

FINAL REPORT
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Project leader: Attila Ósi

Host institution: Hungarian Natural History Museum (MTM)

Project title: **Quest for Mesozoic vertebrates in Hungary**

Participants:

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Réka Kalmár (applied technician, 01.01.2016.-31.11.2019)

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1. Summarized goals of the four-years project (also listed in the original application):

- 1) Project focuses on four main target areas: Iharkút, Ajka, Villány and Alsópere to find Mesozoic vertebrates.
- 2) Continue the systematic excavations in Iharkút (Sz-6, Sz-4 sites) and to prospect for further bone yielding layers of the Csehbánya Formation.
- 3) 3D mapping of the discovered fossils (bones, coprolites, larger plant fossils) to provide an extensive 3D digital map.
- 4) Find and excavate natural outcrops of the Ajka Coal Formation between Ajka and Úrkút.
- 5) Conduct large-scale, annual excavations in the construction site at Villány and screen-washing of the bone-yielding beds of the Mészhegy Formation and Templomhegy Dolomite.
- 6) Excavation and screen-washing of the potential beds of the Alsópere Bauxite and Tés Clay Formations.
- 7) Sedimentological description of all the previously and newly excavated vertebrate sites.
- 8) Taxonomical, systematic and paleobiological descriptions of the identifiable fossils discovered from all the mentioned localities.

2. Results directly related to the project

2.1. Iharkút

2.1.1. Fieldwork

The research team carried out three-week excavations at the Iharkút vertebrate site (Upper Cretaceous, Csehbánya Formation, Bakony) annually, with 22-26 participants. An area of nearly 300 m² potential layers have been excavated and ca. 4.000 new vertebrate remains, hundreds of coprolite finds and plant remains enriched the collections of the Hungarian Natural History Museum. Among the most valuable finds are four partial skulls. Two of these belong to the two crocodile species known only by fragmentary findings, the third is the most complete armored dinosaur skull from Iharkút to date, and the fourth is most probably belongs to *Ajkaceratops*. Between 2016 and 2019, a digital 3D map has been also made at the excavated area. Thousands of bones and teeth were measured with a computerized theodolite machine, which were evaluated by different GIS methods using the Jewel program (B.G.). This study gives an insight into the usability of the 3D modelling methods in fossil mapping

from the measuring processes to the spatial analysis creating 2D or 3D model (Albert et al. 2018).

As an integral part of the excavation, screen-washing was also carried out, contributing thousands of new micro-vertebrate finds (primarily teeth, bone fragments, and eggshell fragments). Final preparation of the specimens has been done in the laboratories of MTM and ELTE.

Collection at the Iharkút Sz-4 site was also continued with the utilization of a three dimensional coordinate system and the measurement of the finds, similarly to the Sz-6 site. Moreover, beside numerous other remains, the excavation yielded important finds, such as the second mandible of the rare lizard *Chromatogenys*, also providing valuable information for taxonomical studies.

In order to widen our knowledge about the Late Cretaceous flora, fauna and paleoenvironment of „Bakony Island”, an extensive prospecting for other outcrops of the Csehbánya Formation (that differ from the currently studied sites stratigraphically and/or spatially) has been done. Thirteen outcrops indicated on geological maps have been surveyed and sampled, of which currently one has indication of vertebrate remains. Prospecting/sampling will continue on these, as well as on other outcrops.

2.1.2. Sedimentary environment

Detailed sedimentological investigation of the Late Cretaceous vertebrate locality of Iharkút was conducted by G.B. Twelve stratigraphic sections were investigated in 15-20 m in length indicating that the terrestrial deposits exposed by Iharkút open pit were formed in an anastomosing fluvial system, where the most important vertebrate site (site SZ-6) were interpreted as a lag deposit formed during an episodic high density flash flood event (Botfalvai et al. 2016).

