

A new bothremydid (Chelonia: Pleurodira) fossil assemblage from the Late Cretaceous (Santonian) of Hungary – additional studies in the historical paleobiogeography of Late Cretaceous bothremydids

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Abstract — At the only Late Cretaceous (Santonian) dinosaur locality of Hungary in the Bakony Mountains (Iharkút locality) turtle remains are the most abundant fossils and because of their preservation they are also the best represented group so far. Since 2000 three partial skulls, two isolated lower jaws, several hind limbs, two partial plastrons, numerous shell fragments and other postcranial bones have been discovered. The skulls and the lower jaws belong to a presently unnamed new bothremydid taxon while the identification of the isolated postcranial material is in progress. The Iharkút bothremydid is a new taxon and a member of the so-called *Bothremys*-group. According to a preliminary cladistic analysis this is the sister taxon of *Foxemys mechinorum* from the Late Cretaceous deposits of southern France. The newly discovered material suggests that members of the *Bothremys*-group first appeared in the Mediterranean and the appearance of bothremydids in North America at the same period can be explained by a sudden migrational event from Europe.

Introduction

The Bothremydidae family is a group of well represented pleurodirian fresh water turtles in the Late Cretaceous herpetofaunas. Because of their unspecialized ecological function the group was widespread in the Late Cretaceous ecosystems. The massiveness of their typical turtle skull helps on the fine preservation during fossilization and further the identification of the material.

The bothremydid fossils from Iharkút were discovered by the team of the Hungarian Dinosaur Expedition between 2000 and 2005. We have collected a large amount of fossils including three partial skulls and two lower jaws belonging to the same taxon. Two of the discovered plastron fragments can also be identified as bothremydids. We regard the isolated postcranial bones (hind limbs, pectoral and pelvic elements, vertebrae) only indirectly as bothremydids because no other turtles are represented so far by identifiable material at Iharkút.

Here we shortly describe the most complete skull (MTM-GYN56) and lower jaw (MTM-GYN57) and make comparisons with *Foxemys mechinorum* which is very probably the closest relative of the Iharkút form. The biogeographical importance of this material is also discussed as the Iharkút bothremydid further clear the questionable biogeographical origin of Santonian bothremydids in North America. All material housed in the Hungarian Natural History Museum (MTM).

Geological setting

The locality is situated near the village Iharkút, in the Bakony Mts, Western Hungary. In the fossil site

the open-pit mining of the bauxite exposed the Csehbánya Formation, which contains the bone-yielding layers. The bones are concentrated in a flood plain and channel deposit consisting of sand, silt, clay and dolomite pebbles, more or less cemented, representing a high-energy depositional environment. Occasionally turtle remains can also be unearthed from siltstone which represents low-energy depositional environment. The age of the bone containing sediments are Santonian which is based on palynological examinations (Knauer & Siegl-Farkas, 1992) and on (Szalai, 2005) paleomagnetic age determination.

Systematic paleontology

Testudines Linnaeus, 1758
Pleurodira Cope, 1864
Pelomedusoides Cope, 1868
Bothremydidae Baur, 1891

Skull morphology

The newly discovered taxon from Hungary is a member of the Pleurodira group because the pterygoid bears a well developed trochlear process, there is a medial process on the quadrate and the foramen palatinum posterius is situated posterior to the orbits (Gaffney, 1979). It also belongs to the Pelomedusoides group because the skull lacks the nasal bones and the prefrontals join in the midline (Gaffney & Meylan, 1988). The skull shows distinct bothremydid features: the quadrate and the basi-sphenoid covers the prootic, the eustachian tube is

separated from the incisura columellae auris (Tong et al., 1998).

General features of the skull — The skull is roughly triangular in dorsal view and slightly slopes anteriorly. The interorbital space is wide, the shape of the well preserved left orbit is subcircular in

lateral view. The temporal cavity is wide and dorsally to this fossa the parietals are damaged. The skull completely lacks the premaxilla, the postorbital, the quadratojugal and the vomer. The left quadrate is damaged.

