A Late Cretaceous (Santonian) terrestrial ecosystem in the western Tethyan archipelago: the Central European Iharkút vertebrate site (Csehbánya Formation, Hungary)

ATTILA ŐSI[1]

[1]Hungarian Academy of Sciences – Hungarian Natural History Museum, Research Group for Palaeontology, Ludovika tér 2, Budapest, 1083, Hungary; e-mail: hungaros@freemail.hu

ABSTRACT

The faunal composition and paleobiogeographic relationships of the single known Mesozoic terrestrial site from Hungary (Central Europe) is reviewed here. This Late Cretaceous (Santonian) locality at Iharkút, discovered in 2000, provided more than 10.000 bones and teeth of close to 30 different vertebrate groups. These include pycnodontiform and lepisosteid fishes, the unique *Hungarobatrachus* and discoglossid, paleobatrachid and pelobatid frogs, albanerpetontids, various types of scincomorph lizards, mosasaurs, bothremydid, dortokid and cryptodiran turtles, sebecosuchian, hylaeochampsid, and two additional unidentified crocodylomorphs, azhdarchid pterosaurs, nodosaurid ankylosaurs, rhabdodontid ornithopods, coronosaurian ceratopsians, basal tetanuran, abelisaurid, and paravian theropods, and at least two different enantiornithine birds. Comparison of the Iharkút fauna with those of other European Late Cretaceous localities from Romania, Austria, France and Spain reveals close similarities in family level, however the genera and/or species of the individual areas are alrealy different. This can be explained first, by the Santonian age of the Iharkút locality being slightly older than the other, Campano-Maastrictian localities, and second by the supposed insular condition of the Iharkút area within the European archipelago. Further similarity with

other European faunas is the mixture of Paleolaurasian, Euramerican, Gondwanan and endemic European forms.

Key words: Late Cretaceous, Santonian, Iharkút, Hungary, continental fauna, endemism, western Tethyan archipelago

Attila Ősi [hungaros@freemail.hu], Hungarian Academy of Sciences – Hungarian Natural History Museum, Research Group for Palaeontology, Ludovika tér 2, Budapest, 1083, Hungary; Tel: 0036-1-2101075/2317, Fax: 0036-1-3382728.

INTRODUCTION

Mesozoic terrestrial vertebrate localities are not as abundant, rich and temporally continuous in Europe as in various other places of the world (e.g. Argentina, western part of North America, or Central and East Asia) and in several cases these sites provided dominantly isolated remains or fragmentary associated speciemens. The relatively poor fossil record along with few localities of terrestrial vertebrate remains is especially true for the early Late Cretaceous (Late Cenomanian–Santonian) period (Buffetaut and Le Loeuff 1991, Weishampel et al. 2004, Barrett et al. 2008, Pereda-Suberbiola 2009, Ősi et al. 2010a). This general phenomenon is usually explained by the relatively high see level characteristic for the Mesozoic (Smith et al. 1994), that resulted in an expanded archipelago rather than a huge and continuous landmass with potential terrestrial, fluvial or lacustrine sedimentary basins in Europe (Dercourt et al. 2000, Csontos and Vörös 2004). The southern part of this region was the western Tethyan archipelago where the extension and existence of islands were strongly influenced by continuous see level fluctuation. One of these islands or perhaps an outpost of a largert island was the Transdanubian Central Range within the Apulia microplate that includes the Iharkút vertebrate locality, described here.

Discovered in 2000, the Late Cretaceous continental vertebrate locality at Iharkút (Bakony Mountains) is the single known Mesozoic vertebrate site in the country and one of the most recent, systematically collected, terrestrial vertebrate sites of Europe (Ősi 2004a, Ősi et al. in press). Iharkút is the only European contiental vertebrate locality of Santonian age supported by sedimentological, palinostratigraphic and magnetostratigraphic evidences (Knauer and Siegl-Farkas 1992, Szalai 2005, Ősi and Mindszenty 2009) thus it plays a very important role in filling the gap among the older (Albian-Cenomanian) and younger (Campano-Maastrichtian) faunas in Europe. Excavations at the site provided more than 10.000 micro- and macrovertebrate remains including associate skeletons that represent approximately 30 different vertebrate taxa. These remains indicate a very diverse fauna of lepisosteid and pycnodontiform fishes, albanerpetontids, anurans, turtles, lizards, crocodyliforms, pterosaurs, non-avian theropod, ornithopod, nodosaurid and ceratopsian dinosaurs, and enantiornithine birds. Besides vertebrate fossils, remains of invertebrates, (such as gastropods, bivalves and insects) and plant fossils (e.g. sporomorphs, seeds, carbonized twigs and treetrunks, leaves) are also abundant in the locality that are critically important in our understanding of the paleoecological background of this ecosystem.

