Limacidae indet. II
<i>Trichia</i> sp. indet.
<i>Helicigona</i> sp. indet.
<i>Tropidomphalus</i> cf. <i>doderleini</i> (Brusina)

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 (*Carychium* and *Succinea* species). *Carychium* 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*, *Pelydtes* 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 *Salamanca*, 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 *Brachycormus-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-

sensation 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 parapophyses), is clearly referable to the Infraorder Scolecophidia. The scolecophidian from Rudabánya is tentatively considered to be a member of the genus *Typhlops*, 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 unrealizable 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 sigmoid 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 6.8 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. hungaris* 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 simi-

lar 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 vertebrae; the centrum length is 7.8 mm. Vertebrae 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 hypapophyses 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 elapid *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 Kohfidisch 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*, *Eryx* (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 (1867) 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 Dobruja (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

Bochenszi (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. *Palaeortyx aff. grivensis* is a small Galliform bird known from La Grive (France) and Gargano (Italy) (Ballman, 1969a, 1976), Rudabánya, Tardosbánya and Sûmeg (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 *Palaeortyx aff. grivensis* and the larger *Miophasianus*. This intermediate sized taxon is approximately the size of *Palaeortyx phasianoides* and/or *Palaeortyx 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 (1933) it agrees in size with *Fulica atra*. Ballmann (1969b) has noted the occurrence of a rail, "Rallidarum 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 strigiform 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 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 (*Locustrelle luscinioides*).

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, *Palaeortyx 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: *Lanthanotherium sanmigueli*, *Galerix* 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 *Galerix* species is represented by an M³ 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 vireti*.

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 endemica* from Can Llobateres, representing an early member of the evolutionary lineage Rudabánya - Can Llobateres - Kohfidisch. The specimens are referred to *Crusafontina aff. endemica*. They are the biostratigraphically most important soricid from Rudabánya. One tiny mandibular fragment with three molars in situ is referred to *Paenelimnoecus aff. repenningi*, in large part because of its biostratigraphic and geographic proximity to the type locality of Kohfidisch, Austria. *Paenelimnoecus crouzeli* from Sansan is markedly earlier in time and smaller in size but would fit well morphologically. One lower jaw fragment bearing M₁ 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

exoedaenodonty, in the strong fusion of the trigonid cusps of M₁, and in the reduction of the M₂ 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 *Plesiodimylus chantrei* compare closely with *Pl. chantrei* from the type locality La Grive. This species is known for its long biostratigraphic 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 atavistic element in the *Metacordylodon* sample. Together with *Crusafontina*, the talpid remains referred to a new species of "*Archaeodesmana*", represent the dominant insectivores in the Rudabánya fauna. However, the most diagnostic element, the I1 with a bifid apex, is not preserved, allowing no more precise referral than genus *Archaeodesmana*. *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 *Lanthanotherium* and by one specimen of *Galerix*, compare with extant S.E. Asian faunas that have humid forest biotopes with thick undergrowth, often close to water bodies. *Crusafontina aff. endemica* is morphologically comparable to the extant species *Anourosorex 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 semiaquatic in their behavior. The desman *Archaeodesmana*, like extant desmans, certainly had a semiaquatic 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 Topál (1989a, b) has demonstrated it for plecotine bats.

PRIMATES

Pliopithecidae or *Incertae sedis* (L. Kordos)

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, *Epipliopithecus* and *Plesiopliopithecus*. Ginsburg & Mein (1980) raised *Anapithecus* to genus rank and referred it to the Subfamily Crouzeliinae (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 Götzenhof (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 Crouzeliinae 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 (Kordos, in progress) reveals that *Anapithecus hernyaki* differs from *Pliopithecus antiquus* (the type of the Pliopithecinae) 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 priensis*" is almost identical in all characters to *Anapithecus hernyaki*.

The crouzeliines 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 Kordos' observations on the Rudabánya assemblage, *Anapithecus hernyaki*'s lower dentition differs significantly from both the pliopithecines and crouzeliines, 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" (Kordos & Begun, 1999).

Hominoidea (D. Begun)

Begun & Kordos (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 impli-

cations (Begun, 2001). Other probable localities for *D. brancoi* are Mariathal in Austria and Ebingen, Trochtelfingen, 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 Bruijn, *et al.*, 1992; Rögl, *et al.*, 1993; Andrews, *et al.*, 1996). Only Salmendingen is younger and probably attributable to MN 10 (Mein, 1986; 1990; Sen, 1996). 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 (Moyá-Solá & Köhler, 1993). An alternative hypothesis is that *Dryopithecus* is in the clade of the African apes and humans (Begun, 1994, 1995; Begun & Kordos, 1997). *Dryopithecus* shares with African great apes and *Australopithecus* a continuous supraorbital torus, a shallow sulcus supratoralis, a prominent glabella, an increase in the anteroposterior 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 & Kordos, 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/Ouranopithecus* 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 facio-dental 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 facio-dental 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

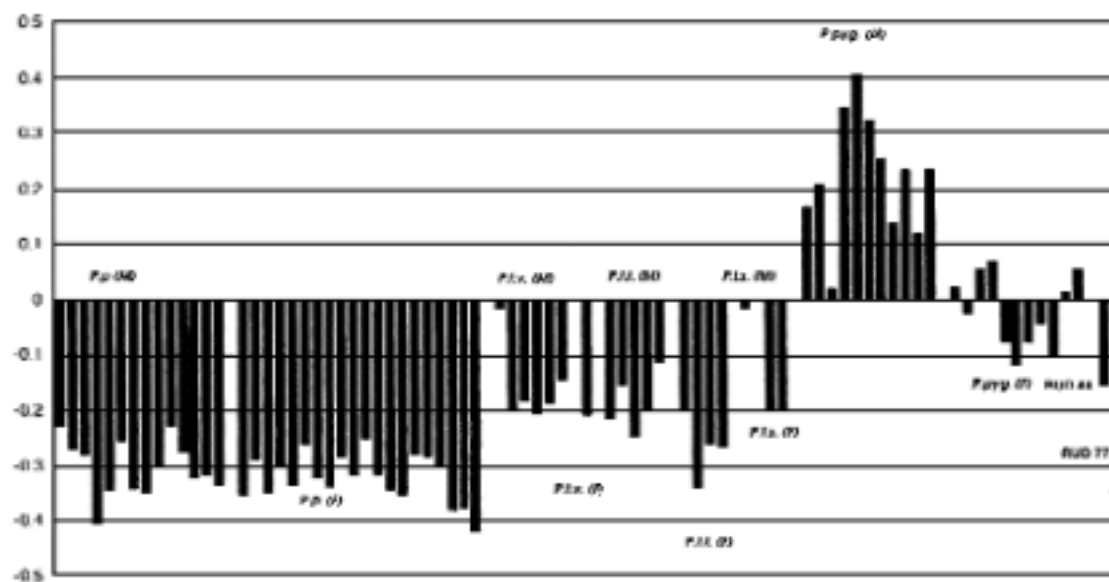
are included within the MV-NUTSHELL computer package (Wright, 1994).

