Middle Miocene (Late Badenian) microvertebrates from Hidas, SW Hungary

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Abstract

Up to the present, no terrestrial vertebrate fauna has been published from the pre-Pannonian Miocene of SW Hungary. In 2022 a microvertebrate assemblage was unearthed from a lime mud bed of the Middle Miocene Hidas Formation, in an abandoned coal mining field close to Hidas in the Mecsek Mts. The herpetofauna and the rodent material are described here. Fossil findings point to the Late Badenian MN 7+8 Zone, which, together with the earlier results based on the marine mollusc fauna, narrows the age of the unit to ~13.5–13.3 Ma. The amphibians and reptiles are aquatic, semiaquatic or periaquatic forms. Sedimentary features and the accompanying freshwater gastropod fauna are indicative of a shallow pond or a paludal depositional environment. Crocodylian finds reported earlier from the Hidas Formation indicate a subtropical climate, just before the end of the Miocene warm period in Central Europe. Among the rodents, glirids and flying squirrels as well as *Democricetodon* and *Megacricetodon* indicate the presence of humid arboreal vegetation around the site. The rodent taxa are well known from the Middle Miocene faunas of northern Hungary, western Romania and from the Upper Freshwater Molasse of southern Germany and Switzerland. The rodent material does not show characteristics of an insular fauna, e.g. gigantism or endemism. Consequently, although the coeval palaeogeography of the region has been described as an archipelago in the Central Paratethys, with the Mecsek Mts. being one of the islands, the area must have had ecological connections towards the northern and eastern parts of the Pannonian Basin, and the marine areas within the archipelago did not form a barrier against the distribution of microvertebrates. The corridor could have been located towards the NE from the Mecsek Mts., across the elevated basement blocks of central Hungary.

Keywords: Herpetofauna, Rodent fauna, Pannonian Basin, Mecsek Mountains, Palaeogeography

1. INTRODUCTION

Microvertebrate assemblages are important indicators of palaeoenvironment, the biochronological position of the faunas and their palaeogeographic relationships. The Pannonian Basin in Central Europe experienced profound palaeogeographic changes during the Neogene. The formation of the basin took place mostly in the Early and Middle Miocene, as a result of large-scale migration and deformation of lithospheric microplates (HORVÁTH et al., 2006). Numerous small vertebrate localities are known in the Pannonian Basin from this time interval, providing useful information on the evolutionary and palaeoenvironmental changes in the area (HÍR et al., 2016, 2017, 2019). However, these are mostly located in the northern and eastern parts of the basin. Only sporadic finds have been reported in the south (Paragovo, Veliko Selo and Leštane in Serbia (MARKOVIĆ & MILIVOJEVIĆ, 2010), several locations in the Mecsek Mts. in Hungary (KORDOS & SOLT, 1984, KORDOS, 1985), or on the eastern border of the basin (e.g., Subpiatră, Vârciorog, Tășad in W Romania) (HÍR et al., 2016, 2017). Here we present a new vertebrate assemblage collected in the SE part of the Mecsek Mts., SW Hungary, and discuss its palaeoenvironmental and palaeogeographic significance.

2. GEOLOGICAL SETTING

The sampled outcrop lies along the SE margin of the Mecsek Mts., in a relatively deep gully system south of the village of Hi-

das (Fig. 1.), at the coordinates 46.248723° N, 18.503948° E. Due to the steep topography, it is dissected by dislocation planes of landslides, but displacement along them is minor and it is possible to assemble the probable sedimentary succession, composed of three conformable layers:

1) Mollusc coquina, composed dominantly of brackish-water taxa: the gastropods *Terebralia* and *Nassa*, and small sized ostreids. The shells are mostly oriented parallel to the bedding plane.

2) Whitish grey lime mud, at least 0.8–1 m thick. Variably porous, crumbling, without visible internal sedimentary structures. In the field it was possible to discern *Planorbis* shells and bone fragments. It must have been deposited in a shallow freshwater environment, like a pool or a swamp.

3) Dark brown lignite, at least 1 m thick. It contains lenses of light grey clay and a few cm thick beds of yellowish white, porous dacite tuff, with mm sized biotite crystals.

The succession can be classified into the coal-bearing Hidas Formation (Fig. 2). Both the *Planorbis*-bearing layers and the coquina with ostreids are typical for the interbeds between the coal layers (CSEPREGHYNÉ MEZNERICS, 1950, BOHNNÉ HAVAS, 1973). The age of the unit is upper Badenian in the regional, Central Paratethys stratigraphy (lower Serravallian in standard global stratigraphy) (SELMECZI et al., 2023). The formation is composed of alternating lignite, clay, marl, mollusc co-
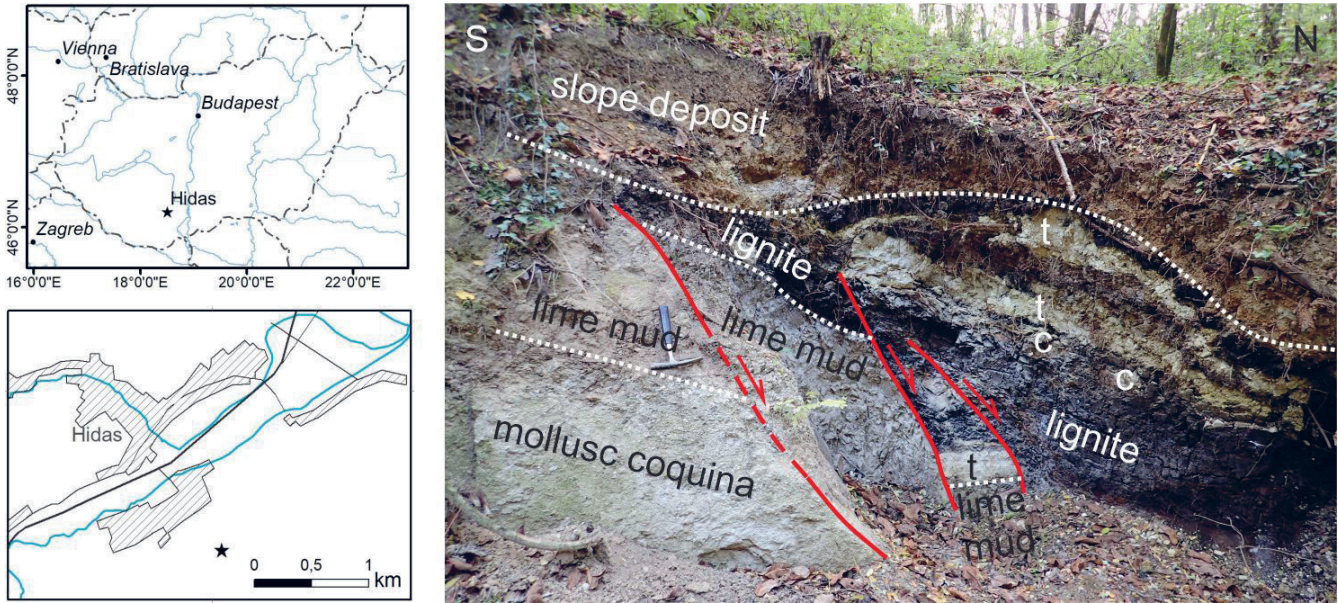
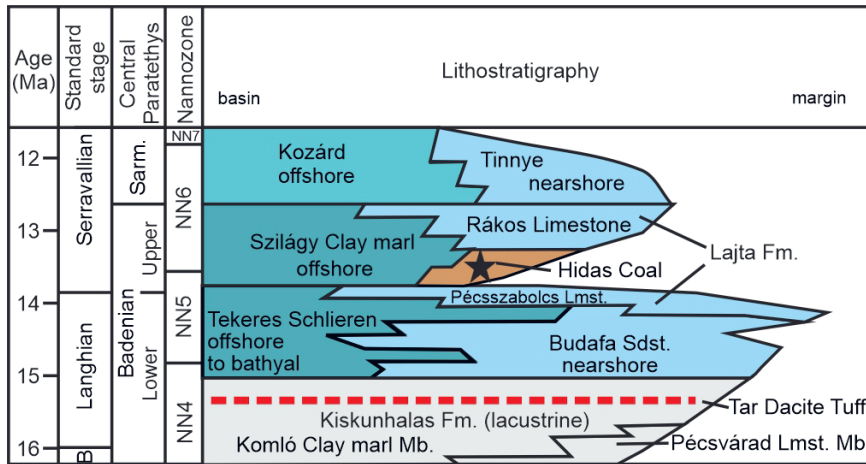**Figure 1.** Location and appearance of the studied outcrop. Abbreviations: t – tuff; c – clay lense.

Figure 2. Stratigraphic position of the fauna (indicated by star). Lithostratigraphy of the Mecsek Mountains after SEBE et al. (2019); chronostratigraphy after KOVÁČ et al. (2018).

quina and lime mud layers and accumulated in brackish and freshwater environments.

