Late Cretaceous (Santonian) *Atractosteus* (Actinopterygii, Lepisosteidae) remains from Hungary (Iharkút, Bakony Mountains)

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ABSTRACT

Remains of lepisosteid fishes are well known from the Upper Late Cretaceous of Europe, but only by fragmentary remains from some Cenomanian and Campanian-Maastrichtian deposits. Here we report various cranial and postcranial remains of gars, discovered in the Upper Cretaceous (Santonian) Csehbánya Formation of Iharkút (Bakony Mountains, Hungary) in the last 15 years. These remains represent one of the most diverse assemblages of lepisosteid fish material remains from Upper Cretaceous continental deposits of Europe. Based on tooth morphology, scale-microstructure and the features of the supracleithrum and the microstructure of the ganoid scales we refer these remains to the genus Atractosteus. Besides some uncertain remains from the Cenomanian of France and Spain, the Santonian aged fossils from Iharkút represent the oldest undisputable occurrence of the family Lepisosteidae in the European continental Cretaceous. Using tooth crown morphology, the surface microstructure of the ganoid scales, and the anatomy of the supracleithrum morphology, a review of the Late Cretaceous lepisosteid record suggests the occurrence of both Atractosteus and Lepisosteus in the European archipelago.
1. Introduction

Gars, or garpikes (Lepisosteidae), are a well-known group of primitive neuropterygian fishes, including extant and fossil taxa. Their evolution, historical biogeography, functional anatomy and interrelationships with other actinopterygian fishes have been the subject of many papers for a long time (Regan, 1923; Hammarberg, 1937; Rayner, 1948; Jollie, 1984; Gottfried & Krause, 1998; Hammarberg, 1937; Jollie, 1984; Kammerer, Grande, & Westneat et al., 2006; Rayner, 1948; Regan, 1923).

Their fossilized remains going back to the Early Lower Cretaceous deposits (Wiley, 1976), and they were recorded all over the world from various localities in North America (including the Arctic region), Central America and Cuba, Africa, Madagascar, Asia and Europe (Grande, 2010).

In Europe, fossil lepisosteid fishes are known from Late Upper Cretaceous (Table 1., Fig. 1) to Oligocene deposits of various localities (Wiley & Schultze, 1984). Their Late Cretaceous European occurrences are listed in Table 1. Up to now, Santonian gar remains from Europe have been reported only from two localities of Hungary. Material from the deposits of the Upper Santonian are very similar to those of ?Dentilepisosteus cf. kemkemensis (see in Grande, 2010 and Cavin et al., 2015).
A single tooth, tentatively referred as 'Lepisosteidae indet. is known from the Middle Cretaceous (Lower Cenomanian) vertebrate assemblage of Fouras-Vauban (Charentes, southwestern France). This small tooth has a conical crown without carinae (Vullo, 2005; Vullo and Néraudeau, 2008), preventing its certain assignment to lepisosteid fishes. A ganoid scale assigned to Stromerichthys sp. has been reported from Les Renardières (Charentes, southwestern France; Vullo, 2005) and from the Cenomanian of Algora and Asturias (Spain; Vullo et al., 2009; Torices et al., 2012). These specimens have been reinterpreted as Obaichthys africana (Cavin et al., 2015).

The Early Campanian lepisosteid fossils (teeth and scales) from Villeveyrac (Hérault Basin, southern France) are considered as Lepisosteidae indet. (Buffetaut et al., 1996). Based on the lanceolate tip of the teeth, these remains were referred to Atractosteus by Sigé et al. (1997).

Teeth, scales, vertebrae and one cranial fragment referred to Lepisosteus and Atractosteus have been reported from the Campanian of Champ-Garimond (Gard, southern France) (Sigé et al., 1997).

The lepisosteid material from the Early Campanian of Ventabren (Bouches-du-Rhône, France), including skull elements and scales, have been described as Atractosteus africana (Arambourg and Joleaud, 1943) (Cavin et al., 1996). This species was regarded as a nomen dubium by Grande (2010).