2.1.3. Fauna

In 2017, a comprehensive study on the ichthyofauna of the Late Cretaceous (Santonian) Iharkút vertebrate locality was published (Szabó and Ósi 2017). These specimens represent at least 9 different fish taxa, among which pycnodontiforms and lepisosteids were already known and published in detail (Szabó et al. 2016 a, b). Since the published material is composed almost completely by micro-remains, and the study reveals a diversity for the Iharkút fish fauna far higher than it was previously expected, the study highlights the importance of screen-washing at other European vertebrae fossil sites.

M.R. and A.Ó. performed the documentation of primitive neosuchian crocodylians from Iharkút belonging to Allodaposuchidae and Paralligatoridae. The first partial to near complete skulls recovered during the 2018 fieldseason are by far the best preserved remains of these taxa and have been generally documented as well. Altogether, the material from Iharkút represents one of the anatomically best known and oldest primitive neosuchians from the Late Cretaceous of Europe and are therefore critical for reconstructing the phylogeny and early evolution of modern crocodylian families (Rabi et al. in prep. a, b).

M.R. prepared anatomical descriptions and phylogenetic analyses of turtles belonging to the stem-turtle *Kallokibotion* and the side-neck turtle families Dortokidae and Bothremydidae from Iharkút. The photographic documentation and graphic illustration of the material has been partially completed as well. The review of skeletal anatomy suggests that the Iharkút dortokid is a new species and a preliminary phylogenetic analysis reveals that it is closely related to an undescribed species from the Late Cretaceous (Maastrichtian) of Transylvania. The study of Iharkút turtles raised some phylogenetic methodological questions in relation to

the analysis of homoplastic traits in morphological taxon-character datasets. The phylogenetic analyses of the Iharkút turtles involved a global morphological revision of related turtles and resulted in a comprehensive dataset and for the first time demonstrate that Mesozoic turtle diversification was driven by the successive break-up of the Pangea supercontinent secondarily overwritten by intercontinental dispersals during the Cenozoic.

Cranial morphometrics, tooth wear pattern, and jaw muscle reconstruction of different species of ankylosaurs have been done to reveal the diversity and convergences in the evolution of feeding adaptations in ankylosaurs. Results demonstrated that dental occlusion in ankylosaurs did exist from the Early Cretaceous and their jaw mechanism was much more complex than previously thought (Ósi et al. 2016a).

New, articulated ankylosaur armor specimens from Iharkút allowed to distinguish the sacral armor of *Hungarsaurus* and *Struthiosaurus*. In addition, the new specimens revealed that the pelvic armor of ankylosaurs could have been much more diverse than previously thought and some characteristic armor elements can be used for generic-level taxonomy as well (Ósi and Pereda-Suberbiola 2017).

Research group published the taxonomy, taphonomy and paleoecological aspects of the 12 partial and incomplete ankylosaur skeletons discovered in Iharkút (Ósi et al. 2019a). Also with the help of these skeletons, the social lifestyle and paleoecology of this enigmatic dinosaur group were analysed in a review paper. Our holistic approach showed that combining palaeontological and biological information is essential and can provide new insights into the behavioural ecology of long extinct vertebrates (Prondvai et al. submitted).

A comprehensive study involving several different approaches and techniques (thin sections, SEM, XRF, quantitative histological analyses) has been performed and published on the eggshell fragments recovered from Iharkút. This study demonstrated the high diversity of eggshell types originating from dinosaurs, squamates and crocodiles and that the most frequent morphotype belongs to some kind of theropod dinosaurs (Prondvai et al. 2017).

A sauropod tooth has been discovered in Iharkút that possibly belongs to a relatively basal titanosauriform. Although a few footprints are known from the Adriatic-Dinaric Carbonate platform (Solt et al. in press), this tooth is the only body fossil from the late Cenomanian-Late Campanian period of Europe indicating that not the disappearance of this group but rather preservational biases are responsible for the lack of sauropod remains from this critical 22 My long period (Ósi et al. 2017).