Only sporadic vertebrate remains have been known from the Hidas Formation so far. From the coal mine in the village of Hidas, KORDOS (1985) reported *Steneofiber* sp., *Diplocynodon* sp. and „crocodile" bones, citing VADÁSZ (1935). KORDOS (1985) also mentions a Rhinocerotidae tooth from the Hidas Formation, from the shaft of the (Jurassic) coal mine near the village of Máza, found at the boundary between the Mesozoic and the overlying Miocene beds. The Hidas Formation does not occur in that area where the basement is overlain by the Lower Miocene, fluvial Szászvár Formation, therefore we consider this mention to have an erroneous lithostratigraphic classification. An otolith assemblage consisting of *Gobius* sp., *Citharus* sp. and Soleidae was reported from the brackish-water layers of the Hidas Formation, (BARANYAI, 2010).

3. MATERIAL AND METHODS

Two tons of sediment were collected from the fossiliferous level at the studied outcrop. They were air-dried on textile in the sunshine and subsequently soaked in water and some H_2O_2. The samples were screen-washed using a sieve system with a 0.5 mm mesh size. Sorting was carried out by the co-workers of the Municipal Museum of Pásztó and by the authors. The fossil material belongs to the collections of the Municipal Museum of Pásztó (MMP. 2022.1.–2022.74. and MMP. 2023.5–2023.28.). The measurements were taken using an MBS-10 stereomicroscope. The dimensions are given in mm. The digital images were taken using a Canon EOS 400 D digital camera equipped with Canon MP-E65 mm and Canon EF 60 mm macro-objectives. The retouches on micromammal teeth were made by JH. The systematics of the rodents follows MCKENA & BELL (1997). The anatomical nomenclature of amphibians and squamate reptiles follows VENCZEL & HÍR (2013), while in rodents the nomenclature of the dental morphology is after CUENCA-BESCOS (1988), DAXNER-HÖCK (2010), DAXNER-HÖCK & HÖCK (2015) for sciurids, MEIN & FREUDENTHAL (1971) for cricetids and DAAMS (1981, 1985) for glirids. Abbreviations in the text: L: maximal antero-posterior length of the occlusal surface of a tooth; W: maximal labio-lingual width of the occlusal surface of a tooth; P4: upper premolar; p4: lower premolar; M1-M2-M3: upper molars; m1-m2-m3: lower molars; fr.: fragment

4. SYSTEMATIC DESCRIPTION

Class: Amphibia LINNAEUS, 1758

Order Urodela DUMÉRIL, 1806

Family Salamandridae GOLDFUSS, 1820

Genus *Lissotriton* BELL, 1839

Lissotriton rohrsi (HERRE, 1955)

Figs. 3A-C

Referred material: One atlas (MMP.2023.5.1), one trunk vertebra (MMP.2023.6.1), one humerus (MMP.2023.7.1).

Description. Atlas. The specimen is well-preserved and might have belonged to a relatively large adult individual. The anterior cotyles are circular and face anterodorsally (i.e., obliquely), whereas the tuberculum interglenoideum is wide and flattened. The neural arch is moderately vaulted and provided with a low and short neural ridge, flanked by two lateral crests delimiting a posteriorly tapering triangle surface (Fig. 3A).

Trunk vertebra. The centrum is opisthocoelous and moderately elongated. The neural arch is vaulted and provided with a high and posteriorly widening neural spine. Pits of various sizes occur on the dorsal margin of the neural spine; however, it is devoid of any pustular sculpture (Fig. 3B).

Humerus. MMP.2023.7.1 represents a proximal fragment. The caput humeri is rounded and well ossified representing an adult individual. The processus dorsalis humeri projects at an angle of about 45° from the main humeral shaft. The crista ventralis humeri is moderately developed.

Comments. The referred remains might have belonged to two different sized individuals, the atlas probably representing a larger individual, compared to the trunk vertebra that corre-
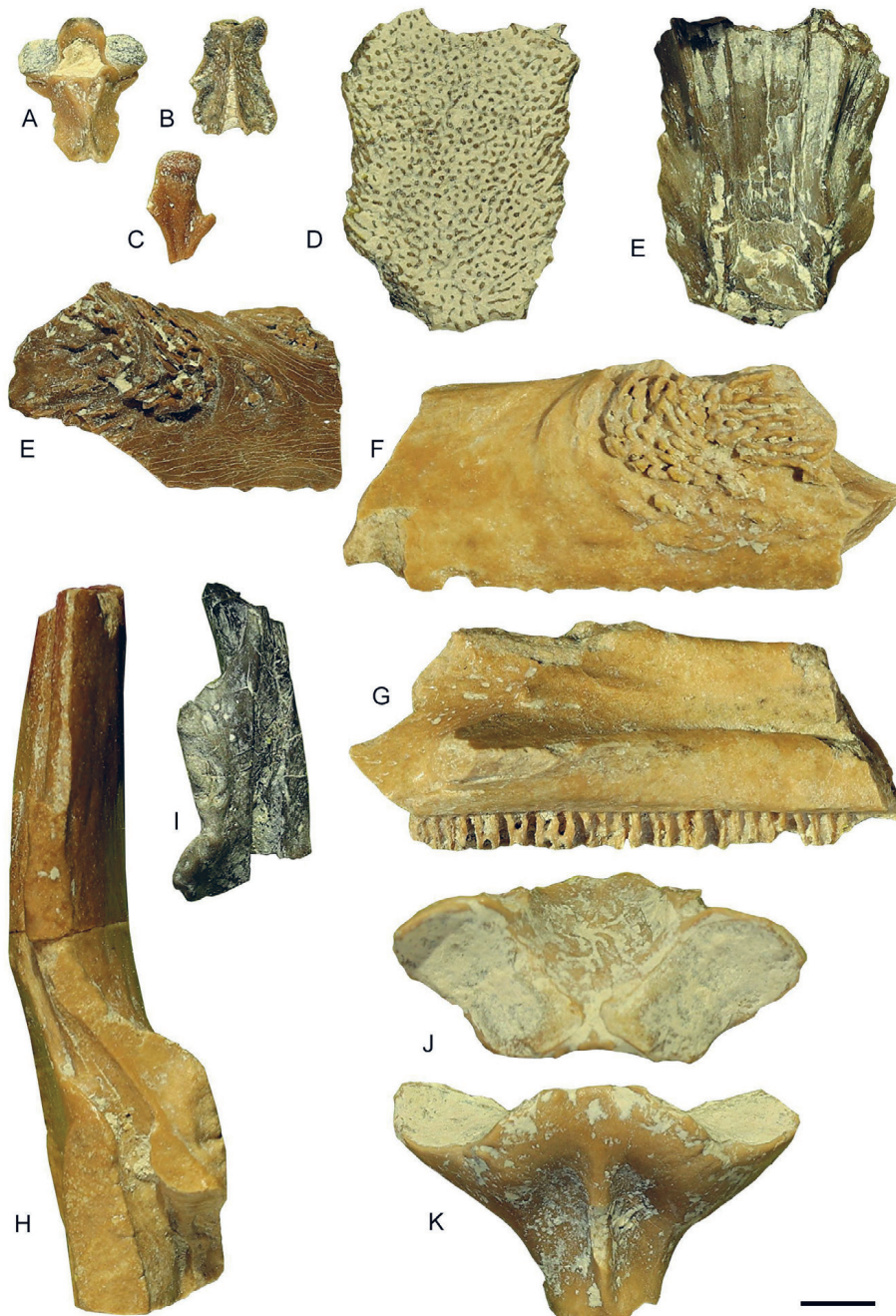

Figure 3. Urodeles and anurans from the middle Miocene of Hidas, Hungary. A-C: *Lissotriton rohrsi*, atlas (A), trunk vertebra (B), humerus (C); D-K: *Latonia seyfriedi*, D, E – frontoparietal; E – G, maxillae; H, I – angulars; J, K – atlas. A, B, D, H, I – dorsal views, J – lateral view, E, K – ventral views, E, F – labial views, G – lingual view, J – anterior view. Scale bar = 2 mm.

sponds to a comparatively smaller individual. In fact, the description of *Lissotriton* (= *Triturus*) *rohrsi* (HERRE, 1955) from the Middle Miocene (MN 6) type locality of Děvínská Nová Ves (Neudorf, Dévényújfalu), Slovakia (ESTES, 1981), corresponds exactly to those of the referred specimens. Assignment of the proximal humerus is based on overall morphological similarity with those of *Lissotriton* members. Unfortunately, apart from the vertebrae, no other skeletal parts in Europe have been referred to this species, considered as part of the *L. vulgaris* group (IVANOV, 2008; VENCZEL & HÍR, 2013; GEORGALIS et al., 2019). An atlantal specimen (MMP.2009.668), referred as *Lissotriton* cf. *rohrsi*, from the Sarmatian (MN 7+8) locality of Felsőtárkány 3/10, N Hungary appears with a less elongated centrum and the tuberculum interglenoideum is slightly divided (VENCZEL & HÍR, 2013, fig. 25). Trunk vertebrae, also with a slightly different morphology (i.e., neural spines not widened at their anterior section, but bifurcating in their posterior part) have been identified as *Lissotriton* aff. *rohrsi* from the Early Miocene (MN 4) locality of Mokrá Western Quarry, Czech Republik (IVANOV, 2008), or as *Lissotriton* sp. (*L. vulgaris* group), possessing higher neural spines, from the latest Miocene (MN 13/14) of Maramena, Greece (GEORGALIS et al., 2019). Further reports of the above taxon are from the Early Miocene (MN 4) of Oberdorf (SANCHÍZ 1998a) and Late Miocene (MN 9) of Götzendorf (MIKLAS, 2002), both from Austria. The material also contains several strongly fragmentary specimens that cannot be identified below the familial level (i.e., Salamandridae indet.).