Lepisosteid scales and teeth were found at the Campanian-Maastrichtian locality of Lo Hueco (Cuenca, Spain). Based on the SEM-observation of the micro-ornamentation of the scales these remains were referred to Atractosteus sp. (Ortega et al., 2015).

The first report of lepisosteid fishes from the Upper Campanian-Lower Maastrichtian of Laño (Spain, Basque Country) based on fragmentary scales, referred to Lepisosteus sp. (Astibia et al., 1990). Later on more fossil gar material was collected from Laño,
corresponding to a left supracleithrum, 9 opisthocoelous vertebrae and numerous ganoid scales. Cavin (1999) described the remains as *Atractosteus* sp., but later the material was referred to indeterminated Lepisosteidae by Pereda-Suberbiola et al. (2015).

Further Campanian-Lower Maastrichtian fish remains (scales and teeth) referred to lepisosteid fishes have been found in Monséret and Campagne-sur-Aude (Aude, southern France) (Tong et al., 1993; Le Loeuff, 1992).

The gar remains (teeth, scales and vertebrae) of the Upper Cretaceous (Campanian-Maastrichtian) of Arraíde (Portugal) were described as *Clastes lusitanicus* and *Clastes pustulosus* (Sauvage, 1897-98). These taxa have been regarded as *nomen dubium* by Grande (2010). This material of *Clastes lusitanicus* includes teeth with lanceolate crown, which could refer to the genus *Atractosteus* (Sigé et al., 1997).

The Early Maastrichtian gar material from Cruzy (Hérault Basin, southern France) includes relatively uncommon lepisosteid scales (Buffetaut et al., 1999).

The Maastrichtian lepisosteid remains reported from Fântânele (Hațeg Basin, Romania) (one fragmentary tooth and ganoid scales) are not well preserved and also smaller than any previously presented Cretaceous gar remains of Europe (Grigorescu et al., 1999). Besides these early finds some lepisosteid remains are known from the maastrichtian of Budzorene (Hațeg Basin, Romania). These remains (teeth and ganoid scales) were described as *Atractosteus* and *Lepisosteus*, based on tooth morphology (Csiki et al., 2008). Some unpublished lepisosteid remains are known outside of the Hațeg Basin (Codrea et al., 2010).

There is a report of Santonian gar teeth and a single vertebra from the Ajka Coal Formation (Ajka, western Hungary, representing a swampy lacustrine environment), western Hungary has been described as Lepisosteidae indet. (Ősi, Bodor, Makádi, & Rabi, 2016 et al., in press). This material comes from a swampy lacustrine environment being contemporaneous with the fluvial deposits of the other locality is the Iharkút vertebrate site 25 km northeast
from of the Ajka site. This assemblage is much more diverse than the remains from Ajka, and it originates from the fluvial deposits of the Csehbánya Formation (Ősi et al., 2012), the latter being produced in the material described here. These tooth remains have lanceolate tips, which feature could refer to *Atractosteus* (Sigé et al., 1997).

Santonian occurrence of gars have been reported recently from Múzquiz (Mexico). A single specimen, collected in the „Los Temporales” quarry in Coahuila State (northern Mexico), was described as *Herreraichthys coahuilaensis*. This species is unique among all lepisosteids in having extremely long lacrimomaxillary series and a relatively wider and shorter premaxilla (Alvarado-Ortega, Brito, Porras-Múzquiz and Mújica Monroy, 2016).

Fossils of Cenozoic lepisosteid fishes are also known from Europe. Among others an extremely short-jawed species, *Masillosteus kelleri* Micklich and Klappert, 2001 has been discovered in the freshwater deposits of the Eocene Messel Formation of Germany (Micklich and Klappert, 2001).

In this paper we describe the lepisosteid remains from the Santonian Iharkút continental vertebrate site of western Hungary, summarize their morphological features, compare them with other European gar fossils, and discuss their Cretaceous–European distribution in Europe.