This paper papers provides an overview of the Iharkút locality with short discussion of the geological background that is followed by the brief review on the vertebrate fauna of the Iharkút locality. Paleobiogeographical aspects of the fauna are also discussed.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Late Cretaceous Iharkút vertebrate locality is situated close to the villages of Németbánya and Bakonyjákó, in the heart of Bakony Mountains of western Hungary, Central Europe (47° 13´ 52´´ N, 17° 39´ 01´´ E, see Fig. 1A). This single known locality is in an abandoned and recultivated open-pit bauxite mine and today, the site and its surroundings belong to the Dino Park Ltd. The discovery of the locality is partly due to the bauxite mining activities in the area. The quest for the „red gold" as the bauxite is frequently called in the region was started in the late 1960's that provided huge open-pit mines (Fig. 1B), the only outcrops of the bone-yielding Csehbánya Formation. This was formerly known only from deep corings related to mining activities.

In a tectonical point of view, the locality is on the Transdanubian Central Range that was on the northern part of the triangular-shaped Apulian microplate between Africa and Europe durng the Mesozoic. Southwards and westwards, this block had direct connection with the southern and eastern Alps (Csontos and Vörös 2004), the latter of which provided the early

Campanian Austrian Muthmannsdorf fauna (Bunzel 1871, Seeley 1881, Buffetaut et al. 2010). Eastwards, the Transdanubian Central Range was relatively close to the Moeasian corner and the famous Haţeg Basin from where an exceptional Maastrichtian terrestrial vertebrate fauna was documented (Nopcsa 1923, Csiki and Grigorescu 2007, Weishampel et al. 2010 and references therein).

Concerning the geological background of the area, as in most parts of the Transdanubian Central Range, the thick basement of the locality is formed by the Upper Triassic Main Dolomite Formation (Fig. 1B, C). Deep (50 to 90 m), tectonically controlled sinkholes on the karstified surface of this dolomite were filled by the bauxite (Fig. 1B). No later than the Santonian, this paleosurface including the vertically expanded bauxite lens started to be covered by deposits of the Csehbánya Formation (Fig. 1B). Bone-yileding beds occur in this formation as an alluvian flood plain deposit consisting of alternating coarse basal breccia, sandstone, siltstone and paleosol beds (Jocha-Edelényi 1988, Ősi and Mindszenty 2009; Fig. 2). Although isolated bones and teeth and plant remains appear in various beds of the formation (including red paleosols, blackish, organic rich clay) the most productive sequence is a greyish, coarse basal breccia covered with sandstone and braunish siltstone (Fig. 2). These beds produced 99% of the vertebrate remains and provided a diverse fauna discussed here.

THE CONTINENTAL VERTEBRATE FAUNA FROM IHARKÚT

Fishes. Fishes are represented by the extinct pycnodontiforms and the lepisosteiforms in Iharkút that latter of which exists today in freshwater or brackish water environments of eastern North America, Central America, and the Caribbean islands. Although some fine-grained and laminated sediments occur in the locality, associated remains of fishes still have not been found (Ősi et al. in press). Concerning pycnodontiforms, isolated lower jaws (prearticulars, Fig. 3A) and teeth are the most abundant remains (Makádi et al. 2006). The prearticulars contain three to four tooth rows that are composed of elongate to circular-shaped teeth (Gulyás 2009). Teeth ususally have smooth grinding surface but apparently, some teeth originally have complex enamel ornamentation (Ősi et al. in press). Gulyás (2009) noted that these pycnodontiform remains belong to the genus *Coelodus* and they are among the few freshwater occurrences of pycnodontiform fishes (Kocsis et al. 2009). The group has not been reported from other Late Cretaceous vertebrtae sites, only the Lower Cretaceous Spanish Las Hoyas locality provided evidence for the group. Lepisosteiform remains are isolated teeth (Fig. 3B, C), a poorly preserved jaw element, vertebrae, and scales. Teeth are conical with lanceolate apex and their base is ornamented by longitudinal ridges. Based on Gulyás (2009) these remains are almost identical with those of *Atractosteus* (or *Lepisosteus* Buffetaut et al. 1996) that has been described from other European vertebrate faunas as well (Buffetaut et al. 1996, Grigorescu et al., 1999).