Family Alytidae FITZINGER, 1843
Genus *Latonia* MEYER, 1843
Latonia seyfriedi MEYER, 1843
Figs. 3D-K, 4A-C.

Referred material: two frontoparietals (MMP.2023.8.1-2.), 25 fragmentary maxillae (MMP.2023.9.1-25), eight angulars (MMP.2023.10.1-8), five atlases (MMP.2023.11.1-5), 15 presacral vertebrae (MMP.2023.12.1-15), one sacral vertebra (MMP.2023.13.1.), one ilium (MMP.2023.14.1.).

Description. Frontoparietal. Both available specimens are azygous and covered dorsally by a strong secondary sculpture. In MMP.8.1. the intertubercular space is infilled by the fine grained light grey matrix (Fig. 3D), whereas the ventral surface displays a medial sagittal fissure line that may correspond to the fusion line of the parietal parts (Fig. 3E). The ventral posteromedial part is developed into a deep concavity that corresponds to the frontoparietal incrassation (ROČEK, 1994).

Maxilla. Most specimens are very damaged. The labial surface, especially on its dorsoposterior part, is covered by a secondary sculpture observed even in the small-sized specimens. The secondary sculpture consists of a framework of irregularly perforated bone (ROČEK, 1994), which is typical for *L. seyfriedi* (Fig. 3E, F). The lingual surface displays a wide and moderately prominent lamina horizontalis delimiting ventrally the pars dentalis; posteriorly the lamina horizontalis projects into a prominent pterygoid process, whereas its base is connected to a crest delimiting a shallow posterior depression (Fig. 3G).

Angular. It is a slightly S-shaped bone with the anterior part curved medially and compressed mediolaterally, whereas its posterior part is more robustly built and widened into a spoon-like pars spatulata (not preserved in any of the available specimens). MMP.2023.10.1. is the largest specimen, rebuilt (i.e., glued together) from two broken parts. The posterodorsal part is broken off at the level of the coronoid process (Fig. 3H); the Meckel's groove is relatively deep, extending sinuously on the dorsal and more anteriorly on the dorsolateral part of the bone. In MMP.2023.10.2. the posterior coronoid process is also preserved, positioned nearly at a right angle to the anterior coronoid process (Fig. 3I).

Atlas. In all the available specimens only the atlantal centra are preserved (Fig. 3J, K). The anterior cotyles are distinctly separated, their articular surface is roughly rectangular, standing obliquely to the horizontal surface at about 45°. The anterior part of the ventral lamina is protruding anteriorly below the deeply concave articular space. The ventral surface of the centrum bears a prominent ventral crest, whereas the posterior cotyle is circular.

Presacral vertebrae. In all specimens only the vertebral centra are preserved (Fig. 4). The centrum is opisthocoelous with a more or less hemicylindrical ventral surface, and with strong dorsoventral flattening (Fig. 4A).

Sacral vertebra. The single specimen preserves only the centrum. It is provided with an anterior and two posterior condyles. The posterior margins of the posterior condyles are damaged (Fig. 4B).

Ilium. The MMP.2023.14.1. specimen preserves the acetabular region of a relatively large individual. The acetabular surface exhibits a sinuous anterior margin extending into a narrowed dorsal surface, whereas anteroventrally it projects beyond the margin of the reduced preacetabular region (Fig. 4C). The supraacetabular region is extensive, but its dorsoposterior part is broken off. The dorsal tubercle is oval and thickened, whereas posterior to it there is a deep supraacetabular fossa.

Comments. Diagnostic features of this large sized alytid frog are among others the widened frontoparietal table bearing an extensive secondary sculpture on the frontoparietal and that the frontoparietal table is more reduced in *Discoglossus* and *Latonia nigriventer* (see in BITON et al., 2013). The labial surface of the maxillae also bears a secondary sculpture, this attribute lacking in *Latonia vertaizoni* (ROČEK, 1994), in *L. ragei* (HOSSINI, 1993), *Latonia* sp. from Maramena (GEORGALIS et al. 2019), and in recent *L. nigriventer* and members of *Discoglossus* (BITON et al., 2013).

Family Palaeobatrachidae COPE, 1865
Genus *Palaeobatrachus* sp.
Figs. 4D-K

Referred material: two frontoparietals (MMP.2023.15.1-2.), three maxillae (MMP.2023.16.1-3.), one sphenethmoid (MMP.2023.17.1.), 12 angulars (MMP.2023.18.1-12), one humerus (MMP.2023.19.1.).

Description. Frontoparietal. The specimen MMP.2023.15.1. preserves the anterior half of an azygous frontoparietal. The dorsal surface displays two well-defined parasagittal crests being parallel in the posterior part of the preserved fragment; however, these diverge at the level of the pineal foramen, reaching the lateral margins of the bone (Fig. 4D). In ventral view, the contact area with the sphenethmoid is marked by a striated area on the anterolateral sides of the bone (Fig. 4E). The second specimen lacks the parasagittal crests and its lateral sides are strongly eroded.

Maxilla. In the available specimens the anteriormost parts contacting the premaxilla and the posterior (i.e., toothless) parts are not preserved (Fig. 4F, G). The maxillary nasal process is moderately high and somewhat damaged. The tooth crowns are
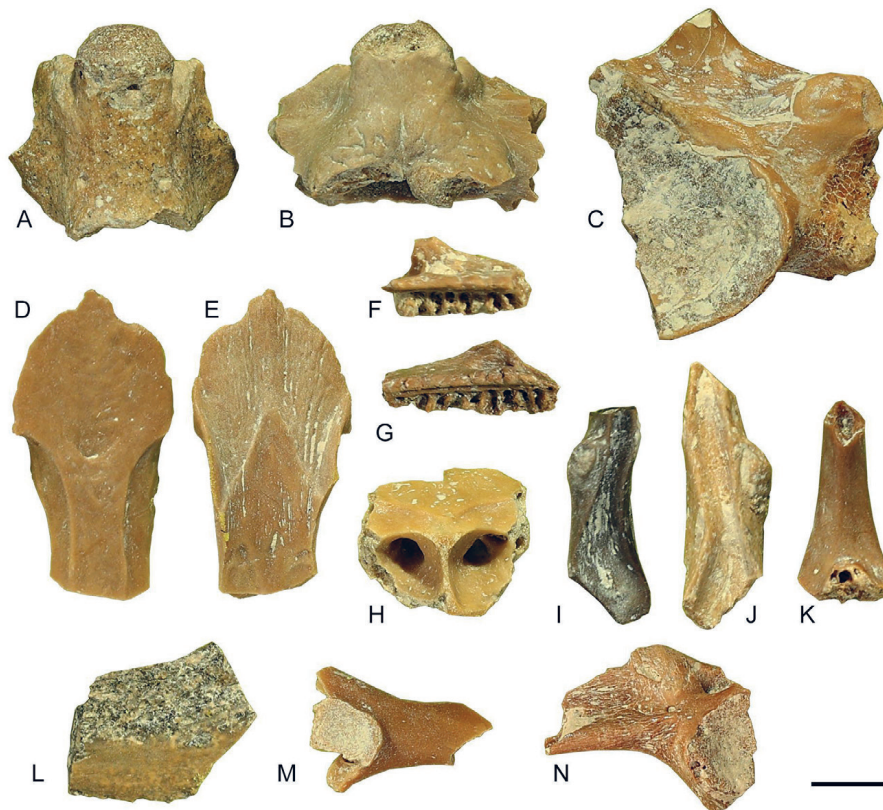
Figure 4. Anurans from the middle Miocene of Hidas, Hungary. A-C: *Latonia seyfriedi*, presacral vertebra (A), sacral vertebra (B) and ilium (C); D-K: *Palaeobatrachus* sp., frontoparietal (D, E), maxillae (F, G), sphenethmoid (H), angulars (I, J) and humerus (K); L, M: *Pelobates* sp., maxilla (L) and ilium (M); N: *Pelophylax* sp., ilium. A, B, E, K – ventral views, C, M, N – lateral views, D, I, J – dorsal views, F, G – lingual views, H – anterior view, L – labial view. Scale bar = 2 mm.

broken off, but the tooth sockets preserve on each side osseous tuberosities, which are typical for palaeobatrachids (SANCHÍZ 1998b).

Sphenethmoid. The only specimen preserved the anterior part of a relatively small individual, indicated by the fact that the rostrum is not completely ossified (Fig. 4H). In anterior view, an obliquely placed bony lamella divides the olfactory canal, situated medially, and the orbitonasal foramen, which conveyed the ophthalmic nerve (canalis ramus medialis nervi ophtalmici), situated dorsolaterally. The former structure is about twice as large as the latter. The dorsal surface of the bone displays an anteriorly tapering crest, which in the living animal marks the contact area of the overlying frontal, situated posteriorly, and the nasal bones, situated anteriorly.