2. **Locality and geological background**

The Iharkút vertebrate fossil site is located in an open-pit bauxite mine near the villages of Bakonyjákó and Németbánya (Bakony Mountains, western Hungary, 47° 13’ 52” N, 17° 39’ 01” E) (Fig. 2A).

In a tectonical point of view, the Iharkút vertebrate locality is on the Transdanubian Central Range, a tectonic block that was situated on the northern part of the triangular-shaped Apulian microplate between Africa and Europe during the Mesozoic (Csontos &and
Vörös, 2004). The oldest rock outcropping at the Iharkút locality is the Upper Triassic Main Dolomite Formation, in which deep (50 to 90 m) tectonically controlled and karstified sinkholes were formed within the Triassic dolomite and were filled up by the Cretaceous (pre-Santonian) Nagytárány Bauxite Formation that was mined in the area from the 1970’s. The bauxite, together with the karstified paleosurface of Triassic rocks, were covered by alluvial flood plain deposits of the Csehbánya Formation consisting of alternating coarse basal breccia, sandstone, siltstone and paleosol beds deposited in a freshwater environment (Jocha-Edelényi, 1988; Ősi & Mindszenty, 2009; Botfalvai, Haas, Bodor, Mindszenty, & Ősi et al., in press 2015). Palynological studies indicate a Santonian age of this formation (Bodor & Baranyi, 2012). Bone-yielding beds which occur in various stratigraphic horizons occur in the Csehbánya Formation that produced a rich and diverse fossil assemblage of isolated and associated bones, teeth and plant remains. The vertebrate assemblage is composed of fishes, amphibians, turtles, mosasaurs, and other lizards, pterosaurs, crocodilians and dinosaurs including birds (Ősi et al., 2012). The Iharkút vertebrate assemblage is dominated by bones of freshwater and semi-aquatic animals while the number of bones of terrestrial animals is subordinate (Botfalvai et al., in press 2015).

The most productive sequence (SZÁL-6 site) is a greyish, coarse basal breccia covered with sandstone and brownish siltstone that produced 99 percent of the vertebrate remains including the fish fossils described in this paper (Fig. 2B-C). At the locality The Csehbánya Formation is only partially covered by the Middle Eocene Iharkút Conglomerate Formation.

3. Material and methods

Lepisosteid remains from Iharkút described here have been collected during the summer fieldworks from 2000-2014, and during also by means of the process of the screen-
washing of the material of the most productive SZÁL-6 site of the Iharkút locality (for site maps within the locality see Botfalvai et al., in press, in press).

All specimens are housed in the Hungarian Natural History Museum (Magyar Természettudományi Múzeum; MTM), where they were cleaned and prepared mechanically in the technical labs of the Department of Paleontology and Geology. The fossils are hardly pyritized, and with a few exceptions, they are dark brownish or black in color.

For scanning electron microscopy (SEM) pictures a Hitachi S-2600N and a Hitachi S-2360N scanning electron microscope was used. For measuring the line-drawings of the scales we used the free version of ImageJ 1.48v, was used.

The fossils are hardly pyritized, and with a few exceptions, they are dark brownish or black in color.

4. Systematic paleontology

Class: Actinopterygii Cope, 1887

Super Division: Holostei Müller, 1844

Division: Ginglymodi Cope, 1872

Order: Lepisosteiformes Hay, 1929

Family: Lepisosteidae Cuvier, 1825

Tribe: Lepisosteini Grande, 2010

Genus Atractosteus Rafinesque, 1820

Atractosteus sp.

(Fig. 3-8, 10)

Material: 1 lacrimomaxillary bone (V.2010.155.1.), 1 frontal (VER 2014.73.), 5 dentary fragments (VER 2014.75.1-2., VER 2014.77., VER 2015.2., VER 2015.3.), 3 unidentified

Remarks: Of the lepisosteid material from Iharkút listed here, not all the elements can be determined at genus level. However, following parsimony we refer all Lepisosteidae remains from Iharkút to *Atractosteus*, until more complete material is discovered.