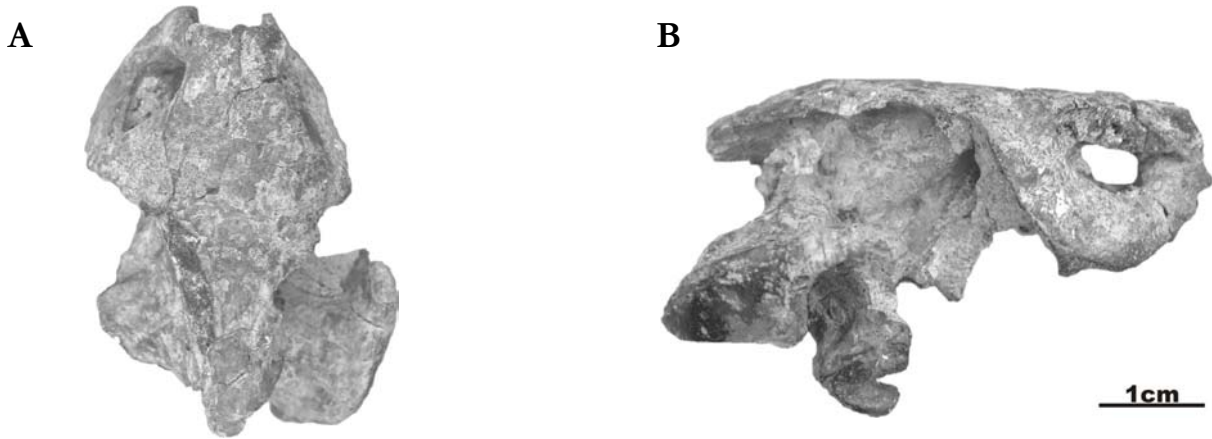


Fig. 1 — The most complete skull of the newly discovered Iharkút bothremydid (GYN56). A: dorsal view, B: right lateral view.

Dermal roofing elements — The prefrontals are rectangular and the apertura narium externa is visible in dorsal view. The prefrontals contact the maxilla laterally, anterior to the orbits. The suture between the prefrontals and the frontals is not visible. Although the skull lacks the premaxilla it seems that the apertura narium externa does not form a prominent separated process. The lateral edges of the parietals are damaged and the suture for the frontals can not be identified. The prefrontal contacts the postorbital anterolaterally. The postorbital is only anteriorly preserved and contacts the jugal with a ventrally visible, roughly antero-posterior suture. The right jugal is well preserved, the left one is only posteriorly damaged. The jugal is a horizontally short element and does not take part in the cheek emargination.

Palatal elements — The maxillae contact the anterior and lower margins of the orbits and form the triturating surface with the palatines. The palatine contacts the maxilla with a transverse suture but the suture with the pterygoid is not visible.

Palatoquadrate elements — There is a pleurodirian pterygoid flange which is wide but do not reach the line of the quadrate laterally. The pterygoid muscle chamber is large and it medially contacts the basisphenoid. The basisphenoid-basioccipital suture is V shaped. Only the right quadrate is preserved, the cavum tympani is not complete. The incisura columellae auris is an undeveloped and

hardly recognizable fissure which is not completely closed. The antrum postoticum is large and its anterior opening is wide. There is an oval, not very well preserved fossa ventral to the incisura which might be the precolumellar fossa.

Discussion — The morphological features suggest that the bothremydid from Hungary is the closest relative of *Foxemys mechinorum*, discovered in Fox Amphoux, southern France. This result is also supported by a preliminary cladistic analysis. In some characters there are differences between the two taxa: in the Iharkút bothremydid the medial edge of the triturating surface is slightly concave in medial view while it is convex in *Foxemys*. The incisura columellae auris is short and not as developed and its posterior opening is narrower than in *Foxemys*. It appears that in the bothremydid from Hungary the eustachian tube has a very narrow contact with the incisura while in *Foxemys* it is separated by bone. Another feature difference is the oval shaped foramen magnum in the Iharkút taxon while *Foxemys* bears a circular foramen magnum (Tong et al., 1998).

Lower jaw

A fully preserved left lower jaw was found isolated from the skull. It bears bothremydid characters such as the triturating surface widens posteriorly, the labial

ridge is blunt and the lingual ridge is S shaped in dorsal view (Gaffney et al., 2003).