Angular. The available specimens are fragmentary, most of them preserving the more robustly built area bearing the coronoid process. However, the specimen MMP.2023.18.1. preserves part of the moderately widened posterior portion (i.e., pars spatulaeformis praearticularis) (Fig. 4I). The Meckel's groove is wide, sinuous and delimited by sharp bony lamellae; the coronoid process appears as a low tuberosity, situated on the lingual side of the angular (Fig. 4I, J).

Humerus. The only available small-sized specimen preserves the distal part of a humerus (Fig. 4K). From the humeral ball, apparently positioned medially, only its base is preserved. The ventral cubital fossa is lacking, a typical feature for palaeobatrachids (see e.g., VENCZEL, 2004: fig. 5: E, F).

Comments. Based on the available specimens, differentiation of the two late Badenian palaeobatrachid species known from the Pannonian Basin (i.e., *Palaeobatrachus hiri* and *P. codreavladi*) is not possible (ROČEK et al., 2021).

Family: Pelobatidae BONAPARTE, 1850
Genus *Pelobates* WAGLER, 1830
Pelobates sp.
Figs. 4L, M.

Referred material: one maxillary fragment (MMP.2023. 20.1.), one right ilium (MMP.2023.21.1.).

Description. Maxilla. The labial surface is shallowly convex and bears a primary sculpture on its dorsal part (Fig. 4L). Unfortunately, the sculpture is mostly eroded preserving only the base of that structure. The lower part of the labial surface is smooth, extending parallel to the ventral (i.e., tooth bearing) margin.

Ilium. The only specimen preserves the labial region and the posterior part of the iliac shaft (Fig. 4M). The iliac shaft is reduced to a dorsal ridge and the dorsal protuberance is lacking. A little wasting is present between the acetabular region and the iliac shaft, due to the presence of a so-called "spiral groove" extending on the medial side of the bone (EVANS & MILNER, 1993).

Comments. Typical features of the above specimens are the presence of a primary sculpture on the maxilla, the nature of the dorsal ridge on the ilium and the lack of the dorsal protuberance. In *Pelodytes* the ilium resembles the genus *Pelobates*, but in the former a small dorsal protuberance is always present on the ilium (VENCZEL & HÍR, 2013: fig. 64).

Family Ranidae BATSCH, 1796
Genus *Pelophylax* FITZINGER, 1843
Pelophylax sp.
Fig. 4N.

Referred material: one fragmentary left ilium (MMP.2023.22.1.)

Description. Ilium. The only specimen preserves the acetabular region and part of the iliac shaft. The anterior half of the acetabulum appears circular and delimits ventrally an extremely deep supraacetabular fossa. The slightly convex dorsal protuberance extends anteriorly to the supraacetabular fossa into the dorsal margin of the posterior part of the iliac shaft. The preacetabular region is reduced.

Comments. The preserved parts of the only specimen are closely similar to the so-called hybridogenetic green frogs, described under the name *Pelophylax* (= *Rana*) *esculentus* (RAGE & HOSSINI, 2000, VENCZEL, 2004, VENCZEL & HÍR, 2013) from various Middle Miocene localities.

Class Reptilia LAURENTI, 1768
Order Squamata OPPEL, 1811
Family Lacertidae OPPEL, 1811
Lacertidae indet.

Referred material: one posterior fragment of a left maxilla (MMP.2023.23.1.), two fragmentary dentaries (MMP.2023.24.1.).

Description. Maxilla. The specimen represents a small posterior part of the maxilla provided with a fragmentary facial process and seven tooth positions. The tooth crowns are cylindrical and bicuspid with a smaller anterior and a larger posterior cusp (Fig. 5A).

Dentary. The dentary displays a relatively deep and dorsoventrally narrow subdental shelf, filled with a fine grained light-grey coloured matrix. The labial surface is smooth with few nutritive foramina. The tooth crowns are cylindrical, and if the apical region is preserved, they display a weakly bicuspid condition (Fig. 5B).

Comments. The specimens might have belonged to a small sized taxon, comparable in size to the living members of *Podarcis* or *Zootoca*.

Family Anguidae GRAY, 1825
Anguinae indet.
Fig. 5C-F

Referred material: one posterior fragment of a right dentary (MMP.2023.25.1.), one trunk vertebra (MMP.2023.26.1.).

Description. Dentary. The specimen preserves a posterior dentary fragment with six tooth positions. The dental parapet is of relatively low height, whereas a medially projecting nearly horizontal crest may correspond to the contact surface of coronoid articulation. The tooth bases are widened mediolaterally, whereas the tooth crown is very worn apically with some trace of a mesiodistal carina. The labial surface is smooth and nearly flat with its ventral part broken off.

Trunk vertebra. The specimen is extremely small with an elongated centrum and displays a smooth ventral surface without any constriction. The cotyle is strongly flattened, the synapophyses are relatively small and the neural canal is enlarged and of roughly triangular shape.

Comments. The specimens despite their fragmentary nature (dentary) or small size (vertebra) appear reminiscent of *Ophisaurus* (VENCZEL & HÍR, 2013). However, based on the available material, a closer assignment is not possible.

Family Colubridae OPPEL, 1811
Colubridae indet. sp. 1
Fig. 5G, H.

Referred material: seven fragmentary vertebrae (MMP.2023.27.1-7).

Description. Trunk vertebrae. The available specimens represent a large sized colubrid snake. The centrum length of the largest vertebra is 7.2 mm. Unfortunately, the neural arch is broken off in all the examples. The main preserved characteristic is that the haemal keel is flattened and spatulate shaped. Small subcotylar tubercles are present in some of the specimens.

Comments. Large sized colubrids with somewhat similar morphology from the early Late Miocene of Litke have been assigned by VENCZEL & HÍR (2015) to "*Coluber*" cf. *caspioides*, or to "*Coluber*" *pouchetii* from the late middle Miocene of Felsőtárkány 3/2. and 3/10 localities (VENCZEL & HÍR, 2013).

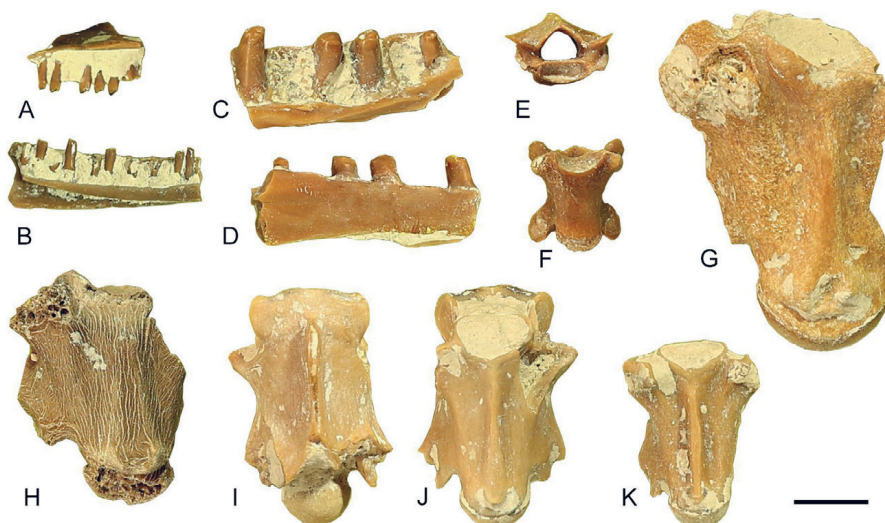**Figure 5.** Squamate reptiles from the middle Miocene of Hidas, Hungary. A, B: Lacertidae indet., maxilla (A) and dentary (B); C-F: Anguinae indet, dentary (C, D) and trunk vertebra (E, F); G, H: Colubridae indet. sp. 1, trunk vertebrae; I-K: Colubridae indet. sp. 2, trunk vertebrae. A-C lingual views, D – lateral view, E – anterior view, F-H, J, K ventral views, I – dorsal view. Scale bar = 2 mm.

Colubridae indet. sp. 2

Fig. 5I-K.

Referred material: 20 fragmentary vertebrae (MMP.2023.28.1-20).

Description. Trunk vertebrae. The specimens are small sized, the centrum length never reaching 5 mm. The neural arch is moderately vaulted, the zygosphene, if preserved, has a shallowly convex anterior margin, whereas the paradiapophyses are differentiated into diapophyseal and parapophyseal portions of roughly equal length. The haemal keel of the trunk vertebrae is prominent and long, extending posteriorly into the vicinity of the condyle in the form of a narrow ridge. In some specimens the posterior part of the haemal keel is slightly flattened dorso-ventrally.

Comments. The morphology of the available specimens, especially those of the haemal keels display a wide range of variation, and therefore, we cannot exclude that the material contains more than one small sized colubrid taxon.

Class Mammalia LINNAEUS, 1758
Order Rodentia BOWDICH, 1821
Family Gliridae THOMAS, 1897
Subfamily Glirinae THOMAS, 1897
Genus *Myoglis* BAUDELOT, 1965
Myoglis meini (DE BRUIJN, 1966)

Table 1. *Myoglis meini* data from Hidas.