5. Description and comparisons

5.1. Cranial elements

Lacrimomaxilla: The single known hardly pyritized lacrimomaxillary bone (V.2010.155.1.; Fig. 3A-B) is 20 mm long with one *in situ* tooth (and two more open...
alveoli in the inner tooth row). Similar to other gar dermal bones, its lateral surface is
ornamented. Although posterior lacrimomaxillary bones are much longer than the anterior
ones, this lacrimomaxillary element is too fragmentary to permit the identification of
its exact position within the upper jaw.

Frontal: The largest identified cranial element is a partial left frontal (VER
2014.73.; Fig. 3F-G). It is flattened dorsoventrally and elongated anteroposteriorly.
On the dorsal surface the ganoin ornamentation can be clearly observed. A descending
lamina, typical for the frontals (Grande, 2010), can be seen on the ventral side of the bone.
Only the medial margin of the bone is preserved, where it was articulated with the right
frontal. On living adult gars the two frontals articulate with each other medially by a
clearly visible suture.

Dermal bones: These remains are skull elements, showing diverse size and shape, and
they cover the dorsal and the lateral sides of the head. The extinct species Lepisosteus
indicus Woodward, 1908 bear unornamented dermal bones making it unique among all
the gars (Gottfried & Krause, 1998; Grande, 2010). The 3 dermal bones, presented here
(VER 2014.74.1-2., VER 2015.1.), are too fragmentary for a precise identification of their
position in the skull.

Dentary: Among the four lepisosteid dentaries from Iharkút (VER 2014.75.1-2.,
VER 2014.77., VER 2015.2., VER 2015.3.) three specimens have preserved teeth, or
preserved alveoli sometimes containing the broken tooth base. The
anteroposterior length of the most completely preserved left dentary (VER 2014.75.1.; Fig.
4A-B) is 73 mm. Of this jaw element 13 alveoli of the inner tooth row are preserved, among
which six contain teeth. A well-preserved, posteriorly wider mandibular
sensory canal Meckelian-groove is clearly visible along the medial side of the dentary. The
preserved fragment is straight with the lateral surface devoid of ganoin (unlike most of the
bones of the gar skull), but it has a smooth, longitudinal striation. An other specimen (VER 2015.2.; Fig. 4G-H), with has a dentary fragment ornamented its ventral surface, ornamented and (VER 2015.2.; Fig. 4G-H) is 6 mm long and dorsoventrally flattened dorsoventrally, and its ventral surface is nicely ornamented, indicating that it is a fragment of representing the anterior segment of the dentary. There is no preserved tooth in it. The other two dentaries do not bear any additional features worth to be mentioned.

The Iharkút lepisosteid dentaries are clearly different from the lepisosteid dentity-fract reported from Armuña (Pérez-García et al., 2016), in having smooth lateral and ventral sides.

Teeth: Lepisosteid teeth from Iharkút are typical for the family. They are apicobasally high, conical and circular in cross section, reaching their maximal thickness at their base, and they are getting narrower and pointed to the tip of the crown. The enamel is dark brown/black and shiny, but on the tip of the crown it is brighter and slightly translucent. Teeth are They show the characteristic typically plicidentine structure (Grande, 2010) well seen in the external structure part of the large teeth. They are strongly striated longitudinally, starting from their base towards the tip (these striae are the outer expressions of the dentine-folds). The striation vanishes around the half of the apicobasal height of the crown. In cross section a central pulp cavity can be observed in the plicidentine structure (Fig. 5A). The tip of most teeth is lanceolate, with a slight constriction beneath the labiolingually flattened part of the crown (Fig. 5F-G). The lanceolate shaped part bears unserrated carinae (Fig. 5G).

A few teeth are have with simple, conical tip (VER 2014.85., VER 2015.33., VER 2015.35.; Fig. 5D-E), and based on their size and apical ex-morphology, they could have been part of the outer row of teeth, tooth row. The tip of most teeth is lanceolate, with a slight constriction beneath the labiolingually flattened part of the crown (Fig. 5F-G). The lanceolate shaped part bears unserrated carinae (Fig. 5G). The tip of most teeth is lanceolateshaped, with a slight
constriction beneath the labiolingually flattened part of the crown (Fig. 5F-G). This lanceolate shaped part bears unserrated carinae (Fig. 5G).