Amphibians. 99% of the amphibian remains were found by screen-washing from different bone-yielding layers of the Csehbánya Formation. The amphibian assemblage is composed of hundreds of isolated fragmentary cranial, mandibular and appendicular elements. Based on the relatively frequent occurrence of frog remains (mostly pelvic elements and limb bones), a new taxon *Hungarobatrachus* has been described (Szentesi and Venczel 2010). Study of its well-preserved and diagnostic pelvic bones suggested a high capacity for jumping and swimming for *Hungarobatrachus* (Szentesi and Venczel 2010). It seems that along with various other tetrapod taxa this frog was also an endemic member of the Iharkút community. Besides the bones of *Hungarobatrachus*, remains of discoglossid and paleobatrachid (Szentesi 2010) and pelobatid frogs (Szentesi Z., pers. comm.) have been also unearthed in Iharkút that indicates a diverse from fauna in this terrestrial-fluvial ecosystem.

The other group of amphibians in the Iharkút fauna is the Albanerpetontidae. This peculiar group of very small bodied animals with Jurassic to Pliocene time range (Venczel and Gardner, 2005) is a frequent element of some Late Cretaceous European faunas (Folie and Codrea, 2005). The albanerpetontid remains from Iharkút are strongly resemble the specimens from the Haţeg Basin and suggest close taxonomic affinities (Ősi et al. in press).

Turtles. As usual in most European terrestrial vertebrate sites, turtle remains, especially their shell fragments belong to the most common fossils in Iharkút. Besides, carapace and plastron remains, cranial (skulls and lower jaws) and postcranial material (vertebrae, appendicular elements) are also relatively abundant. Pereda-Suberbiola (2009) summarized that the European Late Creatceous turtle record of continental faunas is composed of the Solemydidae, Chelydroidea, Kallokibotionidae, Bothremydidae and Dortokidae. Remains of at least the latter two groups occur in the bone-yileding beds of Iharkút and bothremydid turtles are the most abundant in the area (Fig. 3D). Shell fragments of this group refer to relatively large animals with a body length over one meter. Cranial features unambiguously indicate its close relationship to *Foxemys mechinorum* (Tong et al. 1998) an other European bothremydid from the Late Cretaceous of southern France, but important differences have been also noted between the two taxa (Rabi and Botfalvai 2006, Rabi et al. in press). Whereas bothremydid remains are known from various sites in southwestern Europe (Lapparent de Broin and Murelaga 1999, Murelaga and Canudo 2005, Tong et al. 1998) and also from Iharkút (Rabi and Botfalvai 2006), they have not been reported from the Maastrichtian of the Haţeg Basin (Grigorescu 2010) or the Campanian of Austria. Dortokidae, an endemic group to Europe has a similar occurrence also known in southern France, Spain and Iharkút (Pereda-Suberbiola 2009). From the Hungarian site they are known by pelvic elements and shell material (Ősi et al. in press). In addition, a third group, tentatively referred to Cryptodira indet. also occur in the fauna but additional material is need for a more precize taxonomic identification (Ősi et al. in press).

Lizards. Similarly to the Haţeg fauna of Romania (Weishampel et al. 2010), one of the most diverse groups in the Iharkút fauna are scincomorph lizards. Based on numerous fragmentary mandibles and dentaries at least four different taxa can be estabilished (Makádi 2008, Ősi et al. in press). Various of these specimens has be referred to *Bicuspidon* aff. *hatzegiensis* (Makádi 2006), a small-bodied species that was reported from the Haţeg Basin (Folie and Codrea 2005) but, interestingly, not from the southwestern European sites (Pereda-Suberbiola 2009).