Locality:	No. inv.	Position:	L:	W:	Figure:
Hidas	MMP. 2022.6.1.	P4	1.61	1.62	
Hidas	MMP. 2022.5.1.	m3	1.82	1.83	Pl. 1F

Description. P4. It possesses a rectangular outline with rounded angles. The occlusal surface is flat. There are four main ridges: anteroloph, protoloph, metaloph, posteroloph. Anteroloph has free ends in the lingual and labial margin, the other main ridges are fused in the postero-lingual angle (protocone). One additional ridge: the anterior centroloph, is situated between the lingual margin and the centre of the occlusal surface. The ends of this ridge are free.

m3. It has a subtriangular outline. The occlusal surface is flat. The anterior margin is broad, the posterior one is rounded. The enamel of the posterior slopes of the ridges is wrinkled. The four main ridges are: anterolophid, metalophid, mesolophid, posterolophid. The Anterolophid is transversal, the other main ridges are positioned diagonally. There are three secondary ridges: 1. anterior additional ridge (between the anterolophid and the metalophid on the lingual side), it has two short minor ridges on the anterior and the posterior sides; 2. a long, but low developed centrolophid on the posterior side of the metalophid; 3. a short posterior extra ridge between the mesolophid and the posterolophid on the lingual side.

Comments. The biochronological range of *Myoglis* in Europe extends from the Early Miocene to the Late Miocene (MN2-MN10). In the Pannonian Basin the earliest occurrence is from Szentendre (early MN6). The latest record is known from the Richardhof-Wald (MN10), Vienna Basin, Austria. *Myoglis* is a characteristic element of the microvertebrate faunas mirroring a humid climate and forested environment. VAN DER MEULEN & DE BRUIJN (1982) classified *Myoglis* as a member of the "flat molar group" which has a mainly vegetarian diet.

Subfamily Dryomyinae DE BRUIJN, 1967
Genus *Paraglirulus* ENGESSER, 1972
Paraglirulus werenfelsi ENGESSER, 1972

Table 2. *Paraglirulus werenfelsi* data from Hidas.

Locality:	No. inv.	Position:	L:	W:	Figure:
Hidas	MMP. 2022. 7. 1	M2	1.15	1.22	Pl. 1E

Description. M2. It has a rectangular outline. The occlusal surface is concave. The ornamentation on the lingual margin is weak. It has four main ridges and five secondary ridges. The main ridges are: anteroloph, protoloph, metaloph, posteroloph. All of them are labially connected to the continuous endoloph. The anteroloph and protoloph are labially fused. The labial end of the posteroloph is close to the metaloph, but there is no complete fusion. The extra ridges are as follows: 1. a long and centrally positioned anterior extra ridge having free ends between the anteroloph and the protoloph; 2. anterior centroloph having free lingual end, labial end is fused with protoloph; 3. a very long extra ridge between the centrolophs; the labial end fuses with endoloph, the lingual end reaches the base of the anterior centroloph on the labial margin, but a complete fusion is not developed; 4. posterior centroloph is with free lingual end and labial end is fused with metaloph; 5. a short extra ridge develops between the posterior centroloph and the metaloph has free ends; 6. a relatively long, centrally positioned extra ridge has free ends between the metaloph and the posteroloph.

Comments. *Paraglirulus werenfelsi* is a frequent element of the Middle Miocene microvertebrate faunas. In the Pannonian region the biochronological range of this species extends from the MN5 up to the MN10 zone. *Paraglirulus* is regarded as a member of the group „Gliridae II," having an arboreal-scansorial lifestyle (VAN DAM & WELTJE, 1999). VAN DER MEULEN & DE BRUIJN (1982) classified *Paraglirulus* as a member of the "symmetrical molar goup", which has a mainly vegetarian diet.

Family Sciuridae FISCHER DE WALDHEIM, 1817
Subfamily Pteromyinae BRANDT, 1855
Genus *Albanensia* DAXNER-HÖCK & MEIN, 1975
Albanensia albanensis (MAJOR, 1893)

Table 3. *Albanensia albanensis* data from Hidas.

Locality:	No. inv.	Position:	L:	W:	Figure:
Hidas	MMP. 2022. 1. 1	M1	3.25	3.90	Pl. 1A
Hidas	MMP. 2022. 8. 1	p4	3.05	3.12	

Description. M1. It has a subrectangular outline with rounded lingual side, because of the convex lingual wall of the protocone. This lingual wall is crenulated and has two incisions. The lingual cingulum on the base of the protocone is weak. The anteroloph is a continuous ridge from the centre of the protocone up to the anterior margin of the paracone. This ridge has no minor cusps. The protoloph and metaloph converge on the labial side of the protocone in a V-shape. Protoconule is incipient. Protoloph is a continuous ridge (not having a „zigzag form" in the sense of DAXNER-HÖCK, 2004) between the protocone and the paracone, but it bears short anteriorly and posteriorly directed additional ridges. The mesostyle crista on the posterior side of the paracone is well developed. Mesostyle is absent. The metaloph connects the protocone, metaconule and metacone. It has a weak

tendency for „zigzag" formation. Hypocone is incipient. The metacone and metaconule have posterior ledges, but these extra ridges do not reach the posteroloph. The posteroloph is thin and bears minor anteriorly directed additional ridges.

p4. It has a trapezoidal outline with rounded angles. Anterior margin is narrower than the posterior one. On the mesial part of the crown there are two cusps: protoconid and metaconid. They are connected by two ridges: anterolophid and metalophid. The cusps and the ridges enclose the small trigonid basin. Anteroconulid is not developed. An enamel ridge is developed on the posterior slope of the metaconid (on the lingual margin) reaching to the mesolophid. This latter element forms an incipient cusp. There is an incision between the mesolophid and the entoconid. The poorly developed mesoconid on the labial side is connected to the protoconid and the hypoconid by enamel ridges. Posterolophid consists of a series of minor cusps. The surface of the talonid basin is crenulated.

Comments *Albanensia* is a large sized flying squirrel. In the Miocene of the Pannonian Basin three *Albanensia* species are represented:

A. sansaniensis, Szentendre, Hungary, HÍR (2019), HÍR & VENCZEL (2018)

A. albanensis, Gratkorn, Austria, DAXNER-HÖCK (2010); Mikófalva, Hungary, HÍR (2019)

A. grimmi (Felsőtárkány 3/2, Hungary, HÍR (2019); Götzendorf, Richardhof-Wald, Richardhof-Golfplatz, Austria, DAXNER--HÖCK (2004); Pezinok, Slovakia, JONIAK (2016).

A. sansaniensis is the oldest one (MN6), while *A. grimmi* is the youngest one (MN9, MN10).

The systematic position of the *Albanensia* population of Rudabánya (MN9) is open to dispute. KRETZOI & FEJFAR (2005) classified this population as *A. grimmi*, but the dimensions are smaller (HÍR 2019). DAXNER-HÖCK (2010) defined the distinctive characters of *A. albanensis* as follows: smaller dimensions, lower and less crenulated loph(ids) and con(ids), smaller P4/p4, longer m3 with continuous and a small or absent hypoconulid, straight (not zigzag-shaped) protoloph and metaloph, absent or very short protoconule, small hypocone. The classification of the teeth from the Hidas Formation is based mainly on the dimensions and the incipient protoconule and hypocone. The protoloph is undoubtedly straight. The metaloph is disputed, but the "zigzag figure" is not typical. The lingual cingulum is weak.

The *Albanensia* genus became extinct in the early phase of the Late Miocene (MN10). The other flying squirrel genera (*Miopetaurista, Neopetes, Pliopetes, Pliopetaurista, Blackia*) survived the "Vallesian crisis" and occurred in Central Europe up to the Pliocene (MN15 zone).

Forsythia gaudryi (GAILLARD, 1899)

Table 4. *Forsythia gaudryi* data from Hidas.

Locality:	No. inv.	Position:	L:	W:	Figure:
Hidas	MMP. 2022. 9. 1	M1-2	1.92	2.48	Pl. 1B
Hidas	MMP. 2022. 2. 1	M3	2.35	2.28	Pl. 1C
Hidas	MMP. 2022. 3. 1	m1	2.03	2.16	Pl. 1D

Description. **M 1-2**. The occlusal surface has a subrectangular outline with a rounded and convex lingual surface. There are two small incisions in the convex lingual surface. The protoloph and the metaloph converge towards the labial margin of the protocone. A short secondary ridge (protoconule) is directed anteriorly from the lingual part of the protoloph into the anterosinus. The metaloph is broad, two cusps (metaconule) are incorporated into this ridge. The posteroloph is poorly developed related to the other ridges. In the deepest part of the sinuses the enamel is not crenulated.

M3. It has a subtriangular outline, with rounded angles. The two main cusps are the protocone and the paracone. In the mesial surface there is the anteroloph, which extends from the protocone to the anterior surface of the paracone. The protoloph extends between the protocone and the paracone. Anteroloph and the protoloph are transversal and parallel. A small protoconule is developed on the lingual part of the protoloph. Hypocone is developed as a small cusp on the posterior slope of the protocone. The posterior slope of the paracone bears a weak mesostyle crista. The weakly developed posteroloph has a semicircular shape and closes the central basin. The surface of the central basin is crenulated by irregular secondary ridges.

m1. It has a trapezoidal outline, the posterior width is larger than the anterior one. The four main cusps are situated in the four angles of the occlusal surface: protoconid (antero-labial), metaconid (antero-lingual), hypoconid (postero-labial), entoconid (postero-lingual). Lower developed conulids are the mesostylid on the posterior slope of the metaconid and the mesoconid between the protoconid and the hypoconid. Mesoconid is connected to the labial main cusps via the ectolophid. It bears a transversal enamel ridge which reaches the labial margin. The protoconid and the metaconid are connected by the anterolophid and the metalophid. The anterolophid is stronger and anteriorly protuberant. The metalophid is thinner. The two main anterior cusps and the ridges enclose the small trigonid basin. There is a deep notch between the mesostylid and the entoconid. The central part of the occlusal surface is occupied by a large talonid basin. This basin is posteriorly bordered by a posterolophid.