The lanceolate teeth (referable to *Atractosteus*) from Iharkút are similar to the teeth published from several Late Cretaceous localities (e.g. Sauvage, 1897-98; Buffetaut et al., 1996; Ősi et al., 2016), but different from the pointed gar teeth reported by Pérez-Garcia et al. (2016), and Grigorescu, Venczel, Csiki and Limberea (1999), and the pointed *in situ* fangs published by Cavin, Martin and Valentin (1996). The apexes of the lanceolate gar teeth from Iharkút slightly differ from those of the extant *Atractosteus spatula* (Lacépède, 1803), which has fangs with higher, more elongated lanceolate apex. The tip of most teeth is lanceolate shaped, with a slight constriction beneath the labiolingually flattened part of the crown (Fig. 5C, F, G). This lanceolate shaped part bears unserrated carinae (Fig. 5G). A few teeth are with simple, conical tip (VER 2014.85., VER 2015.33., VER 2015.35.; Fig. 5B, D, E), and based on their size and apex morphology they could have been part of the outer row of teeth.

The teeth from Iharkút are similar to the teeth published from other Late Cretaceous localities (e.g. Sauvage, 1897-98; Buffetaut et al., 1996; Grigorescu et al., 1999; Ősi et al., in press), but different from the *in situ* teeth published by Cavin et al. (1996). The apex of the lanceolate gar teeth from Iharkút are slightly different from the tips of the lanceolate teeth of the extant *Atractosteus spatula* (Lacépède, 1803), which has fangs with higher, more elongated lanceolate apex.

### 5.2. Postcranial elements

**Supracleithrum:** A single, nearly complete right lepisosteid-supracleithrum (VER 2015.246., Fig. 6) has been found at the Iharkút site (Fig. 6). Supracleithrum is a dermal element of the pectoral girdle of lepisosteid fishes. The anteriorly extending lateral
A canal runs through this bone element anteroposteriorly, that enters the supracleithrum bone anterolaterally (near to the dorsal process), and exits it posteromedially. There is a ganoin-ornamentation on the dorsolateral surface of the bone. The supracleithrum has a dorsal and a ventral process, although only the base of the ventral process is preserved, not preserved, only fragmentary. The of the dorsal process bears no projecting ridges, which feature refers to the genus *Atractosteus* (see Wiley, 1976).

The Iharkút lepisosteid supracleithrum is similar to that of the extant *Atractosteus spatula* in contour and in the lack of projecting ridges on the anterodorsal processal socket (see Grande, 2010). The Iharkút specimen is also similar to the lepisosteid supracleithrum published by Cavin (1999) in having a simple ganoin-ornamentation consisting of relatively extended surfaces of ganoin, instead of a pattern of small, dot-like spots of ganoin.

However, this ornamentation is also much less complex than those seen in *Atractosteus turanensis* (see Nessov & Panteleeva, 1999), *Lepisosteus osseus* (see Grande, 2010), and all *Atractosteus* and *Lepisosteus* supracleithra published by Wiley (1976).

The Iharkút lepisosteid supracleithrum is similar in shape to those seen in *Atractosteus* spatula (see Grande, 2010), but it is visually different both in shape and ornamentation from *Atractosteus turanensis* (see Nessov & Panteleeva, 1999), *Lepisosteus osseus* (see Grande, 2010), and the lepisosteid supracleithra published by Wiley (1976) and Cavin (1999).