Tooth histology of the Iharkút crocodiles revealed significant difference between the enamel structure and growth of these four, ecomorphologically different forms. Most importantly, structures similar to the Hunter-Schreger bands characterizing mammalian enamel and the so called wavy enamel first described in the herbivorous hadrosauroid dinosaurs were also observed in the *Iharkutosuchus* teeth. The fact that the former clades are all characterized by effective oral food processing suggests that these dental histocharacters are feeding-related evolutionarily adaptive features that convergently appeared in these distantly related clades (Horváth et al. 2019).

More than 2000 coprolites have been found in Iharkút and analyzed by a wide range of methods. Results pointed out that most of the coprolites are from aquatic carnivorous animals (e.g. lepisosteiform fish, *Pannoniasaurus*). Inclusions within the coprolites resulted in some interesting fossils including gar scales or coalified plant fossils as well (Segesdi et al. 2017).

The morphometric, microstructure and wear pattern analysis of neornithischian dinosaur teeth from Iharkút has been documented. Results demonstrate that the teeth of the ceratopsian *Ajkaceratops* are practically indistinguishable from those of *Mochlodon* based on morphometric or microstructural characters, only wear pattern can be used to distinguish the teeth of the two herbivorous animals (Virág and Ósi 2017).

2.2. Ajka

2.2.1. Fieldwork and vertebrate fauna

Research team has begun exploring and documenting detailed sedimentological and paleontological findings of the Upper Cretaceous Ajka Coal Formation in the Csinger Valley. A detailed geological profile of the excavation was made and large quantities of samples were screen-washed from several layers. Thousands of vertebrate fossils have been found, including micro- and macroscopical specimens. At present all groups discovered in Ajka (*Lepisosteiformes*, *Pycnodontiformes*, *Pannoniasaurus*, *Iharkutosuchus*, neosuchian crocodiles, turtles, paravian and nodosaurid dinosaurs) overlaps with the much more diverse fauna from Iharkút. This clearly indicates that although different environments existed in the two areas, these taxa were most probably present in both environments (Ósi et al. 2016b, Ósi and Botfalvai submitted). The sedimentological description of the newly created outcrops of the Ajka Coal Formation and the detailed comparison of the microvertebrate assemblages from Ajka and Iharkút are tasks still to be done.

2.2.2. Amber inclusions

During the last 150 years, a high number of amber, known as „ajkaite” was collected from the Late Cretaceous (Santonian) Ajka Coal Formation (Ajka-Csingervölgy, Bakony Mts., Hungary). An extremely wide range of inclusions was discovered inside the amber stone specimens. Three stones were investigated for possible vertebrate inclusions (e.g. hair, feathers, etc.) in the Deutsches Elektronen SYNchrotron (DESY, Hamburg, Germany). However, vertebrate inclusions are yet not discovered, two of the 3D models, revealing a *Hersiliidae* spider and a pseudoscorpion, are currently under study (Szabó 2019a.; Novák et al., in prep.).

2.3. Villány

2.3.1. Sedimentology

The sedimentology and taphonomy of the Middle to Late Triassic Villány vertebrate sites (Construction and Road-Cute sites) were analysed in detail. Results indicate that the sediments of the Construction vertebrate site were formed in a subtidal to peritidal zone of the inner ramp environment, while the depositional environment of the Road Cut section represents a nearshore, shallow marine environment characterized by high siliciclastic input from the land (Botfalvai et al. 2019).

2.3.2. Fauna

The Middle and Late Triassic fish fauna of the two Villány vertebrate sites is comparatively described. The unearthed fauna (including piscivorous and durophagous sharks, and various osteichthyans) reveals a marked faunal shift between two fossil-bearing formations at the boundary of the Ladinian and the Carnian (Szabó et al. 2019).