Mosasaurs. Interestingly, isolated remains of mosasaurs are frequent fossils in the Iharkút locality. This dominantly marine, predatory group of squamates is represented by several skull and mandible elements, teeth, a large number of vertebrae (Fig. 3E) and some elements of the pelvic and pectoral girdles of various sizes. The remains indicate its basal position among mosasaurs and represent a new genus (Makádi 2005, Szentesi et al. 2006). The largest specimens refer to a total body length of an adult animal close to six meters so it was suggested that they were the top predators of the fresh waters of the Iharkút area. The abundance and large size-variation of these animals along with stable isotope data taken from their teeth (Kocsis et al. 2009) indicate that, in spite of their primarily marine habitat, their occurrence in this lacustrine environment was not occasional but continuous (Makádi 2005, Ősi et al. in press). Mosasaur fossils from other continental deposits are unknown all around the world, thus these remains are of great importance because well demonstrates that, similarly to some groups of marin fishes and mammals today, mosasaurs were able to inhabit freshwater environments (Makádi 2005).

Crocodylomorphs. As usually seen in Cretaceous continental vertebrate faunas and this is the case in Iharkút, the crocodylomorphs are a diverse and relatively abundant group represented by at least four different taxa (Ősi et al. in press). Based on numerous, labio-lingually flattened and mesio-distally finely serrated, triangular teeth and some dentary and cranial elements, the ziphodont *Doratodon* has been identified from the site (Rabi 2008). Cranial elements of *Doratodon* are extremely rare thus the Hungarian remains are particularly important for a better understanding of its phylogenetic position. Originally, this poorly known mesoeucrocodylian has been described on the basis of an incomplete, fused mandible, a fragmentary maxilla and teeth from the Lower Campanian Gosau Beds of Austria (Bunzel 1871, Buffetaut 1979), and has been also recorded from the Campanian of Spain (Company et al. 2005), the Maastrichtian of the Haţeg Basin, Romania (Martin et al. 2006) and possibly from Upper Cretaceous beds of Italy (Delfino 2001).

An other mesoeucrocodylian has been unearthed from Iharkút, and based on labio-lingually compressed isolated teeth without true serration on the carinae its close relationship has been suggested with the Early Cretaceous European *Theriosuchus* (Ősi et al. in press). Recently, the survival of *Theriosuchus* has been revealed from the Maastrichtian of the Haţeg Basin (Martin et al. 2010), so the occurrence of the genus in the Santonian of Iharkút seems to be quite realistic.

Neosuchians are represented by at least two taxa. The first, known by isolated cranial and mandibular elements and isolated teeth (Fig. 3F), actually shows close affinities with alligatoroids (Rabi 2006). Some new remains, however, questioned this hypothesis and rather suggest a more basal position within Eusuchia, close to *Allodaposuchus* discovered in various European sites such as in the Haţeg Basin, southern France and perhaps in Spain (Nopcsa, 1928; Delfino et al., 2008; Buscalioni et al., 2001; Martin 2010). Additional material is essential to clarify its systematic position.

Iharkutosuchus makadii, a basal hylaeochampsid eusuchian is the fourth and best known crocodyliform in Iharkút. A number of cranial and mandibular remains including complete skulls (Fig. 3M), mandible and teeth of different ontogenetic stages provide insight into the paleobiology of this peculiar small-bodied eusuchian. This species possesses an extremely heterodont dentition with flat, multicusped grinding teeth (the autapomorphic character of the genus), closed supratemporal fenestrae even in early ontogenetic stages, and various unusual cranial and mandibular features that were suggested to be related to the special jaw mechanism, dental occulsion and oral food processing of the animal (Ősi et al. 2007, Ősi 2008a). Cranial adductor muscle reconstruction, analysis of the temporal region, dental wear features and enamel microstructure revealed an effective dental occlusion performed by a complex jaw mechanism combined with a latero-medial mandibular movement. Transverse movement of the lower jaws during the powerstroke are also known in sphagesaurids (Pol 2003, Ősi in prep.), but whereas it was essential only for side switching of the active, occluding sides in the Brazilian forms, the transverse movement of *Iharkutosuchus* was applied also for effective occlusion and grinding the food even in this phase (Ősi and Weishampel 2009).