Vertebrae: 453 opisthocoelous vertebrae are known from the bone-yielding beds of the Csehbányra Formation at Iharkút. Most specimens are only vertebral centra, but on some specimens the lateral parapophyses, and dorsally the bases of the paired neural spines are also preserved. The vertebrae are variable in size and shape (Fig. 76). Anterior abdominal vertebrae are much lower dorsoventrally than the other abdominal
Whereas some specimens are short and squattish, some are elongated and gracile, representing different parts of the backbone. The anterior abdominal vertebrae are much lower dorsoventrally (Fig. 7A-B). The anteroposterior length of the vertebral centrum of the largest specimen (VER 2014.97.; Fig. 7C-D) is 13 mm, the dorsoventral height is 9 mm, and the mediolateral width is 15 mm. Whereas some specimens are short and squattish, some are elongated and gracile, representing different parts of the backbone (Fig. 9C). The anterior abdominal vertebrae are much lower dorsoventrally (Fig. 6A-B). The caudal vertebrae are more elongated anteroposteriorly (Fig. 7E-F) than the abdominals.

The vertebrae from Iharkút have features similar to the specimens published by Dutheil (2000), Gayet et al. (2001), Kear et al. (2009), Martinelli and Teixeira (2015), Ősi et al. (2016) and Sauvage (1897-98). The vertebrae from Iharkút have features similar to the specimens published by Sauvage (1897-98), Dutheil (2000), Gayet et al. (2001), Kear et al. (2009) and Martinelli and Teixeira (2015). The vertebrae of the genera *Lepisosteus* and *Atractosteus* are macro/morphologically identical.

Scales: Ganoid scales referred to lepisosteid fishes are known from Iharkút, referred to lepisosteid fishes. These ganoid scale fossils are thick dorsoventrally and rhomboidal in shape (Fig. 8A-F). A haft-like, anterodorsal process is present for their attachment to the body. On some lateral line scales (Fig. 8F) dorsally to this process a tooth-like peg is also present for the connection with the dorsally adjoining scale ("peg-and-socket" articulation; Grande, 2010). These scales bear a thick layer of ganoin on their lateral surface, which substance-showings a typically tuberculated surface in electron microscopical view (Fig. 8G-J). On several specimens from Iharkút the edge of the ganoin-layer is wavy bordering the bony substance of the scale. The size of the scales varies from 2x3 mm to 19x25 mm.
The scales of from Iharkút are similar in outer morphology to some published scales from other localities (Becker, Chamberlain Jr., Robb, Terry & Garb, 2009; Grigorescu et al., 1999; Pérez-Garcia et al., 2016; Sauvage, 1897-98), but clearly differ from the scales published by Buffetaut et al. (1996), and those of *Atractosteus africanus* (see Cavin et al., 1996) in having less complex ganoin pattern those published from other localities (Sauvage, 1897-98; Grigorescu et al., 1999; Becker et al., 2009), but clearly differ from the scales published by Buffetaut et al. (1996), and those of *Atractosteus africanus* (see Cavin et al., 1996) in having visibly different shaped ganoin-layer on the bony base of the scales.

5.3. Taxonomic assignment

The members of the order *Lepisosteiformes* were described in great detail by López-Arbarello (2012).

Based on the results of a phylogenetic analysis by Grande (2010) the Iharkút fossils belong to Lepisosteidae because the teeth have plicidentine tooth structure (ch. 41 by of Grande, 2010) and the supracleithrum there is has a concave dorsal articular facet on the supracleithrum (ch. 93 of by Grande, 2010). The Iharkút form is a member of Lepisosteinae, since lacrimomaxillary bones are present (ch. 42 of by Grande, 2010), and they can be referred to the tribe *Lepisosteini* because the dentary teeth are arranged as an outer lateral row of small, similar sized conical teeth and an inner medial row of greatly enlarged fangs (ch. 39 of by Grande, 2010).

Unfortunately, neither the single character (ch. 54 of by Grande, 2010): symphysis of lower jaw occurs along the medial surface of anterior right and left dentaries with anterior ends pointing anteriorly) of *Lepisosteus* listed by Grande (2010), nor the three characters (ch. 40 of by Grande, 2010): collective shape of laterally expanded part of vomerine heads, ch. 80 of by Grande, 2010: tooth plates associated with second and third hypobranchials, ch. 104 of...
by Grande, 2010: anterior end of first coronoid curves medially and expands broadly to a flat symphysis) described in Atractosteus can not be observed in the Iharkút material.