Hypoconulid is not developed. Irregular secondary ridges start from the posterolophid and expand to the centre of the talonid basin.

Comments and discussion. *Forsythia* is a middle-sized flying squirrel genus, which is extremely rare. Referring to DAXNER-HÖCK (2010) it has been found in the faunas of the MN 7+8 zone. DE BRUIJN et al. (2003) described *Forsythia* from the Anatolian locality Çandir (MN6). ZIEGLER & FAHLBUSCH (1986) classified *Forsythia* aff. *gaudryi* from the Early Miocene MN4 localities of Rembach and Erkertshofen, which were later referred to *Aliveria luteyni* by DE BRUIJN (1999).

Forsythia evolved from the Early Miocene *Aliveria*, which is the common ancestor of the genera *Forsythia* and *Albanensia* (DE BRUIJN et al. 1980). In the Pannonian Basin *Forsythia* has only been reported from the MN7+8 locality Gratkorn (Austria), where a complete lower toothrow was described by (DAXNER-HÖCK, 2010) and an M1-2 was reported from Egerbocs (MN7+8, Northern Hungary) by HÍR (2001).

Family Cricetidae ROCHEBRUNE, 1883
Subfamily Cricetinae ROCHEBRUNE, 1883
Genus *Democricetodon* FAHLBUSCH, 1964
Democricetodon freisingensis (FAHLBUSCH, 1964)

Description. M1. Anterocone has two units, but they are not divided. Sulcus or groove are absent in the mesial surface. The lingual anteroloph reaches the base of the protocone and closes

Table 5. *Democricetodon freisingensis* data from Hidas.

Locality:	No. inv.	Position:	L:	W:	Figure:
Hidas	MMP. 2022. 10. 1	M1	2.21	1.41	
Hidas	MMP. 2022. 11. 1	M1	2.23	1.46	
Hidas	MMP. 2022. 12. 1	M1	2.02	1.34	
Hidas	MMP. 2022. 14. 1	M1	2.21	1.46	Pl. 1G
Hidas	MMP. 2022. 15. 1	M1	2.24	1.34	
Hidas	MMP. 2022. 16. 1	M1	2.07	1.18	
Hidas	MMP. 2022. 17. 1	M1	2.04	1.48	
Hidas	MMP. 2022. 18. 1	M1 fr.		1.41	
Hidas	MMP. 2022. 19. 1	M1 fr.		1.40	
Hidas	MMP. 2022. 20. 1	M2	1.61	1.43	
Hidas	MMP. 2022. 21. 1	M2	1.67	1.48	
Hidas	MMP. 2022. 22. 1	M2	1.71	1.60	
Hidas	MMP. 2022. 23. 1	M2	1.61	1.47	
Hidas	MMP. 2022. 24. 1	M2	1.50	1.32	
Hidas	MMP. 2022. 25. 1	M2	1.57	1.40	
Hidas	MMP. 2022. 28. 1	M3	1.26	1.30	
Hidas	MMP. 2022. 29. 1	m1	1.85	1.32	
Hidas	MMP. 2022. 30. 1	m1	1.90	1.33	
Hidas	MMP. 2022. 31. 1	m1	1.76	1.22	
Hidas	MMP. 2022. 32. 1	m1	1.96	1.40	
Hidas	MMP. 2022. 33. 1	m1	2.03	1.33	
Hidas	MMP. 2022. 34. 1	m1	1.92	1.41	
Hidas	MMP. 2022. 35. 1	m1	1.97	1.33	
Hidas	MMP. 2022. 36. 1	m1	1.90	1.26	
Hidas	MMP. 2022. 40. 1	m2	1.76	1.43	Pl. 1M
Hidas	MMP. 2022. 41. 1	m2	1.81	1.47	
Hidas	MMP. 2022. 42. 1	m2	1.75	1.39	
Hidas	MMP. 2022. 43. 1	m2	1.74	1.33	
Hidas	MMP. 2022. 44. 1	m2	1.75	1.44	
Hidas	MMP. 2022. 45. 1	m2	1.68	1.39	
Hidas	MMP. 2022. 49. 1	m2	1.72	1.43	
Hidas	MMP. 2022. 47. 1	m3	1.71	1.30	Pl. 1N
Hidas	MMP. 2022. 46. 1	m3 fr.	1.68		

the protosinus. In a similar way the labial anteroloph reaches the base of the paracone and closes the anterosinus. A well-developed parastyle is frequent (5 of 9 specimens). Anterolophule is branched (V-shaped) (8 of 9 specimens) or simple (only the lingual branch is found in 1 of 9 specimens). The two branches connect the anterior angle of the protocone and the two units of the anterocone. The labial spur of the anterolophule (anteromesoloph) is long, it reaches the labial margin, or the parastyle (8 of 9 specimens). In one case it is absent. Protolophule is double (4 of 9 specimens) or only the posterior branch is present (5 of 9 specimens). Paracone posterior spur is rare and remnant (short) (2 of 9 specimens). The long mesoloph is regular. It always reaches the labial margin. Entomesoloph is absent. Metalophule is short and posterior. A remnant anterior metalophule is found in 4 of 9 specimens, but it does not reach the hypocone, or the anterior arm of the hypocone.

M2. Lingual and labial arms of the anteroph reach the anterior base of the protocone and the paracone and close the anterosinus and the protosinus. The anterosinus is deeper. Double protolophule is regular. Mesoloph is long, reaches the labial margin (5 of 6 specimens), or short (1 of 6 specimens). Entomesoloph is absent. A double metalophule is frequent (4 of 6 specimens). In

two cases the anterior metalophule is a remnant and does not reach the hypocone or the anterior arm of the hypocone.

M3. Anterosinus and protosinus are closed. Protosinus is shorter. Protolophule is double. Mesoloph is long and reaches the labial margin. Entomesoloph is absent. Hypocone and metacone are reduced. Metalophule is anterior.

m1. The anteroconid consists of two or three units, but they are either not divided, or only superficial grooves are found in the mesial surface in the juvenile unworn molars. The labial anterolophid reaches the anterior base of the protoconid and closes the protosinusid. Lingual anterolophid is not developed and the anterosinusid is open. Anterolophulid is branched (V-shaped). The lingual branch runs to the lingual unit of the anteroconid. The labial branch runs to the labial unit of the anteroconid (4 of 8 specimens) or to the labial anterolophid (4 of 8 specimens). The long mesolophid is regular (reaches the lingual margin). The ectomesolophid can be complete and long (5 of 8 specimens) (it connects the anterior arm of the hypoconid and the labial margin of the toothcrown), or it can be short (3 of 8 specimens) (no connection with the anterior arm of the hypoconid).

m2. The labial anterolophid is well developed, reaches the anterior base of the protocone and closes the protosinusid. The lingual anterolophid is short and closes the small anterosinusid. The long mesolophid is regular (as in m1). The ectomesolophid is short, never reaches the anterior arm of the hypoconid. Posterosinusid is relatively wide and closed by the posterolophid.

m3. Anterolophids are developed as in m2. Mesolophid is long. A complete ectomesolophid is found in one case. In the other molar it is absent. Entoconid is reduced. Posterosinusid is ellipsoid and closed by the posterolophid.

Comments. The abstract of the *D. freisingensis* original diagnosis (FAHLBUSCH, 1964) is as follows: well developed and long labial eperon of the anterolophule of M1, double protolophule is frequent in M2, less frequent in M1; anteroconid is wide and indented in m1.

The possibility of the distinction of *D. gaillardi* and *D. freisingensis* is a subject of a long discussion. FAHLBUSCH (1964), BAUDELOT (1972) and HEISSIG (1995) underlined the similarity of the two species. HEISSIG (1995) realized the presence of the doubled anterolophulid of m1 in the type material of *D. freisingensis* (Giggenhausen) and the simple anterolophulid in the type material of *D. gaillardi* (Steinheim). Referring to MARIDET & SEN (2012) the distinctive characters among others include: the labial margin of the M1 the paracone and metacone are in line in *D. gaillardi*, but in *D. freisingensis* the metacone is situated in a more labial position. These observations can be useful in samples of statistically significant quantities. Taking into consideration that the debate concerning the synonymy of *D. gaillardi/D. freisingensis* is not closed, we do not follow the proposal of MARIDET (2003).