Besides cranial remains dozens of well-preserved postcranial material of crocodyliforms including vertebrate, pectoral and pelvic elements, limb bones, and dermal scutes have been also found. Their relatively conservative features, however, prevent their more precize taxonomic assignment.

Pterosaurs. Pterosaurs with extremely lightly built skeletal elements are rare in most of the continental vertebrate sites, especially in fluvial sediments deposited in high energetic levels. Among the European Late Cretaceous sites Iharkút is one of the richest that provided numerous cranial and postcranial remains of azhdarchid pterosaurs (Ősi et al. in press). Based on a complete, edentulous mandible and more than 45 additional symphyseal tips (Fig. 3K, L) a new genus and species, *Bakonydraco galaczi* has been described (Ősi et al. 2005). In addition, an elongate premaxillary tip has been discovered and referred to this genus (Ősi et al. 2011). This great abundance of the *Bakonydraco* jaw fragments clearly indicates that this animals were quite abundant in the Iharkút ecosystem. The postcranial material including numerous cervicals, pectoral girdle remains and limb bones is most probably belongs to the same genus, and if this is true than, along with the cranial material, a wing span of 3-4 meters of the Hungarian azhdarchid can be estimated.

Due to the absence of any diagnostic features, some bones could be referred only to Pterodactyloidea, among which a posterior, articular region of a mandible may suggest the occurrence of an other group of pterosaurs in the area, becasue the glenoid shows some different morphology, compared to that of *Bakonydraco* (Ősi et al. 2011). In the Late Cretaceous of Europe, besides azhdarchids, the occurrence of ornithocheirids in the Campanian Grünbach Formation of Austria (Wellnhofer 1980) an pteranodontids from the Maastrichtian of the Haţeg Basin (Jianu et al. 1997) has been also advocated. Recent studies, however, demonstrated that the diagnostic part of the Austrian remains belong to Azhdarchidae and the rest is non-diagnostic within Pterodactyloidea (Buffetaut et al. 2011). The material of the Haţeg Basin mentioned by Nopcsa (1914) is actually a maniraptoran sacrum (Ősi and Főzy 2007). Thus, the only supported clade of Late Cretaceosus European pterosaurs is the Azhdarchidae (Pereda-Suberbiola 2009).

Ornithischians. Three different members of ornithischian dinosaurs can be demonstrated in the Iharkút fauna. The most abundant and best known is *Hungarosaurus tormai*, a medium-sized (total body length: 4 meters) ankylosaur known at least by five partial skeletons and hundreds of isolated bones (Fig. 3H, I). Phylogenetic analyses unambiguously showed that it is closely related to the other European ankylosaur, *Struthiosaurus* known from all main Late Cretaceous (Campanian to Maastrichtian) ecosystems and they are basal members of the Nodosauridae (Pereda-Suberbiola and Galton. 2001, Garcia and Pereda-Suberbiola 2003, Ősi 2005). A diagnostic feature of *Hungarosaurus* is the unusual limb proportion with a gracile forelimb almost as long as the hindlimb. Features of the appendicular skeleton together with the presence of paravertebral elements situated along the epaxial musculature indicate that *Hungarosaurus*, similarly to the Early Cretaceous Australian *Minmi*, could have been a cursorial animal (Molnar and Frey 1987, Ősi and Makádi 2009).

In contrast to the other European Late Cretaceous sites, rhabdodontid dinosaurs are among the rarest elements of the Iharkút fauna (Ősi 2004b, Fig. 3J). Cranial and mandibular remains and a femur show some diagnostic features of a new taxon within rhabdodontids and clearly distinguish it from *Rhabdodon* of southwestern Europe and *Zalmoxes* of the Haţeg Basin in Romania (Weishampel et al. 2003). Although histological studies still in preparation, the Iharkút rhabdodontid appears to have been even smaller (total body length approximately 2 meters) than its other European cousins.