Nevertheless, it seems that there are some other morphological features available for distinguishing the two genera. Sigé et al. (1997) noted that the lanceolate crown morphology of the teeth is characteristic only for Atractosteus. The dentition of the extant Lepisosteus and Atractosteus species verifies this theory (see Grande, 2010; Kammerer et al., 2006). Most of the gar teeth from Iharkút have lanceolate tip, which referring them to Atractosteus.

Wiley (1976) differentiates Atractosteus from Lepisosteus in having no projecting ridges on the supracleithrum. The single known Iharkút lepisosteid supracleithrum bears no does not bear projecting ridges, which feature strengthens shows anthe Atractosteus affinity.

Furthermore, other authors (e.g. Gayet & Meunier, 1986, 2001; Gayet, Meunier & Werner et al., 2002) pointed out that the arrangement of ganoin tubercles on the external surface of the scales (see Fig. 7 and 8) clearly distinguishes the extant lepisosteid genera from one aneach other. Measurements were taken on the lateral surface of a two well preserved scales (VER 2015.39. and VER 2015.116.) with having a shiny, thick ganoin- layer (scale specimens VER 2015.39. and .; Fig. 7G-JVER 2015.116.). The diameter of the ganoin tubercles was measured on 4-4 points on the examined scales, altogether on 596 tubercles ranges between 2.91 μm to 7.84 μm (430446 measured tubercles on specimen VER 2015.39., and 166 measured tubercles on specimen VER 2015.116.). The average diameter of the tubercles is 5.65 μm. The distances between the tubercles were also measured also to between 0.26 μm and 5.99 μm on the same 4-4 points on both scales. Altogether 1392 inter-tubercular distances have been measured (1078379 measurements on specimen VER 2015.39., and 314 measurements on specimen VER 2015.116.). The average distance between the tubercles is 2.09 μm. Comparison of the final our results with measurements on
other lepisosteid scales we can conclude indicates that the parameters of the micro-
oration of the Iharkút gar scales are close belong to that of genus Atractosteus (Fig. 9
and Table 2.8).

At sum up, among the lepisosteid remains from Iharkút the teeth, the scales and the
supracleithrum and scales clearly indicate the presence of the genus Atractosteus in the fauna.
Although the lepisosteid specimens from the Csehbánya Formation of Iharkút are all isolated
elements, following parsimony, we refer the material into the same genus and speciesbelieve
that they belong to the same genus, until more complete material justifies the
opposition otherwise.

6. Discussion

The discovered vertebrate fauna of the Iharkút locality fills an underrepresented
temporal gap in the Late Cretaceous vertebrate record of Europe (Ősi et al., 2012). The
Atractosteus material of Iharkút is of great importance, since these remains are not only teeth,
scales and vertebrae, but also a supracleithrum and various other cranial and mandibular
elements and a supracleithrum that helps in furthera better understanding of the anatomy of
this Santonian lepisosteid (Fig. 10). The occurrence of this genus in the Santonian western
Tethyan archipelago further outlines some distributional patterns and biogeographical
inferences.

Besides some uncertain remains from the Cenomanian of western Europe (Vullo &and
Néraudeau, 2008; Vullo et al., 2009) the Hungarian remains represent the oldest undisputable
evidence of Lepisosteidae from the European archipelago. Nevertheless, some of the western
European remains tentatively refered to lepisosteiforms (e.g. Vullo &and Néraudeau, 2008)
may suggest at least a mid-Cretaceous occurrence of lepisosteids in the western part of the
European archipelago. This can be a possible scenario since Onichthys (regarded as
Atractosteus inby Grande, [2010]) from the Cenomanian of Morocco (Cavin & and Brito, 2001) definitely indicates the occurrence of the family in the southern region of the western European archipelago.