The earliest occurrence of *D. freisingensis* is described in Sansan (type fauna of the MN6 zone) (MARIDET 2003). The numeric age of Sansan is the subject of a long debate. Some published data are as follows: FEJFAR & HEINRICH (1997): 12.5 Ma, KRIJGSMAN et al. (1994, 1996): 12.7-13.0 Ma, KÄLIN (1997): 13.9 Ma, KÄLIN & KEMPF (2009): 14.1 Ma, SEN (1997): 15.2-15. Ma, STEININGER (1999): the top of MN6 at 13.5 Ma, base of C5ABn palaeomagnetic chron. We presume that the age between 13.9-14.2 Ma is the most probable, because it is in line with the first occurrence of *D. freisingensis* in the Swiss molasse: Niderwis, which is dated to 14.1 Ma by KÄLIN & KEMPF (2009). In the Bavarian molasse the FAD of this species

is dated to 14.2 Ma by PRIETO & RUMMEL (2016). The latest occurrences of *D. freisingensis* are documented in the MN8 faunas of southern Germany and Switzerland containing *Deperetomys*. These 12 faunas are listed by PRIETO (2012). The numerical age of them is estimated between 13.8 and 13.3 Ma (KÄLIN & KEMPF, 2009).

In the Pannonian Basin *Democricetodon* cf. *freisingensis* was reported from Mátraszőlős (HÍR & KÓKAY 2004, 2011), northern Hungary. The morphology of the Mátraszőlős finds is identical to the type population of *D. freisingensis* from Giggenhausen (after the description of MARIDET, 2003), but the dimensions are rather large. The Mátraszőlős localities were correlated with the latest part of the Badenian (HÍR et al., 2017). The report of *D. freisingensis* from Subpiatră by HÍR & VENCZEL (2005) is not reliable because the classification of the material was emended as *Democricetodon brevis* (HÍR, 2020). The occurrence of the species in the MN9 fauna of Rudabánya (KRETZOI & FEJFAR, 2005) is mysterious. The morphology is undoubtedly referable to *D. freisingensis,* but the main dimensions are smaller and the biochronological position is late MN9.

Democricetodon sp.

Table 6. *Democricetodon* sp. data from Hidas.

Locality	No. inv.	Position:	L:	W:	Figure:
Hidas	MMP. 22. 13. 1	M1	1.83	1.18	Pl. 1H
Hidas	MMP. 22. 26. 1	M2	1.47	1.25	
Hidas	MMP. 22. 37. 1	m1	1.62	1.13	Pl. 1L
Hidas	MMP. 22. 38. 1	m1	1.51	0.99	
Hidas	MMP. 22. 39. 1	m1	1.67	1.19	

Description. M1. Anterocone is undivided. The anterior surface is smooth, and the sulcus or groove are absent. The labial part is wider, the lingual part is narrower and continued in a lingual anteroloph. It reaches the base of the protocone and closes the protosinus. The labial anteroloph is situated between the labial base of the anterocone and the anterior base of the protocone. Anterolophule extends from the centre of the anterocone to the anterior angle of the protocone. The anterolophule bears two short and slightly developed labial eperons, both of them reach the anterior base of the paracone. Protolophule is posterior and connected to the centroloph close to the posterior angle of the protocone. Mesoloph is moderately developed. The tip of the mesoloph reaches the anterior base of the metacone. Metalophule is short and connected to the posteroloph.

M2. The lingual and labial anteroloph are both well developed and both reach the anterior surfaces of the protocone and the paracone closing the protosinus and the anterosinus. Protosinus is shallow, anterosinus is deeper. Protolophule is double. Mesoloph is long and terminates in a mesostyle. Metalophule is short and connected to the posteroloph.

m1. Anteroconid is simple. The mesial surface is smooth. Labial anterolophid is well developed and reaches the anterior base of the protoconid closing the protosinusid. Lingual anterolophid is absent. The lingual base of the anteroconid and the anterior base of the metaconid are close to each other and shut the anterosinusid. The anterolophulid-metalophulid-anteroconid structure is special. Anterolophulid is absent (2 of 3 specimens) or very short (1of 3 specimens). Metalophulid is connected to the anteroconid (3 of 3 specimens). Mesolophid is long and terminates in a mesostylid. Sinusid is closed by a cingulum. Poster-

olophid reaches the posterior base of the entoconid at a low level and the posterosinusid is not closed.

Comments and discussions. Initial observation of the metrical and morphological characteristics of the small sized *Democricetodon* finds of Hidas suggests they are close to *Democricetodon mutilus*. But in the territory of the Upper Freshwater Molasse (Southern Germany and Switzerland) no particular precedents exist for the coexistence of *D. freisingensis* and *D. mutilus*. The latter species has a long biochronological range from the late MN4 to the end of MN6 (MARIDET, 2003, KÄLIN & KEMPF, 2009; PRIETO & RUMMEL, 2016). The younger (MN8) occurrences are disputed. These are as follows:

Giggenhausen. There are five molars published. They were first classified as *D.* cf. *mutilus* nov. subsp. by FAHLBUSCH (1964). Among the morphological characteristics the wide anterocone in the M1 and the presence of ectomesolophid is mentioned in m1 by MARIDET (2003). He underlined the close relationship with *D.* cf. *mutilus* from Vermes 2.

Kleineisenbach. The three molars of *D.* cf. *mutilus* reported were regarded as the descendant of *D. mutilus* by FAHLBUSCH (1964). Referring to the description of PRIETO (2007) the frequent lingually directed anterolophulids in m1 and the frequent interrupted ridges are characteristic in the Kleineisenbach material.

Vermes 2. The material consists of one lower toothrow and an m3. It was classified as *D.* cf. *mutilus* (ENGESSER et al. 1981). In more recent descriptions (MARIDET, 2003, PRIETO, 2007) the occurrence of an enamel ridge in the mesial surface of the M1, the poorly developed ectomesolophids, the lingually directed anterolophulids in m1 are mentioned. According to PRIETO (2007) the Vermes 2 small sized *Democricetodon* can be classified as a new species. MARIDET (2003) drew a different conclusion: he confirmed the original classification. The biochronological position of Vermes 2 is the subject of a long debate. The list of different concepts is the following: AGUILAR (1982): MN 7+8; ENGESSER et al. (1981): MN8; KÄLIN (1997): MN5; KÄLIN & KEMPF (2009): MN5; HEISSIG (1997): MN5; MARIDET (2003): MN 7+8; PRIETO (2007): MN8.

The *Democricetodon* cf. *mutilus* materials of the three localities discussed above are limited, as is the sample from Hidas. Nevertheless, we can conclude that a close relationship of the Hidas finds with *D.* cf. *mutilus* from Giggenhausen, Kleineisenbach and Vermes 2 is not probable, because some characteristic morphological elements of the three Upper Freshwater Molasse assemblages are not found in Hidas, e.g., enamel ridge in the mesial surface of M1, lingually directed anterolophulids in m1, ectomesolophids in lower molars, and interrupted ridges.

Megacricetodon minor (LARTET, 1851)

Table 7. *Megacricetodon* data from Hidas.

Locality:	No. inv.	Position:	L:	W:	Figure:
Hidas	MMP. 2022. 27.1	M2	1.34	1.12	
Hidas	MMP. 2022. 5.1	m2	1.29	0.98	

Description. M2. It has a rectangular outline, which is smaller and more elongated than the M2s of the *Democricetodon* species. The lingual and labial arms of the anteroloph reach the anterior base of the protocone and the paracone and close the anterosinus and the protosinus. Protosinus is shallow, anterosinus is deeper. Protolophule is posterior. Mesoloph is short and reaches the anterior surface of the metacone. Paracone posterior spur is

short and weak. The lingual and labial sinuses are closed by the weakly developed cingulums. Metalophule is transversal, it starts from the centre of the hypocone. Posteroloph reaches the posterior base of the metacone.

m2. It has a rectangular outline, which is smaller and more elongated than the m2s of the *Democricetodon* species. In the mesial surface the labial anterolophid is complete and closes the anterosinusid. Lingual anterolophid is short, no protosinusid. Mesolophid is short and reaches the posterior base of the meta-

conid. Posterolophid reaches the posterior base of the entoconid and closes the posterior sinusid. Lingual sinusid is open, labial sinusid is closed by a cingulum.