The third and most surprising group of ornithischians in Iharkút are the ceratopsians. Although some controversial teeth and vertebrae from northwestern Europe have been assigned to this dominantly Asian and North American group (Godefroit and Lambert 2007, Lindgren et al. 2007), cranial (rostral bone and premaxillae, Fig. 3N) and mandibular (seven predentaries up to now) remains from Iharkút provided the first indisputable evidence for their European existing (Ősi et al. 2010b). The bones of this newly described, small-bodied coronosaurian, *Ajkaceratops kozmai*, show very close affinities with the Central Asian Late Cretaceous bagaceratopsids (*Bagaceratops* and *Magnirostris*) and demonstrates well that ceratopsians were wide-spread on the whole northern Hemisphere, including the European archipelago.

Non-avian theropods. Although the non-avian theropod material is very scanty, a number of bones and teeth were diagnostic to determine at least three different taxa. The largest, having been most probably the top-predator of the terrestrial ecosystems, is a basal tetanuran, known on the basis of hundreds of isolated teeth. These 3–4 cm large, labio-lingually flattened, distally curved, and mesio-distally serrated teeth (Fig. 3G) are almost identical with the theropod teeth from the Campanian of Austria and with the '*Megalosaurus dunkeri*' teeth from the Barremian of the Isle of Wight suggesting the presence of a relict tetanuran in the Santonian-Campanian European archipelago (Ősi et al. 2010a).

For today, it is evident that abelisauroid theropods were rare but important members of the European Late Cretaceous faunas (Buffetaut 1989, Carrano and Sampson, 2008). Besides the lands of southwestern Europe, they also inhabited the Santonian Iharkút site that is supported by a pedal ungual phalanx (Ősi et al. 2010a) and an undescribed femur (Ősi and Buffetaut in prep.). The third group of non-avian theropods are paravians. Based on a single, but diagnostic scapulocoracoid, a new, small-bodied, dromaeosaurid-like theropod, *Pneumatoraptor fodori* has been described (Ősi et al. 2010a). In addition, a number of paravian remains including teeth, caudals and limb bones have been documented, and although they are probably belong to *Pneumatoraptor*, they are non-diagnostic for a more precize determination.

Birds. Almost a dozen of bird bones (limb elements) are known from Iharkút among which a few has been referred nearly to Enantiornithes (Ősi 2008b). Among the enantiornithine bones, a complete tarsometatarsus was described as *Bauxitornis mindszentyae* that shows great similarities with other avisaurid taxa (Dyke and Ősi 2010). Besides the Hungarian bones, remains of Late Cretaceous enantiornithines have been unearthed also in southern France (Walker et al. 2007) but still unknown from the Haţeg Basin, Romania and from the Spanish localities.

'Missing' taxa. An interesting point of the Santonian Iharkút fauna is the absence of sauropod and hadrosaurid dinosaurs and the mammals. These taxa are always occur in most of the other European sites of Spain, France and Romania (Pereda-Suberbiola 2009). Whether their absence is the result of preservational circumstances and additional material is needed to discover them, or these groups indeed did not inhabit this area in the Santoninan, cannot be answered at the moment.

DISCUSSION

Although the Santonian Iharkút assemblage is the oldest among the Late Cretaceous European faunas (Campanian in Austria, Campano–Maastrichtian in France and Spain and Maastrichtian in Romania), its composition is more or less similar to the younger ones, at least in family level, and the differences unambiguously due to their different age, their isolation within the archipelago and preservational circumstances. Concerning paleobiogeography, various terrestrial faunal provinces have been applied in the literature to demonstrate the origin and composition of the different faunas (see e.g. Cox 1980, Russell 1993, Le Loeuff 1998, Pereda-Suberbiola 2009). It is generally accepted that the European Late Cretacoeus sites, including Iharkút, are composed of a mixture of Paleolaurasian (North America+Asia+Europe), Euramerican (Europe+North America) and Gondwanan forms (Russell 1993, Pereda-Suberbiola 2009, Weishampel et al. 2010). This complexity is mainly explained by the „buffer" status of the European archipelago between Asia and North America (Russell 1993, Benton et al. 2010). Besides the immigrants from these paleoprovinces, some taxa endemic to Europe were also summarized by Pereda-Suberbiola (2009), which, indeed, played an important proportion of the different faunas. In the following, the different tetrapod groups of the Iharkút fauna are collected according to their origin area.