Description and comparison — The lower jaw is similar to *Foxemys* because there is an antero-posterior ridge on the wide triturating surface which is sharp anteriorly and becomes lower and rounder posteriorly, the triturating surface is concave in the middle, the lingual ridge is as high as the labial ridge anteriorly, but posteriorly the lingual one is placed higher than the labial one and the fossa meckelii is distinctly separated from the sulcus cartilaginis meckelii. There is no depression on the posterior part of the triturating surface similar to *Foxemys* and unlike *Bothremys*.

Some important differences can be recognized on the lower jaws of *Foxemys* and the Iharkút bothremydid. The sulcus cartilaginis meckelii is dorso-ventrally more expanded and almost reach the symphysis, unlike in *Foxemys*. The lingual ridge is in deeper position anteriorly than the ridge on the triturating surface while it is as high as the labial one on the jaw of the *Foxemys*. The angular, the coronoid and the surangular are complete and they appear to be generally similar to that of *Foxemys*. The articular of the Iharkút bothremydid can not be compared to *Foxemys* where it is not preserved (Tong et al., 1998).

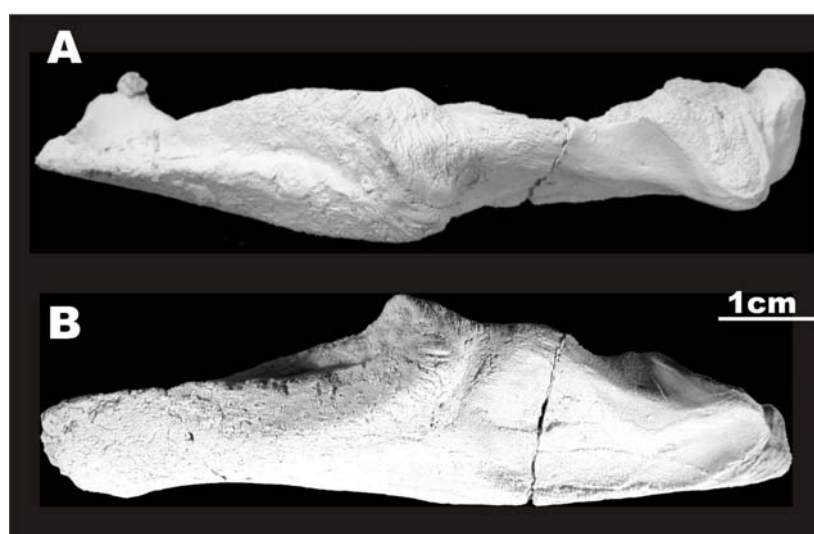


Fig. 2 — Isolated bothremydid left lower jaw from the Iharkút locality (GYN57). **A**: occlusal view, **B**: labial view. The arrow indicates the ridge on the triturating surface.

Paleobiogeographical significance of the discovery

The paleobiogeographical importance of the Iharkút bothremydid is given by its Santonian age in which stage the family is not well represented. The Bothremydidae group is particularly suitable for paleobiogeographical analysis because they have only been discovered in non-marine sediments so they could be regarded as fresh water forms and they were highly diversified during the Late Cretaceous with a wide distribution area. As the bothremydid fossils compared to other Late Cretaceous reptiles are quiet abundant and the cranial material is frequently well preserved, they allow useful phylogenetical studies for dividing basal and derived forms. So far bothremydids can be regarded as an ancestrally Gondwanan group. The oldest discovered member is *Cearachelys* from the Albian of Brasil which is a close relative of the basal *Galianemys* from the Cenomanian sediments

of Morocco (Gaffney et al., 2001, 2002). The next known step in the dispersion of the group happened during the Santonian when two new genera appeared in the Mediterranean: *Karkaemys* from Jordan and the unnamed Iharkút taxon (Zalmout et al., 2005; Botfalvai, 2005). Members of the group have also been unearthed in the Santonian of North America and the genus *Bothremys* have been described from two localities (Zalmout et al., 2005). All the mentioned Santonian forms can be included in the so-called *Bothremys*-group. The geographical origin of the genus *Bothremys* is questionable because it appeared in the same stage with the European forms. In this case it must be decided whether the *Bothremys* group was originated from North America and than migrated to the Mediterranean or it happened in reverse order. This question has not been fully clarified although three derived genera are known from the Campanian and Maastrichtian of Europe and so the European