The placodont remains from the Triassic of Hungary have been described in detail. The oldest specimen, a maxilla fragment from the Late Anisian of Forrás Hill (near Felsőörs,

Transdanubian Range) is identified as *Paraplacodus broilii* based on dental morphology. From the Carnian of the same tectonical unit, there are two isolated teeth and a dentary fragment which belong to *Placochelys placodonta*. The youngest specimen is a placochelyid tooth fragment from the Rhaetian of the Keszthely Mountains.

The richest assemblage of placodont remains is from the Ladinian of the Villány Mountains. Cranial elements are referred to as *Cyamodus* sp. Teeth that occur in this site are similar to that of *Cyamodus* sp. described from Slovenia and both assemblages are among the last occurrences of the genus in the European Triassic. The Villány site is considered as a gap locality because of the rarity of Ladinian placodont occurrences in the German-Alpine sedimentary basins and a new, unsampled area along the northern coast of the Tethys playing an important role in the biogeography of placodonts (Gere et al. in press).

M.S. described the new eosauroptrygian semi-aquatic sauropsid remains from the Middle Triassic (Ladinian) Templomhegy Dolomite of Villány, which were unearthed during the systematic fieldworks of previous years. The occurrence of *Nothosaurus* cf. *mirabilis*, *N.* cf. *marchicus*, *N. giganteus*, and *Simosaurus* sp. has been pointed out in the fauna. The faunal composition from Villány highly resembles that of the Upper Muschelkalk of Germanic Basin. Along with the widespread taxa, the possible remains of *N. marchicus* prove the hypothesis that this small-sized *Nothosaurus* was present outside of the Germanic Basin too. Besides the isolated elements, a probably associated skeleton of a small-sized eosauroptrygian specimen is also known. In the case of these semi-aquatic reptiles, habitat partitioning is suggested based on the different presumed sizes of the adult individuals, moreover, the diverse dentition and skull morphology also indicate trophic specialization (Segesdi and Ósi submitted).

Archosauromorph fossils, including the enigmatic, long-necked reptile *Tansytropheus* have been described from Villány (Ósi et al. submitted). These fossils are of great importance for a better understanding of the poorly known semi-aquatic to terrestrial vertebrate fauna of the Middle to Late Triassic of Central Europe.

2.4. Alsópere

The fourth main goal of the project was to identify and survey an outcrop of the Albian Alsópere Bauxite Formation which yielded a ziphodont crocodyliform tooth in 1950. As a result of an extensive study of geological maps, reports and databases, the original site has been identified and sampled. Based on teeth and bone material, a surprisingly diverse assemblage was recovered, including hybodontid sharks, lepisosteiform/semionotiform, pycnodontiform, amiiform, and indeterminate fishes, more ziphodont ?paralligatorids/?atoposaurids, indeterminate archosaurians, ?theropods. Moreover, hundreds of indeterminate remains were also recovered from the relatively small (~50 kg) sample.

This composition of the assemblage indicates that the enclosing sediment was not deposited on land (as expected, considering that these red bauxitic clays were traditionally assigned to the top of the Alsópere Bauxite Formation) but rather in a shallow marine/lagoon environment where some taxa lived while the remains of others were washed/reworked into. Thus these fossiliferous red bauxitic clays might actually belong to the overlying Tés Clay Marl Formation and contain both terrestrial and marine taxa (Makádi et al. 2019). Other outcrops of the Alsópere Bauxite and of the overlying Tés Clay Marl Formation were surveyed and sampled. Among these, one of the Alsópere sites also yielded some microvertebrate material and will be subjected to large-scale sampling.

The material is important because with their Albian age they are unique in the Carpathian Basin and its surrounding. Nevertheless, more complete specimens could also provide information about the evolution of lineages which are present 15 million years later in the Iharkút fauna on the same tectonical and probably palogeographical unit.

3. Other results related to the project

Beside the four main target areas, various other vertebrate findings in Mesozoic sediments have been published that also enrich our knowledge on the Mesozoic vertebrate diversity of Central Europe.