Paleolaurasian forms. Among the Paleolaurasian taxa collected by Pereda-Suberbiola (2009), discoglossid frogs, albanerpetontids and polyglyphanodontine lizards occur in Iharkút. The pelobatid frog remains (Szentesi Z. pers. comm.) indicate the European occurrence of the group and with their Cretaceous record from Asia and North America they can be regarded as paleolaurasian forms. The European albanerpetontid record goes back to the Early Cretaceous (Gardner and Böhme 2008) and discoglossids and polyglyphanodontines could reach Europe no later the the early Late Cretaceous. As it was intepreted for the doubtful ceratopsian material from Sweden and Belgium, ceratopsians may have Paleolaurasian affinities. Before the discovery of *Ajkaecratops* from Iharkút, however, 'bagaceratopsids' were known exclusively from Central Asia, so the Iharkút ceratopsian can be regarded as a member of a Eurasian group.

Taxa with Euramerican affinitites. According to the available fossil record from Iharkút, paleobatrachid frogs and the nodosaurid *Hungarosaurus* show certainly Euramerican origin. Pereda-Suberbiola (2009) also noted the alligatoroid crocodylians from this paleoprovince and listed their Hungarian occurrence described first by Rabi (2006). However, as mentioned above, new material questioned the alligatoroid affinities of this crocodylian so the origin of this crocodylian is still controversial.

Gondwanan immigrants. Bothremydid turtles (Lapparent de Broin, 2000 Gaffney et al. 2006) and abelisaurid theropods (Buffetaut et al. 1988) are the classic examples for taxa with Gonwanan origin that inhabited Europe during the Cretaceous. Both groups are present in the Santonian of Iharkút along with the poorly known mesoeucrocodylian, *Doratodon* with ziphosuchian (or sebecosuchian) affinities that is also regarded as a Gonwanan immigrant. Remains of bothremydids and *Doratodon* are restricted to Upper Cretaceous sediments so their earlier than Santonian existence in the European archipelago is ambigous. Abelisaurids are known from the Albian of France (Accarie et al. 1995) so it can be supposed that this group reached the archipelago at least in the Early Cretaceous. The recently published abelisauroid *Berberosaurus* from the Early Jurassic of Morocco (Allain et al. 2007) raise the possibility of a much earlier, Jurassic arrival of the first members of the group into Europe.

Endemic European taxa. Concerning their origins, perhaps the most interesting faunal elements of Iharkút are *Hungarobatrachus*, dortokids, hylaeochampsids, and rhabdodontids which have been found exclusively in Europe. Among these, only *Hungarobatrachus* is the only taxon that has been metioned from a single site (Iharkút), but of course, additional material of other European (or outside of Europe) sites can change this and perhaps can help to clarify its phylogenetic position.

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Figure captions:

Figure 1. **A**, Location map of the Iharkút vertebrate locality (Upper Cretaceous (Santonian) Csehbánya Formation, Bakony Mts, western Hungary). **B**, Shematic section of the open-pit Iharkút (middle Eocene limestones and late Eocene conglomerates occur northwards; after Ősi and Mindszenty, 2009).

Figure 2. Shematic statigraphic section showing the main palaeoenvironments and lithofacies associations at Sz-6 site (after Tuba et al., 2006 and Ősi and Mindszenty 2009)

Figure 3. Some of the vertebrate fossils from the Late Cretaceous (Santonian) Iharkút locality. A, Pycnodontiformes indet. left lower jaw in occlusal view; B-C, Lepisosteidae indet. teeth; D, bothremydid turtle carapax fragment in ventral view; E, Mosasauridae indet. dorsal verebra in dorsal view; F, Neosuchia indet. tooth in ?anterior view; G, basal tetanuran tooth in ?lateral view; H, *Hungarosaurus tormai* tooth in ?lingual view; I, *Hungarosaurus tormai* dermal armour element in dorsal view; J, Rhabdodontidae indet. dentary tooth in lingual view; K, *Bakonydraco galaczi* tip fragment of the mandible in occlusal; L, and lateral view; M, *Iharkutosuchus makadii* (holotype) skull in dorsal view; N, *Ajkaceratops kozmai* rostral bone and premaxilla in left lateral view.