Cameron (1995, 1997) has identified a number of sexually distinctive features in the extant hominid facio-dental 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



Text-fig. 3 - Histogram of Size Component PCA histogram including *Pan* and *Pongo* as well as the most complete fossil specimens RUD 44 (male) and RUD 77 (female).

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; Moyá-Solá *et al.*, 1990). While it is difficult to determine whether these primates coexisted in both time and space, it has been argued that they show adaptations indicating that they partitioned their niches to allow "noncompetitive sympatry". 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 Geológiai Szolgálat 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.

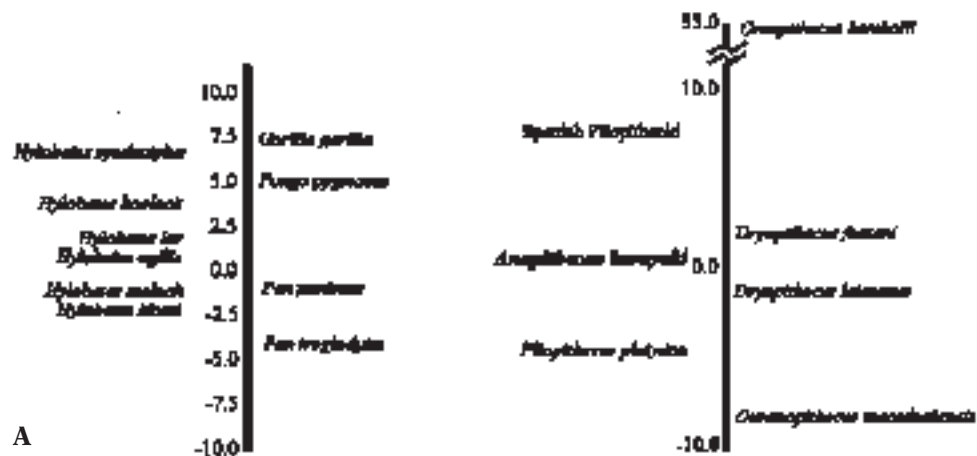
TABLE 2 - *Shearing Crest and Microwear Pit Percentage Data for Available Primate specimens from Rudabánya.*

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

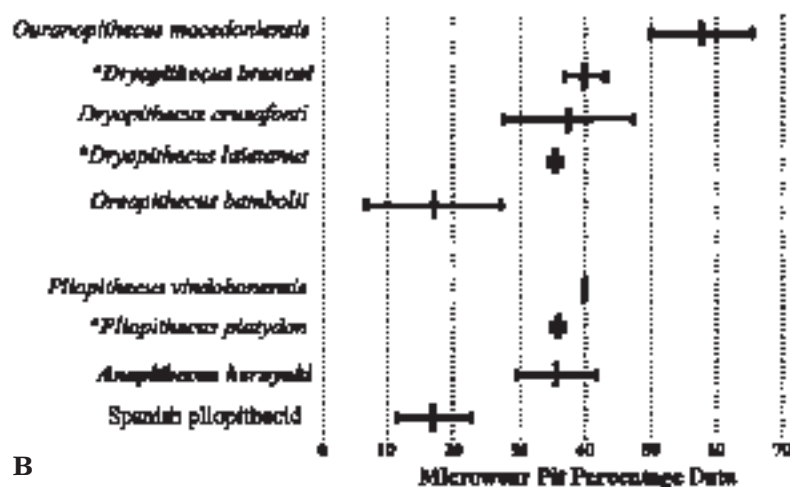
Tshear is the summed lengths of shearing crests 1-8.

Replicas of all worn M₂s 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 Microware 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*



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 asterisk, where ranges (n=2) are presented.



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. brancoi* 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 brancoi* pit percentage values fell within the *Anapithecus heryaki* range. Statistical comparisons of *A. heryaki* 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 heryaki* was predominantly a soft-fruit eater. Further, the microwear evidence indicates that *Dryopithecus brancoi* 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 differ-

ences 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 primate 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.

LAGOMORPHA (S. Sen)

At Rudabánya lagomorpha 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 fontannesi*, its last occurrence is reported in the Spanish locality of Terrassa (MN 10).

RODENTIA

Cricetidae, Sciuridae, Gliridae and Eomyidae
(G. Daxner-Höck and O. Fejfar)

Rudabánya rodents belonging to the families Sciuridae, Cricetidae, Gliridae and Eomyidae include: Sciuridae - *Spermophilinus bredai*, *Blackia miocaenica*, *Hylopetes* sp., *Miopetaurista* sp., *Albanensia grimmi*; Cricetidae - *Eumyarion* aff. *latior*, *Democricetodon* sp., *Kowalskia* cf. *schaubi*, *Microtocricetus molassicus*; Gliridae - *Paraglrulus werenfelsi*, *Glis* aff. *minor*, *Myoglis ucrainicus*, *Muscardinus hispanicus*, *Muscardinus* aff. *vallesiensis*, *Glirulus lissiensis*. Eomyidae - *Eomyops 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 *Eumyarion latior*, is known to occur in Central Europe during the middle and late Miocene, while *Microtocricetus molassicus* is known to occur only in early late Miocene horizons (MN 9-10) of western, central and eastern Europe (Wellcome *et al.*, 1991; Fahlbusch & Mayer, 1975; Kowalski, 1993; Daxner-Höck, 1996; Topachevskii & Scorik, 1992).

Among the Rudabánya flying squirrels and sciurids, *Albanensia grimmi* 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 *Hylopetes* 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 turcolensis* 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 *Paraglrulus werenfelsi*, *Muscardinus hispanicus*, *Muscardinus* aff. *vallesiensis* and *Glirulus lissiensis*, and better quality material of *Myoglis ucrainicus* and *Glis* aff. *minor*.

Although descending from early Miocene glirid lineages, four species (*M. vallesiensis*, *M. hispanicus*, *M. ucrainicus* and *G. minor intermedius*) first occurred in MN9. The eomyid *Eomyops 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. *gaillardi* 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 *Eumyarion*. 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 rhenanum* 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 Amphicyonidae 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. These taxa represent a diversity of adaptational types, including small, omnivorous Melinae and Mephitinae (*Taxodon* cf. *T. sansaniensis*, Melinae gen et sp. indet., *Proputorius*) and small hypercarnivorous Mustelinae (e.g., *Martes* cf. *M. filholi*, cf. *Trochictis* 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, *Ursavus primaevus* and *U. brevirohinus*. 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 *Simocyon 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 jordani*, 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 Eppelsheim (Germany).

Although sabertooth felids are absent, Rudabánya does include two members of the Felidae, *Pseudailurus lorteti* and its smaller relative *P. turnauensis*. Both of these are relatively well known from Astaracian deposits, but are less common in Vallesian ones (Werdelin, 1996). A hypercarnivorous Viverridae, *Semigenetta grandis*, is also represented at Rudabánya, and is more abundant in the material than either of the felid species.