3.1. Triassic vertebrates from the Keszthely Mountains

The collection of the Mining and Geological Survey of Hungary houses several yet undescribed Mesozoic vertebrate finds. Though these are scarce remains, they indicate (as it was with the Villány Triassic marine vertebrate site) the potential of these localities. Two of these are from Triassic rocks at Rezi in the Keszthely Mountains. Besides the above mentioned placodont tooth, a partial fish imprint from the Norian Rezi Dolomite Formation was determined as a “ganoid type” Actinopterygia indet. (Gere et al. 2019).

3.2. The Gerecse crocodile

Together with project collaborators A.Ö. and M.R. described a partial skeleton of a large bodied marine thalattosuchian crocodylomorph from the Early Jurassic of the Gerecse Mountains as a new taxon *Magyarosuchus fitosi* (Ősi et al. 2018). The detailed anatomical and phylogenetic study of this species highlighted its transitional morphology and therefore great importance for understanding the early evolution of pelagization in marine crocodylomorphs (Ősi et al. 2018).

3.3. Fish research

Lower Cretaceous (Valanginian-Hauterivian) fish remains, collected in 1960-62 at Hárskút were described (Szabó 2017). The first record of the hexanchoid genus *Crassodontidanus* from the Jurassic of Magyaréregy (Mecsek Hills, Hungary), together with the revised summary of hexanchiform fossil record of Hungary was published (Szabó 2018). A Late Jurassic fish fauna, unearthed at the long-known Eperkés Hill (Bakony Mts., Hungary; Pálihálás Formation), including both chondrichthyans and osteichthyans, revealing the oldest Hexanchidae shark (*Notidanodon* sp.), was detailed by Szabó (2019b). A re-discovered, articulated specimen of *Dapedium* sp., found in the Early Jurassic (Toarcian) Úrkút Manganese Ore Formation was published that significantly contribute to the evolutionary history of Dapediidae fish through the end-Triassic Mass Extinction (Szabó and Pálfy 2019).

3.4. Paleoecology in the Maastrichtian Hateg Island

As an area closely related to Iharkút, a detailed taphonomical investigation of the famous vertebrate assemblage of Tuste site (Maastrichtian, Hateg Basin) were conducted. The results of this study answered several questions connected to the bone accumulation processes at the site and provided further evidences that the megaloolithid eggs and the hadrosaur hatchling bones were buried at the same time due to the same events indicating their common origin (Botfalvai et al. 2017).

3.5. Filling the Cenomanian-Campanian vertebrate hiatus

A Coniacian sauropod tracksite have been discovered and published from the Island of Hvar. The new trackways further strengthen the earlier hypothesis that sauropods were present in

the western Tethyan archipelago during the late Cenomanian – late Campanian period (Solt et al. in press).

In addition, a diverse Turonian and a possibly Coniacian-Santonian vertebrate fauna have been discovered in the northern Calcareous Alps, Austria. These assemblages are of great importance since continental vertebrates from the Cenomanian to Santonian interval of Europe are extremely scarce, and provide a small but significant link between older and younger vertebrate faunas in the region (Ősi et al. 2019b).

4. Further results

4.1. Gábor Botfalvai completed his PhD defense in 2018.

4.2. Kinga Gere completed her MSc defense and became a PhD student of the Eötvös University in 2018

4.3. Martin Segesdi completed his MSc defense in 2020.

5. Presentation of the results

Research team presented their results among others on the following international meetings:

- European Association of Vertebrate Paleontologists, Lisabon, Portugal
- Hungarian Paleontological Meetings (anually)
- 8th Symposium about Dinosaur Palaeontology and their Environment, Burgos, Spain
- 8th Secondary Adaptation of Tetrapods to Life in Water, Berlin, Germany
- Taphos 2017, Vienna, Austira
- MTE 13 - Mesozoic Terrestrial Ecosystem and Biota, Bonn, Germany

6. Publications cited here and related to the project

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