The sample is modest, but it is enough for the classification. *Megacricetodon minor* is a frequent and regular element of the Middle Miocene vertebrate faunas in the Pannonian Basin from the MN5 to the MN7+8 zones. Only minor morphological differences are visible in this series of *Megacricetodon minor* populations (Hír pers. obs.).
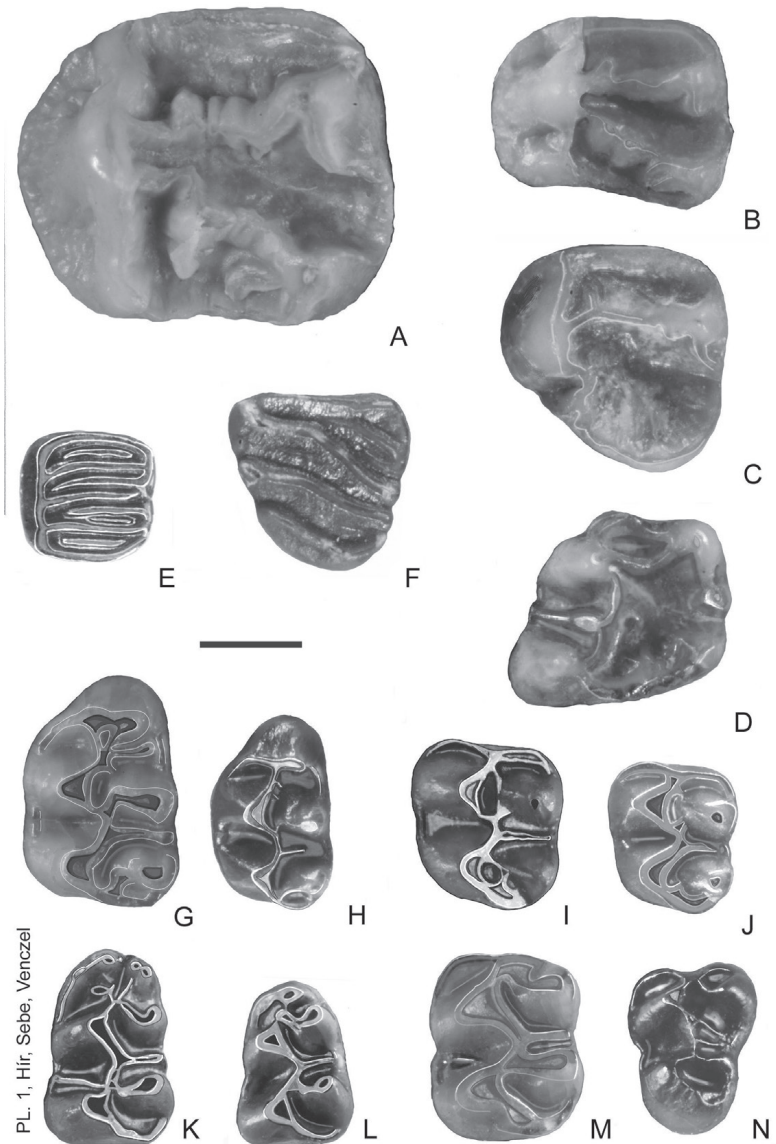

PL. 1, Hír, Sebe, Venczel

Plate 1. Occlusal surfaces of the studied Rodent molars. All are figured in the left side position. The originally right-side molars are graphically reversed. Scale bar = 1mm

	Taxa	Position:	No. inv.	
A.	*Albanensia albanensis* (MAJOR, 1893),	M1,	MMP. 2022. 1. 1.	reversed
B.	*Forsythia gaudryi* (GAILLARD, 1899),	M1-2,	MMP. 2022. 9. 1.	reversed
C.	*Forsythia gaudryi* (GAILLARD, 1899),	M3,	MMP. 2022. 2. 1.	
D.	*Forsythia gaudryi* (GAILLARD, 1899),	m1,	MMP. 2022. 3. 1.	
E.	*Paraglirulus werenfelsi* ENGESSER, 1972	M2,	MMP. 2022. 7. 1.	reversed
F.	*Myoglis meini* (DE BRUIJN, 1966),	m3,	MMP. 2022. 5. 1.	reversed
G.	*Democricetodon freisingensis,* (FAHLBUSCH, 1964),	M1,	MMP. 2022. 14. 1.	reversed
H.	*Democricetodon* sp.,	M1,	MMP. 2022. 13.1.	
I.	*Democricetodon freisingensis* (FAHLBUSCH, 1964),	M2,	MMP. 2022. 20. 1.	
J.	*Democricetodon* sp.,	M2,	MMP. 2022. 26. 1.	
K.	*Democricetodon freisingensis* (FAHLBUSCH, 1964),	m1,	MMP. 2022. 33. 1.	reversed
L.	*Democricetodon* sp.,	m1,	MMP. 2022. 37. 1.	
M.	*Democricetodon freisingensis* (FAHLBUSCH, 1964),	m2,	MMP. 2022. 40. 1.	
N.	*Democricetodon freisingensis* (FAHLBUSCH, 1964),	m3,	MMP. 2022. 47. 1.	reversed

Geologia Croatica

5. DISCUSSION

5.1. The age of the fauna

The coexistence of *Albanensia albanensis*, *Forsythia gaudryi* and *Democricetodon freisingensis* is referable to the MN7+8 zone (13.5–11.1 Ma, STEININGER 1999) and a late Badenian age. Similar assemblages in the Pannonian Basin are the faunas from Mátraszőlős with *D.* cf. *freisingensis*., *D. brevis*, *Albanensia* sp. and a rich late Badenian mollusc fauna (HÍR & KÓKAY 2004, 2011). The microvertebrate material of Hidas strengthens the earlier ideas on the late Badenian age of the Hidas Formation in the Mecsek Mts., which has been estimated as between 13.3–13.7 Ma (SELMECZI et al., 2023), and brackets the age of the unit to ~13.5–13.3 Ma.

5.2. Palaeoenvironmental reconstruction

The fossil lissamphibians and reptiles from Hidas appear as a low diversity assemblage, and each taxon is represented by only a few specimens, with the exception of the alytid frog *Latonia seyfriedi*, which is the most abundant species in the oryctocoenosis. A proportion of the recorded amphibians represent aquatic (e.g., *Palaeobatrachus*) or semiaquatic forms (e.g., *Pelophylax*), while other taxa probably preferred periaquatic environments (*Lissotriton* sp., *Latonia seyfriedi*). The sedimentary facies of the fossil-bearing layer – composed of lime mud, lacking bedding, with a crumbly structure – together with the enclosed freshwater gastropod fauna, indicates a shallow pond or a paludal environment, where the listed aquatic herpetofauna could find a suitable habitat. The additional vertebrate fossils had probably been washed into the pond from the immediate surroundings. The pelobatid frog (*Pelobates sp.*), based on the preference of recent taxa, might have been a burrower in the aerated sandy soils along lakes or rivers. The small number of indetermined lizards and snakes occurred probably around these aquatic habitats. Nevertheless, the lack of natricinae snakes (which prefer freshwater) is noteworthy, as well as the absence of elapids and viperids. From the rodent taxa, glirids and flying squirrels as well as *Democricetodon* and *Megacricetodon* indicate humid arboreal vegetation around the site (WEERD & DAAMS 1978, DAAMS et al. 1988). Additionally, the cited presence of the alligatoroid crocodylian *Diplocynodon* (VADÁSZ 1935, KORDOS 1985), according to MARCKWICK (1998), indicates a relatively mild palaeoclimate: a mean annual temperature of at least 15.3 °C with a mean temperature of the coldest month of at least 5.5 °C. This shows that although the Hidas Formation was deposited after the Miocene Climatic Optimum (17–15 Ma, ZACHOS et al. 2001), the climate was still warm enough for subtropical taxa to inhabit the area. In fact, the accumulation of the formation took place just before the Miocene warm period ended in Central Europe (~14–13.5 Ma), with an increase in seasonality, growing oscillations in humidity and the extinction of numerous thermophilic groups (BÖHME 2003).

5.3. Palaeogeographical relationships

It was by the end of the Middle Miocene that the lithospheric units comprising the basement of the Pannonian Basin reached a geographical configuration that more or less corresponds to the present-day situation (HORVÁTH et al., 2006). At the time of the accumulation of the Hidas Formation, the palaeogeography of the Pannonian Basin is described as an archipelago in the Central Paratethys (HÁMOR, 2001; KOVÁČ et al., 2007, 2017, Fig. 4; NAGYMAROSY & HÁMOR, 2012, Fig. 3.16), with the Mecsek Mts. being one of the islands. Before the studied time period,

around the end of the early Badenian, reconstructions indicate that sea troughs of bathyal depths existed in the Mecsek area, with connections towards the Mediterranean (BÁLDI et al., 2002, SZABÓ et al., 2022). The faunal assemblage of Hidas desribed here shows no characteristics typical of insular faunas, e.g., gigantism or endemism. Most of the taxa are identical to those reported from coeval assemblages in north Hungary and Western Romania (HÍR et al., 2016, 2017, 2019). This means that the Mecsek area had some ecological connections with the northern and eastern part of the Pannonian Basin, and the sea branches or embayments of the Central Paratethys within the archipelago did not form a barrier against the distribution of microvertebrates. Considering the above cited palaeogeographic information, the corridor could have been located towards the NE from the Mecsek Mts., across the elevated basement blocks of central Hungary shown in NAGYMAROSY & HÁMOR (2012).

6. CONCLUSIONS

The fossil microvertebrate material of Hidas is modest, but it allows some conclusions to be drawn from the data. The fauna and the enclosing sediment indicates varied environments, lakes or swamps surrounded by forests. The biochronological position of the fauna can be classified as MN 7+8 based on the presence of *D. freisingensis, Forsythia gaudryi* and *Albanensia albanensis*. Together with the Badenian molluscs of the formation, this can be correlated to the late Badenian in the regional, Central Paratethys stratigraphy, or to the lower Serravallian in standard global stratigraphy. This interpretation is in accordance with the earlier classifications based on the stratigraphic position and the mollusc fauna. The studied material represents the first middle Miocene microvertebrate fauna from southern Hungary. The rodent taxa described herein are well known from the Middle Miocene faunas of northern Hungary and from the Upper Freshwater Molasse of southern Germany and Switzerland. From these findings we can conclude that ecologically, the mainland of the Mecsek region was not an isolated territory during this time period, and some passable corridors (land bridges) existed from here towards other parts of the Pannonian Basin that allowed faunal exchange.

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