The most surprising aspect of the carnivoran assemblage of Rudabánya lies in the dearth of hyaenas. Only some fragmentary specimens tentatively assigned to cf. *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.

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 *Stegotetabelodon gigantorostri*. These species are typical proboscideans for the European Vallesian.

Deinotherium giganteum is represented by a dp4 and another milk molar fragment in that the deinother 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 Kőbánya 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^3 and M_3) 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 posttrites have 1-3 internal conelets and undeveloped conules. In some cases the secondary trefoil is visible. Cement is lacking.

Material referred to *Stegotetabelodon gigantorostri* 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 half 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-

nate position. This phenomenon becomes more visible during the wear of the crests.

PERISSODACTYLA

Equidae, Hipparion s.l. (R.L. Bernor, M. Armour-Chelu, T. Kaiser and R. Scott)

Kretzoi 1983 named a new species of "Hipparion" from Rudabánya based on a complete metatarsal III, "*Hipparion intrans*". In a more detailed description of the hipparion material collected solely under the direction of Kretzoi, Bernor *et al.* (1993a) reported the occurrence of an advanced member of the *Hippotherium primigenium* lineage at Rudabánya. In a subsequent comparison with the Götzendorf (MN 9/10, Vienna Basin, Austria) hipparion assemblage, Bernor *et al.* (1993b) later concurred that the Rudabánya hipparion represented an advanced population of the *Hippotherium primigenium* lineage and suggested a late MN 9 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 assemblages would appear to have become vicariantly separated from the German late MN 9 – MN 11 hipparions to the west. The small Sümeg hipparion appears to be most closely related to the small Greek MN 10 form *Cremohipparion macedonicus*, 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 pre-fossette 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 Csákvár (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-Höck, 1996; Steininger *et al.*, 1996; Bernor *et al.*, 1999). By the same argument, Götzendorf and Sümeg are most plausibly correlative with Pannonian G, circa 9.7 – 9.0 Ma (sensu Rögl & Daxner-Höck, 1996).

Tapiridae (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.

Chalicotheriidae (L. de Bonis, R.L. Bernor and J. Franzen)

The Rudabánya fauna contains the relatively rare occurrence of the chalicotheres, *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 chalicotheres 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 chalicotheres would appear to be a central European form and may prove to be distinct from western European Vallesian chalicotheres.

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 (Rhinocerotini) species cannot be related to one of the known *Dicerorhinus* species of the Miocene. It shows more similarities to the small, middle Miocene *Dicerorhinus steinheimensis* than to the well known large species *Dicerorhinus schleiermacheri* 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, *Hoploaceratherium 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 *Hoploaceratherium*.

All three rhinoceroses had low crowned teeth indicative of browsing, and all three are believed to have inhabited a wooded or bush habitat. Whereas *Hoploaceratherium* 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 more specific information about the stratigraphic correlation of the site other to say that Rudabánya is the youngest known locality with *Lartetotherium*.

ARTIODACTYLA

Suidae (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 tetraconodont, *Parachleuastochoerus* sp. nov.

Kretzoi (in Kretzoi *et al.*, 1976) listed the following suid taxa from Rudabánya: *Korynochoerus palaeochoerus*, *Conohyus ferreus* (n. sp.) and *Listriodon splendens*. We have found no evidence of *Listriodon* 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 crusafonti* (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 peccary-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 (*Dorcatherium nauti*), 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 *Dorcatherium nauti*, first described from Eppelsheim, Germany. It is more advanced than upper molars of middle Miocene *Dorcatherium* (Fahlbusch, 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 paracone ribs are strong and somewhat inflected forwardly, but metacone ribs are weak or absent. The posterior crest of the protocone is bifurcated. On most lower molars there is a *Palaeomeryx*-fold. On M_3 the hypoconulid lobe has a central fossette. On P_4 the lingual end of the metaconid crest has twin flanges directed anteriorly and posteriorly. Fairly large and robust upper canines are still present. The Rudabánya deer appears to be a little changed descendant of Eppelsheim *Euprox dicranocerus* (larger size and higher first tine) or more probably a contemporaneous close relative evolving towards *Lucentia pierensis*.

Micromeryx flourensianus is known by more than 60 specimens from Rudabánya. The tiny *Micromeryx flourensianus*, type species of this moschid genus, is mainly a middle Miocene species, but has been reported as late as the Vallesian of Spain (Morales & Soria, 1981) and has been reported from China. It had enlarged male upper canines and is thought to have been without antlers. The P_4 's usually show fusion of paraconid with metaconid forming a closed wall along much of the lingual side of the tooth. Thenius (1950) has pointed to the dangers of confusing the teeth with those of *Lagomeryx*. Shoulder height in *Micromeryx* was only about 40 cm. Judged from a reconstructed skeleton in Basel (Heizmann, 1976; fig.7), the legs were longer than in modern *Muntiacus*. Habitual body conformation may have been like

that of the modern African neotragine antelope *Neotragus moschatus* (hind legs flexed under the lowered rear of the body; see Kingdon, 1982:192-194; Estes, 1991: 42), and unlike a modern *Capreolus capreolus*.

Boselaphine bovids are known from the middle Miocene onwards. The Rudabánya boselaphine is known by more than 70 specimens. It is assigned to *Miotragocerus* sp. on the evidence of a distal end of a right horn core, 1992/66, about 90 mm long. The tip itself is missing and the top of the anterior keel is just visible at the base of the fragment. The termination of the anterior keel some way 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.

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

With a tragulid, two cervoids and two bovids, 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 cervoid representation and the presence of *Dorcatherium* 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). Köhler (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 *Dorcatherium* 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 \pm 0.5 Ma (Balogh, 1984) and 11.4 Ma \pm 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 proteid amphibian *Mioproteus* 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 romani* 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 sanmigueli*, *Postpalerinaceus* sp., *Crusafontia* aff. *endemica* and *Archeodesmana* n. sp. are advanced forms that support an MN 9 correlation. The erinaceid *Postpalerinaceus* 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., *Microtocricetus molassicus*, *Kowalskia* cf. *schaubi*, *Albanensia grimmi*, *Miopetaurista* sp., *Eomyops catalaunicus*, *Trogonotherium minutum* and *Anomalomys rudabanyensis* and *Myoglis ucrainicus*. The rodents further biochronologically characterize the Rudabánya fauna as follows: 1) mainly middle Miocene rodents (*Eumyarion latior*, *Spermophilinus bredai*, *Paraglrulus werenfelsi*, *Myoglis meini*) associated with 2) late Miocene first appearing taxa (*Microtocricetus molassicus*, *Albanensia grimmi*, *Glirulus lissiensis*, *Muscardinus* aff. *vallesiensis*, *Myoglis ucrainicus*, *Kowalskia* cf. *schaubi*) but without 3) *Progonomys*, *Parapodemus*, modern *Kowalskia*-species and *Pliopetaurista*. 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 MN10, a period when middle Miocene species were almost completely replaced (Daxner-Höck, 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 *Amphicyon*. Many of these archaic taxa carry over into the Turolian making them unuseful for correlation.