origin had been rather supported. Because no Santonian genera had been described from Europe, except *Karkaemys* this theory needs more support. The new discovery from Hungary helps understanding the unknown migration route of the North American *Bothremys*. The first possibility is that the *Bothremys* ancestors had migrated directly from Gondwana being more closely related to the Albian basal forms than to the European ones. The other explanation says that *Bothremys* or its unknown ancestors arrived from the direction of the Atlantic Ocean and the

Mediterranean was the base of their radiation. Our investigations suggest that the Hungarian taxon is the closest relative of *Foxemys* so if the phylogenetical position of *Foxemys* is correct the bothremydid described here is more primitive compared to *Bothremys*. In this case it is rather probable that *Bothremys* ancestors appeared in the Mediterranean and after a short time they migrated to North America. This migration route is also supported by the presence of *Karkaemys* in the Santonian of Jordan which is a more derived form compared to *Bothremys*.

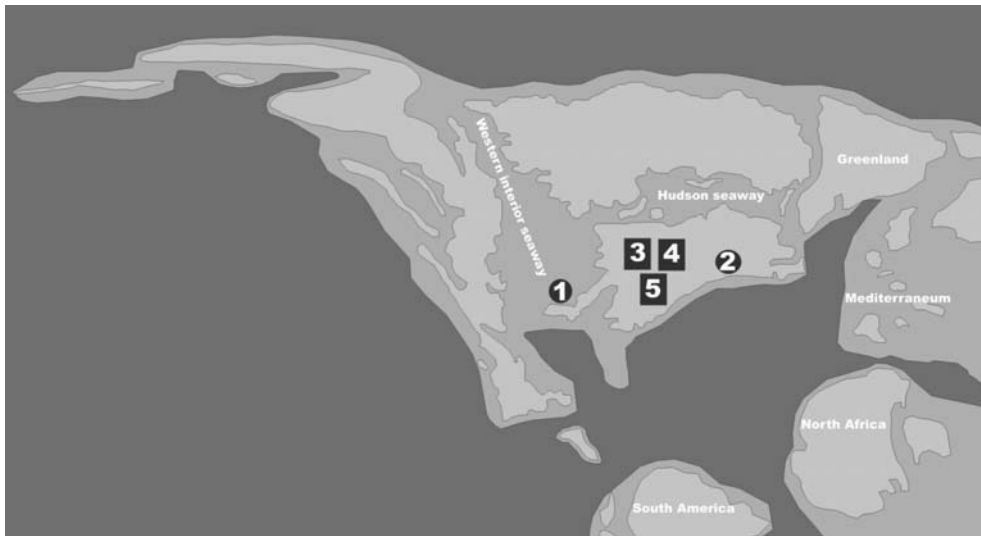


Fig. 3 — Distribution of Late Cretaceous bothremydid turtles in North America. Circles mark Santonian occurrences and squares mark Maastrichtian genera. 1 & 2: *Bothremys barberi*, 3: *Bothremys cooki*, 4: *Taphrosphys sulcatus*, 5: *Bothremys barberi*. Paleogeographic map data are modified from Scotese (1997), biogeographic data are based on Zalmout et al. (2005).



Fig. 4 — Distribution of bothremydid turtles in the Mediterranean during the Late Cretaceous. Circles mark the Santonian taxa, squares mark the Late Campanian-Early Maastrichtian ones. 1: *Iharkút* bothremydid, 2: *Karkaemys arabicus* (Jordan), 3: *Rosasia soutoi* (Portugal), 4: *Foxemys mechinorum* (France), 5: *Polysternon provinciale* (France), 6: *Elochelys convenarum* (France). Paleogeographical map modified from Buscalioni et al. (1999), biogeographic occurrences after Zalmout et al. (2005). Only members of the *Bothremys*-group are indicated.

Acknowledgments

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