The cooccurrence of *Deinotherium giganteum* and *Tetralophodon* 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) correlative 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, *Tapirus* cf. *priscus*, and chalicotheres, *Chalicotherium* aff. *goldfussi*, are a characteristic association for MN 9.

The rhinoceroses *Hoploaceratherium belvedereense* 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 (Hellmund, 1995). The tetracondont *Parachleuastochoerus* 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 *Lucentia* aff. *piemensis* 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.

PALAEOZOOGEOGRAPHY 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 (GFRI's) 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 GFRI's. Dice's index is the one most commonly used (neo-zoological) faunal resemblance

TABLE 3 - *Rudabánya vertebrate faunal list*

VERTEBRATE TAXA	FAD	LAD	ECOLOGY
Pisces		Pices	
Pices indet.			
Amphibia			
Caudata			
Proteidae			
<i>Mioproteus caucasicus</i>	MN5	MN16	lacustrine environments
Salamandridae			
<i>Chelotriton sp., type I</i>	MP12	MN9	lacustrine environments
<i>Chelotriton sp., type II</i>			
<i>Salamandridae new form</i>	MN 4	MN9	lacustrine or wet environments
<i>Salamandridae indet.</i>			
<i>Triturus sp.</i>	L. Mio.	Recent	lacustrine environments
<i>cf. Triturus sp.</i>			
Anura			
Discoglossidae			
<i>Latonia gigantea</i>	MN4	MN15	wet environments
<i>Bombina sp.</i>	MN1	Recent	wet environments
<i>cf. Discoglossus sp.</i>	? MP30	Recent	
Discoglossidae inc. sedis		Recent	wet environments
<i>cf. Discoglossidae</i>			
Palaeobatrachidae			
<i>Palaeobatrachus sp.</i>	? MP6	MN16	lacustrine environments
<i>cf. Palaeobatrachus sp.</i>			
Pelobatidae			
<i>Pelobatidae indet.</i>	MP7	Recent	possibly sandy environments
Pelodytidae			
<i>Pelodytes sp.</i>	MP16	Recent	moderately wet environments
Hylidae			
<i>Hyla sp.</i>	MN4	Recent	
Ranidae			
<i>Rana sp.</i>	? MP17	Recent	wet environments
Reptilia			
<i>Trionyx sp.</i>			
<i>Geomyda sp.</i>			
<i>Testudo cf. kalksburgensis</i>			
<i>Testudo sp. I</i>			
<i>Testudo sp. II</i>			
<i>Scolecophidia indet.</i>			
Typhlophidae			
<i>Typhlops sp.</i>	?	MN12?	tiny burrowing snake
?Leptotyphlopidae gen. and sp. indet.			
Colubridae			
<i>Natrix sp.</i>			
Colubridae Indet. A			
Colubridae Indet. B			
Elapidae			
<i>Naja romani</i>	MN4	MN11	cobra
<i>Serpentes indet.</i>			
Aves			
Anatidae			
<i>Anas aff. velox</i>			aquatic [duck]
<i>Anas sp.</i>			aquatic [duck]
Phasianidae			
<i>Miophasianus aff. medius</i>			bird fauna typical of lake forest environment
<i>Palaeortyx aff. grievensis</i>			bird fauna typical of lake forest environment
<i>Palaeortyx cf. phasianoides/intermedius</i>			bird fauna typical of lake forest environment
Rallidae			
?Miorallus sp.			bird fauna typical of lake forest environment
Strigidae			
<i>Strix cf. brevis</i>			bird fauna typical of lake forest environment
<i>Athene sp.</i>			bird fauna typical of lake forest environment
Sylviidae			
<i>Acrocephalus sp.</i>			bird fauna typical of lake forest environment
<i>Locustella sp.</i>			bird fauna typical of lake forest environment
Corvidae			
<i>Corvus sp.</i>			bird fauna typical of lake forest environment
Mammalia			
Insectivora			generally idicative of water and forest
Erinaceidae			
<i>Lanthanotherium sanmigueli</i>	MN 9	MN 11	compares with SE Asian tropical faunas

<i>Galerix sp.</i>			compares with SE Asian tropical faunas
<i>Postpalerinaceus n. sp.</i>	MN 9	MN 9	
Metacodontidae			
<i>Plesiosorex aff. styriacus</i>	MN 4		
Soricidae			
<i>Dinosorex n. sp.</i>	MN 7/8	MN 9	
<i>Crusafontia aff. endemica</i>	MN9	MN9	extant ecomorph in montain forests of SE Asia
<i>Paenelimnoceus aff. repenningi</i>	MN 6	MN 10	
Dimylidae			
<i>Metacordylodon aff. schlosseri</i>	MN 5	MN 9	likely semiaquatic
<i>Plesiodimylus chantrei</i>	MN4	MN 11	
Talpidae			
<i>Archeodesmana n. sp.</i>	MN 9	MN 9	certainly semiaquatic
<i>Talpa sp.</i>	MN 2	Recent	
Chiroptera			
Vespertilionidae			
<i>Eptesicus campanensis</i>	MN 6		no "true" tropical forms, but tropical marshy woods
<i>Eptesicus n. sp.</i>	MN 9		no "true" tropical forms, but tropical marshy woods
<i>cf. Miotrellus risgoviensis</i>	MN 6		no "true" tropical forms, but tropical marshy woods
Primates			
?Pliopithecidae			
<i>Anapithecus hernyaki</i>	MN 7/8	MN 9	subtropical forest, arboreal, suspensory, ate soft fruits
Hominidae			
<i>Dryopithecus brancoi</i>	MN 7/8	MN 9	subtropical forest, arboreal, suspensory, ate soft fruits
Rodentia			
Cricetidae			
<i>Eumyarion aff. latior</i>	MN 4	MN 9	ground of the forest-open country (elevations)
<i>Democricetodon n. sp.</i>	MN 9	MN 9	ground of the forest-open country (elevations)
<i>Microtocricetus molassicus</i>	MN 9	MN 11	riaprian environment; folivor (reed vegetation)
<i>Kowalskia cf. schaubi</i>	MN 9	MN 9	ground of the forest-open country (elevations)
Sciuridae			
<i>Albanensia grimmi</i>	MN 9	MN 9	arboricol, frugivor, canopy of the forest
<i>Miopetaurista sp.</i>	MN 7/8	MN 9	arboricol, frugivor, canopy of the forest
<i>Hylopetes sp.</i>	MN 4	present	arboricol, frugivor, canopy of the forest
<i>Blackia cf. miocaenica</i>	MN 1	MN 11	arboricol, frugivor, canopy of the forest
<i>Spermophilinus bredai</i>	MN 5	MN 10	probably fossorial, soft ground of the forest
Gliridae			
<i>Paraglrus werenfelsi</i>	MN 7/8	MN 9	arboricol, frugivor/granivor, canopy of the forest
<i>Glis sp. (cf. minor Kowalski)</i>	MN 9	MN 9	arboricol, frugivor/granivor, canopy of the forest
<i>Myoglis ucrainicus</i>	MN 9	MN 9	arboricol, frugivor/granivor, canopy of the forest
<i>Muscardinus hispanicus</i>	MN 7/8	MN 10	arboricol, frugivor/granivor, canopy of the forest
<i>Muscardinus aff. vallesiensis</i>	MN 9	MN 9	arboricol, frugivor/granivor, canopy of the forest
<i>Glirulus lissiensis</i>	MN 4	MN 14	arboricol, frugivor/granivor, canopy of the forest
Eomyidae			
<i>Eomyops catalaunicus</i>	MN 9	MN 12	arboricol, frugivor/granivor, canopy of the forest
Castoridae			
<i>Trogonotherium minutum</i>	MN 4	L. Plio.	aquatic
Anomalomyidae			
<i>Anomalomys rudabanyensis</i>	MN 9	MN 9	probably fossorial, soft ground of the forest
Lagomorpha			
Ochotonidae			
<i>Eurolagus sp.</i>	MN 5	MN 10	
Carnivora			
Viverridae			
<i>Semigenetta grandis</i>	MN 9	MN 9	hypercarnivorous, subtropical forest
Mustelidae			
<i>Taxodon cf. sansaniensis</i>	MN 5	MN 9	terrestrial, omnivore
<i>Melinae gen. et sp. indet.</i>			terrestrial, omnivore
<i>Proputorius sp.</i>	MN 5	MN 12	semiaquatic, terrestrial, invertebrate-eater
<i>Martes cf. filholi</i>			terrestrial
<i>cf. Trochitis sp.</i>			
<i>Paralutra jaegeri</i>	MN 5	MN 9	aquatic
<i>Paralutra n. sp.</i>			aquatic
Ursidae			
<i>Ursavus primaevus</i>	MN 6	MN 11	terrestrial, omnivore, predom. meat-eater
<i>Ursavus brevihinus</i>	MN 4	MN 11	terrestrial, omnivore, predom. meat-eater
Procyonidae			
<i>Alopecocyon sp.</i>	MN 4	MN 13	terrestrial, omnivore
<i>Simocyon diaphorus</i>	MN 9	MN 9	terrestrial, carnivore, meat and bone eater
Amphicyonidae			
<i>Amphicyon n. sp.</i>	MN9		terrestrial, omnivore/scavenger
Nimravidae			
<i>Sansanosmilus jourdani</i>	MN 6	MN 9	terrestrial, carnivore, meat-only

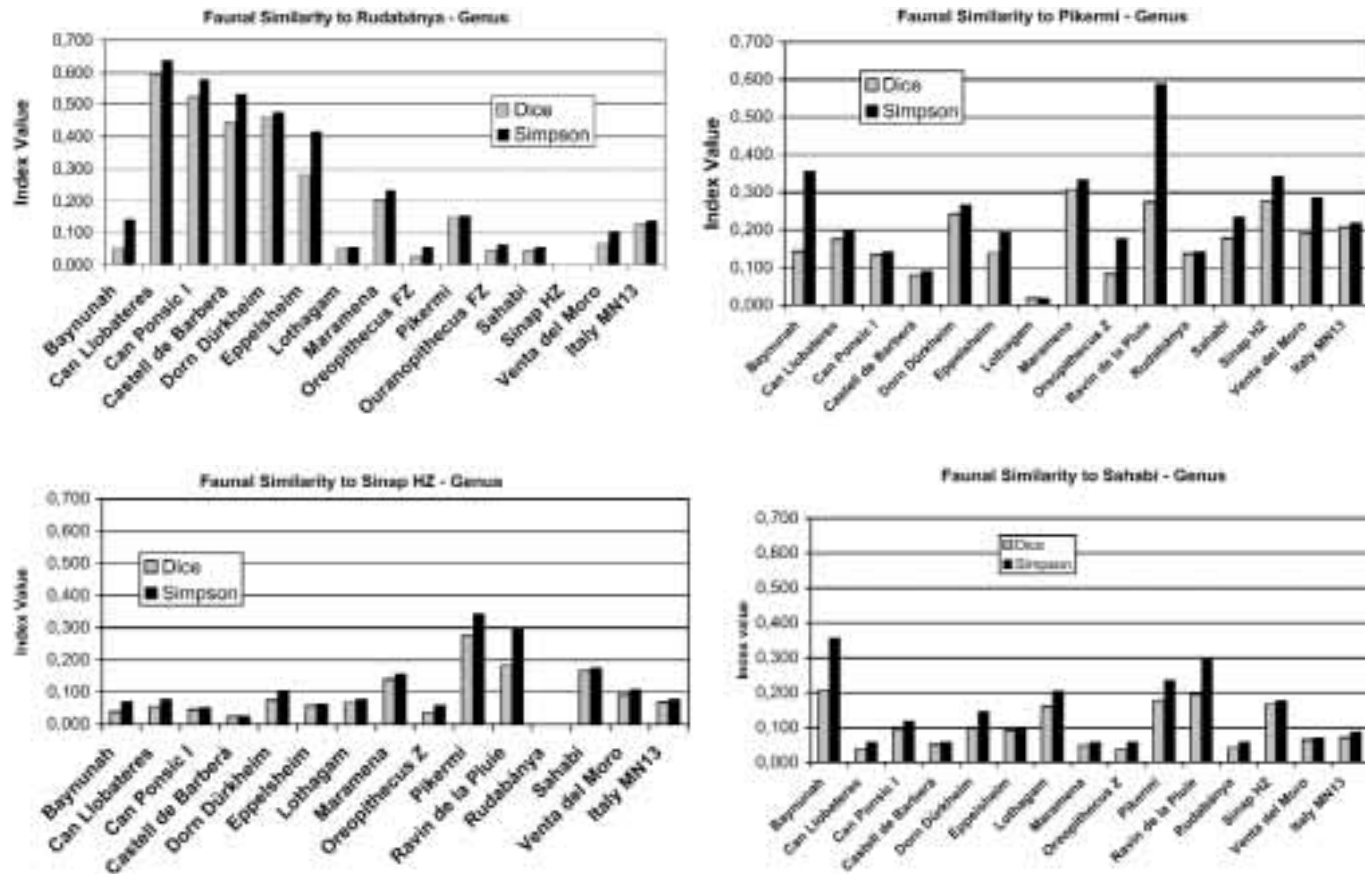
Felidae				
<i>Pseudaelurus turnauensis</i>	MN 4	MN 11		terrestrial, carnivore, meat-only
<i>Pseudaelurus lorteti</i>	MN 4	MN 9		terrestrial, carnivore, meat-only
Hyaenidae				
<i>cf. Thalassictis montadai</i>	MN 7/8	MN 9		terrestrial open country, carnivore, meat and bone eater
Proboscidea				
Deinotheriidae				
<i>Deinotherium giganteum</i>	MN 6	L. Plio.		brachydont browser
Gomphotheriidae				
<i>Tetralophodon longirostris</i>	MN 7/8	L. Plio.		brachydont browser/grazer
<i>Tetralophodon cf. longirostris</i>	MN 7/8	L. Plio.		brachydont browser/grazer
" <i>Stegotetrabelodon</i> " <i>gigantorostri</i>	MN 9			brachydont browser/(grazer?)
Perissodactyla				
Equidae				
<i>Hippotherium intrans</i>	MN 9			running form, mixed graze/browse, deer ecomorph
<i>Hippotherium small sp.</i>	MN 9			likely more grass eating than H. intrans
Tapiridae				
<i>Tapirus cf. priscus</i>	MN 9	MN 11		brachydont, browser, subtropical woodland environments
Chalicotheriidae				
<i>Chalicotherium aff. goldfussi</i>	MN 9	MN 12		brachydont, browser, subtropical woodland environments
Rhinocerotidae				
<i>Hoploaceratherium belvederense</i>	MN 9	MN 10		All brachydont; subtropical woodland environments
<i>Aceratherium incisivum</i>	MN 6	L. Plio.		brachydont browser
<i>Lartetotherium aff. sansaniensis</i>	MN 4	MN 9		brachydont browser; wide habitat tolerance
Artiodactyla				
Suidae				
<i>Propotamochoerus palaeochoerus</i>	MN 7/8	MN 14		omnivore
<i>Parachleuastochoerus n. sp.</i>	MN 9			? Hard object frugivore, omnivory
Tragulidae				
<i>Dorcatherium nauii</i>	MN 4	MN 13		browser, subtropical woodland environments
Cervidae				
<i>Lucentia aff. pierensis</i>	MN 9	MN 11		browser, subtropical woodland environments
Moschidae				
<i>Micromeryx flourensianus</i>	MN 2	MN 11		browser, subtropical woodland environments
Bovidae				
<i>Miotragocerus sp.</i>	MN 9	MN 15		browser, subtropical woodland environments
Bovidae, smaller sp.				

indices, while Simpson's index has long been used by paleontologists and additionally adjusts for differences in sample sizes, which is an issue in this analysis.

The Rudabánya fauna exhibits its strongest resemblance with the Spanish MN 9 localities of Can Llobaters 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: Amphicyonidae, Castoridae, Cervidae, Chalicotheriidae, Deinotheriidae, Erinaceidae, Eomyidae, Gliridae, Hominidae, diverse Mustelidae, ?Pliopithecidae (*Anapithecus hernyaki* at Rudabánya only), low crowned Rhinocerotidae, Sciuridae, Soricidae,



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).

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.

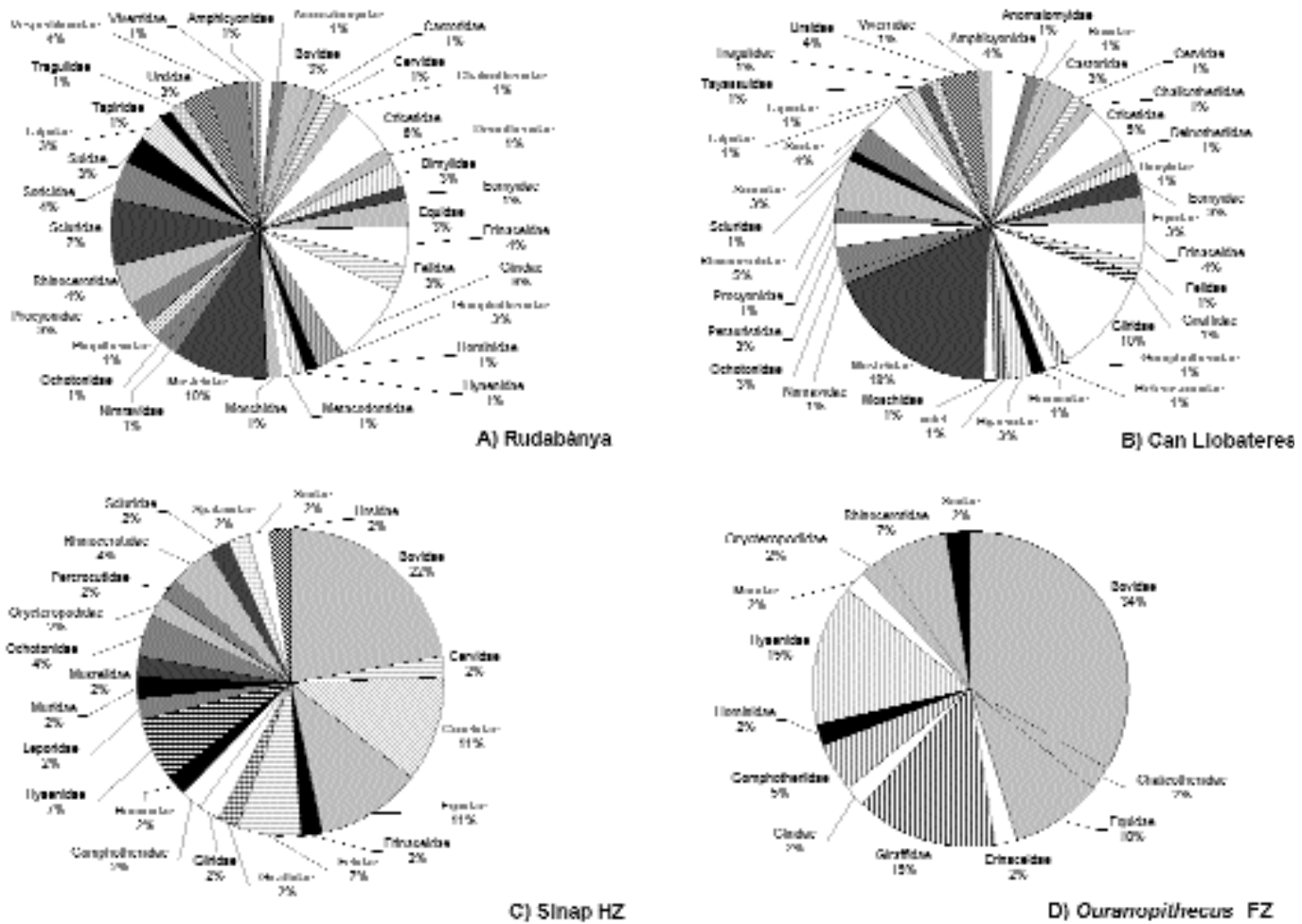
VI) PALAEOCLIMATE ESTIMATES FROM BIOTIC PROXIES

(J. Damuth, J.A. van Dam and T. Utescher)

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. 6 - Pie-diagram of the mammalian family composition of the following assemblages: a) Rudabánya; b) Can Llobateres; c) Sinap Hominid Zone; d) *Ouranopithecus* Faunal Zone.

1800mm/yr. 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

100% (mean: 92.2%) the resulting climate intervals are considered as reliable. The climate data are summarized in table 4. The mean annual temperature 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, 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 climate with warm summers and mild winters (Cfa Köppen-type climate; Köppen, 1931).

As stated above, the Rudabánya flora most probably existed in a very wet habitat. This is also obvious from the floral composition. Approximately 60% of the extant reference taxa of the fossil assemblage presently occur in the alluvial wetland 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 coexistence approach. However, the mean annual precipitation calculated for the Rudabánya flora is consistent with data obtained from neighboring, about time-equivalent localities. The precipitation map for the circum-alpine realm in an early Late Miocene time slice based on the analyses of 28 megafloras shows rates of over 1000 mm all over the Eastern Paratethys (Bruch *et al.*, in press).

VII) PALEOECOLOGY

(R.L. Bernor, M. Fortelius and L. Rook)

The Rudabánya fauna has a subtropical aspect indicative of equable climates (Tables 3, 4). Basing on Kretzoi *et al.* (1976) data, Damuth *et al.* (this paper) characterized the Rudabánya flora as typical of warm temperate, permanently humid climate with warm summers and mild winters.

Andrews *et al.* (1997) stressed close community ecology comparisons between Rudabánya and the early middle Miocene (MN 6) localities of Paşalar (Turkey) and Sansan (France). In support of their paleoecologic characterization, Andrews *et al.* (1997) cite the common occurrence of semiarboreal species, abundant browsing herbivores and common frugivores and insectivores. As stated above, the Rudabánya fauna includes an interesting mixture of archaic European taxa commingled with broader Eurasian immigrant taxa. Table 3 summarizes this research group's current understanding of the age and ecology of the fauna, which we summarize further below.

The Amphibia all suggest the existence of persistent wet conditions at Rudabánya. The snakes have a distinctly subtropical character highlighted by the occurrence of a cobra (*Naja romani*) and taxa all of which became extinct in Central Europe before the end of the Miocene. The avian fauna includes many aquatic forms and is typical of a

TABLE 4 - Rudabánya paleoclimatic values.

N taxa with climate data	30,0
MAT_L [°C]	15,6
MAT_R [°C]	15,7
MAT_% coexisting taxa	93,3
CMM_L [°C]	5,0
CMM_R [°C]	5,1
CMM_% coexisting taxa	90,0
WMM_L [°C]	25,6
WMM_R [°C]	26,3
WMM_% coexisting taxa	90,0
MAP_L [mm]	897,0
MAP_R [mm]	1297,0
MAP_% coexisting taxa	93,3
MMPWM_L [mm]	83,0
MMPWM_R [mm]	89,0
MMPWM_% coexisting taxa	100,0
MARP_L [mm]	86,0
MARP_R [mm]	89,0
MARP_% coexisting taxa	86,7

lake-forest environment.

The mammals are particularly useful for paleoecologic reconstruction. Within the insectivores are found strong indications of subtropical environments such as those that exist today in S.E. Asia. Specifically, the erinaceids *Lanthanotherium sanmigueli* and *Galerix sp.* closely comparable with insectivores living in S.E. Asia today. The soricid *Crusafontia aff. endemica* is most like extant *Anurosores squamipes* living today in montane forests of S.E. Asia. The dimylid insectivore *Metacordylodon aff. schlosseri* was likely semiaquatic, while the talpid *Archeodesmana n. sp.* was certainly semiaquatic. Clearly, the Rudabánya paleolake margin afforded year round warm and equable conditions to maintain this diverse insectivore fauna.

The rodent fauna has a number of species that clearly persist from the middle Miocene of central and western Europe. The diverse sciruids, glirids and comyids suggest forested conditions. The castorid, *Trogonotherium minutum* was an obligatory aquatic form.

The Carnivora include several lineages that continue from earlier Miocene times of central and western Europe, and include: *Semigenetta*, *Proputorius*, *Ursavus* (*U. primaevus* and *U. brevirhinis*), *Amphicyon*, *Sansanosmius* and *Pseudailurus* (*P. turuensis* and *P. lorteti*). The high diversity of mustelids, with which cooccur a viverrid, primitive ursids, nimravid and felids are characteristic of subtropical 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 conditions that prevailed at Rudabánya.

The ungulates further support the interpretation of subtropical forests at Rudabánya. The proboscidean species were all browsers. *Deinotherium giganteum* and *Tetralophodon cf. longirostris* constitute a characteristic proboscidean element for MN 9 of central Europe.

The analysis of *Hippotherium primigenium* verifies its mixed browse/graze dietary behavior. This taxon, along with the smaller hipparion and the hyaenid cf. *Thalassictis montadai* support the hypothesis that more open country mesophytic 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*, *Aceratherium incisivum* and *Lartetotherium aff. sansaniensis* – all were brachydont browsers and are characteristic taxa of central European subtropical/ warm temperate Miocene faunas.

The suids *Propotamochoerus palaeochoerus* and *Parachleuastochoerus* 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; **hypodont** 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 hypodont forms. In fact, the only hypodont 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 hypodont and mesodont forms in their faunas than either Rudabánya or Can Llobateres: 57% hypodont and mesodont forms at Sinap HZ and 51% forms in the *Ouranopithecus* FZ (Text-fig. 7).

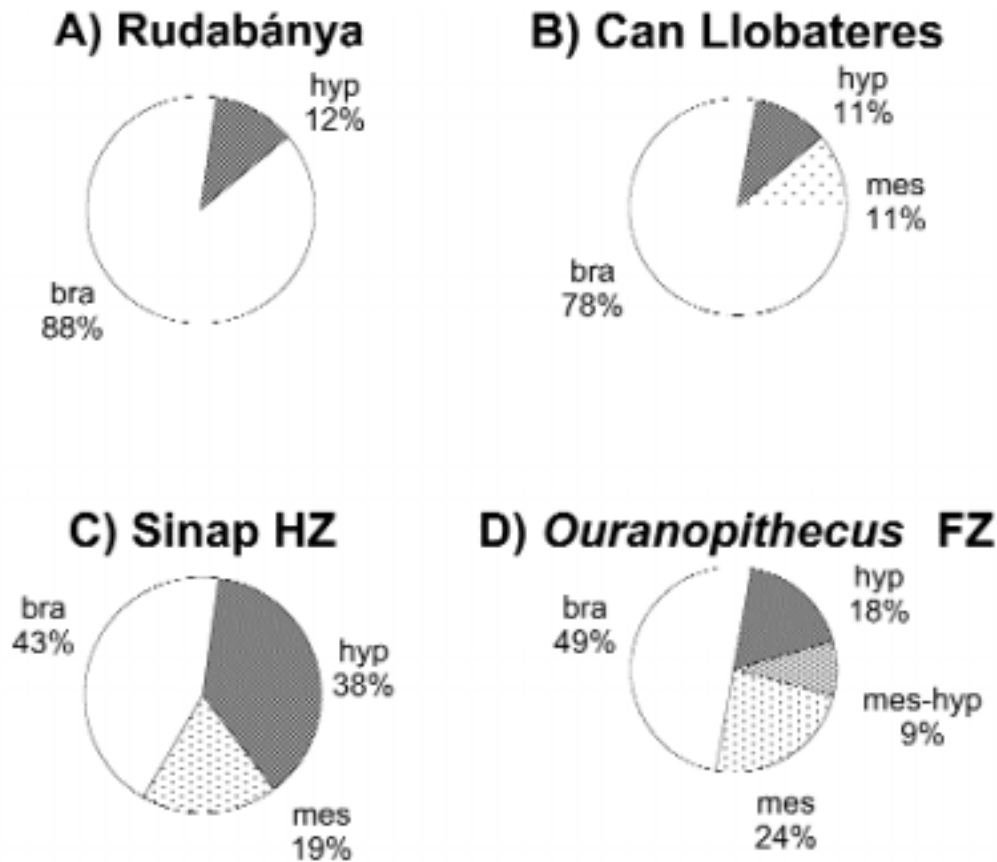
VIII) LATE MIOCENE EUROPEAN HOMINID EVOLUTION

LATE MIOCENE PERIMEDITERRANEAN HOMINID (s.l.) EVOLUTION

The hominid fossil record of Spain (J. Agustí and M. Llenas)

The late Aragonian-Vallesian record of higher primates in the Vallès-Penedès Basin is one of the most abundant and complete from western Eurasia. The first anthropoid record in the Vallès-Penedès Basin occurs at Sant Quirze, in levels of late Aragonian age (*Megacricetodon ibericus* Zone of Agustí & Moyá-Solá, 1991), well before the beginning of the Vallesian (Garcés *et al.*, 1997). The faunal assemblage from Sant Quirze is very similar to that of other late Aragonian European localities such as La Grive M and includes the cervid *Stehlinoceros elegantulus* (Azanza & Menéndez, 1990). The presence of the flying squirrel and the large castorids indicates the existence of humid, forest conditions during this time (Mein, 1970, Aldana, 1992). Castell de Barberà is similar to Sant Quirze in its abundance of wet, forest indicators such as tragulids, castorids, flying-squirrels and dormice. This humid character is similar to that found in some early Vallesian localities such as Can Llobateres. In contrast, the late Astaracian locality of Lower Hostalets has a more open character. In general, and despite the presence of *Dryopithecus*, the latest Aragonian levels are characterized by the absence of forest or humid climate indicators, such as castorids or flying-squirrels, and by low diversities of dormice rodents.

The beginning of the Early Vallesian in the Vallès-Penedès (*Megacricetodon ibericus*-*Hipparion* Zone of Agustí & Moyá-Solá, 1991) is characterized by the presence of the first *Hippotherium* representatives (*Hippotherium primigenium catalanicum*), but the rest of the association is composed of the same elements as the latest Aragonian with even more accentuated dry conditions. No hominoid remains have yet been found in these levels. In contrast, localities of late early Vallesian age included in the *Cricetulodon* Zone (Can Ponsic, Santiga, Can Llobateres 1) are characterized by a very different faunal association, and again includes large castorids, flying-squirrels, tragulids, and tapirids. After an earliest Vallesian “gap”, the hominoid record suddenly increases in the late early Vallesian with the occurrence of *Dryopithecus* in the localities of Can Ponsic and Can Llobateres 1. These faunal assemblages reflect a recovery of more forested, humid conditions comparable with those present in the late middle and early late Aragonian. This is also the time when hominoids (*Dryopithecus laietanus*) attain their highest levels of representation. The boundary between the early and late Vallesian is clearly defined in the Vallès-Penedès Basin by the “Mid-Vallesian Crisis” (Agustí & Moyá-Solá, 1990). This event involved the sudden disappearance of most of the humid elements characterizing early Vallesian localities such as Can Llobateres 1 (rhinocerotids, suids, cervids) and replacement by eastern immigrants (dry-adapted suids like *Schizochoerus*, large sivattherine giraffids



Text-fig. 7 - Ungulate crown height contrast between a) Rudabánya; b) Can Llobateres; c) Sinap Hominid Zone; d) *Ouranopithecus* Faunal Zone. **B**rachidont, **M**esodont, **H**ypsodont.

and boselaphine bovids). 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 (Moyá-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 existed 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 meteai* 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 meteai*. 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 bioprovinces 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; Agustí *et al.*, 1996, 1999). Both *Ouranopithecus macedoniensis* and non-cercopithecoid eucarrhines (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 Tyrrhenian) experienced warmer and possibly wetter conditions, and persisted longer than elsewhere in Europe. Terminal Miocene paleogeographic changes in the Tyrrhenian 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 (the 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 insignificant temporal gap between the last appearance of *Dryopithecus* in Can Llobateres (about 9.5 Ma; Agustí *et al.*, 1996) and the first occurrence of insular faunas in the Marmes 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 *Australopithecus/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 being 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; Moyá Solá *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 lake-side 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-taxa 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 Solá *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 is 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 homoplasious.

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 was largely endemic to central Europe, having some biogeographic connections to west 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.

ACKNOWLEDGMENTS

The Multidisciplinary Research Project at Rudabánya directed by Professors Raymond L. Bernor and Laszlo Kordos was funded by the National Geographic Society and LSB Leakey Foundation. We gratefully acknowledge their generous support throughout the course of this project. Professor Lorenzo Rook offered invaluable assistance in assembling this compendium and in developing new zoogeographic and paleoecologic interpretations of the Rudabánya fauna with Bernor during his stay in the Laboratory of Evolutionary Biology, Howard University. He wishes to acknowledge support for this work by a CNR-NATO Outreach Fellowship. Bernor and Kordos thank all contributors to this compendium, the staff of the Geological Institute of Hungary, and the people of Rudabánya for their assistance throughout our years of work there. We dedicate this contribution to Professor Miklos Kretzoi (Budapest) and Mr. Gabor Hernyák (Rudabánya). Without their considerable contribution and commitment to Rudabánya, this work could not be realized.

We suggest that whomever reads and cites this work, acknowledge the individual authors by the section they have authored. As an example:

SYNDLAR, S., 2003, Snakes: In Bernor R.L. *et al.*, Recent Advances on Multidisciplinary Research at Rudabánya, Late Miocene (MN9), Hungary: a compendium. *Palaeontographia Italica*, 89: 1-34, Pisa.

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