Most of the Late Cretaceous European lepisosteid remains are, however, isolated, scanty remains of teeth, scales and vertebrae without more precise taxonomical identification. Atractosteus has been described from the Early Campanian of southern France (Cavin et al., 1996), where the--These authors concluded that this material belongs to A. africanus previously described as 'Paralepidosteus' africanus (Arambourg & and Joleaud, 1943) from the Late Cretaceous Senonian of Niger and suggested an Euroafrican continental faunal exchange from Africa towards Europe. On the basis of the microstructure, however, Gayet and Meunier (2001:fig. 2) pointed out that the scales of this French material resemble those of Lepisosteus, a hypothesis further supported by the simple conical tooth crown morphology preserved in the jaw element (Cavin et al., 1996:fig. 2; Sigé et al., 1997). Grande (2010) is of the opinion that neither the type of Atractosteus 'Paralepidosteus' africanus, nor the French material bear diagnostic features of the genus Atractosteus, and he refers to them as Lepisosteidae indet.

Regarding additional Late Cretaceous lepisosteid remains from Europe, teeth and scales have been described from the Lower Campanian beds of Villeveyrac, southern France (Buffetaut et al., 1996). Though this material does not bear any diagnostic features listed by Grande (2010), the teeth with lanceolate crown morphology suggest the presence of Atractosteus in this fauna (Sigé et al., 1997). This is also the case with the lepisosteid remains from the Campanian of Champ-Garimond (France), in which the lanceolate teeth suggest the presence of Atractosteus (Sigé et al., 1997). A supracleithrum, 9 vertebrae, and numerous scales have been assigned to Atractosteus from the Maastrichtian of Laño (Cavin, 1999), that was later referred to Lepisosteidae indet. (Pereda-Suberbiola et al., 2015). In
addition, some skull bones, teeth, opisthocoelic opisthocoelous vertebrae and scales are known from the Campaniano-Maastrichtian of Lo Hueco, Spain. On the basis of the microstructure of the ganoid scales Ortega et al. (2015) pointed out that these remains can be assigned to *Atractosteus*. The ganoid scales from the Cenomanian of Portugal (Sauvage, 1897-98; Jonet, 1970-71, 1981; Sauvage, 1897-98), France (Vullo & Néraudeau, 2008) and Spain (Torices, Barroso-Barcenilla, Cambra-Moo, Pérez-García, & Segura, 2012; Vullo, Bernárdez, & Buscalioni, 2009; Vullo et al., 2009; Torices et al., 2012) now suggest a lepisosteiform (obaichthyid) rather than a possible amiiform affinity (Cavin et al., 2015). These scales from the Cenomanian of Portugal identified as remains of *Stromerichthys* by Jonet (1970-71, 1981) and the remains of *Paleoniscidae indet.* described by Sauvage (1897-98) were reidentified as scales of *Obaichthys africanus* Gande, 2010 (Cavin et al., 2015). However, Jonet (1981) described scales also from the Cenomanian of this locality as 'Paralepidosteus cacemensis' and 'Lepidotes minimus', but these remain are very similar to those of *?Dentilepisosteus kemkemensis* (see Cavin et al., 2015; Grande, 2010).

Concerning the Maastrichtian remains from the Haţeg Basin, Romania, additional material is known from different localities (Codrea et al., 2010; Weishampel, Csiki, Benton, Grigorescu, & Codrea, 2010; Weishampel et al., 2010; Codrea et al., 2010) since the publication of the first remains (Grigorescu, et al., 1999), but with a few exceptions (e.g. Csiki, Joncescu, & Grigorescu et al., 2008) their detailed description is still to be done. The lepisosteid material of the Santonian-Santonian of Ajka (Hungary) (Ősi et al., 2016 in press), and the Campaniano-Maastrichtian lepisosteid material described as *Clastes lusitanicus* by Sauvage (1897-98) includes teeth with *Atractosteus*-like, lanceolate tips.

Assuming this information on the European Upper Late Cretaceous record it can be well supported seen, that based on tooth morphology, and scale microstructure and morphology of the supracleithrum at least two different types of lepisosteid fishes have been
recorded so far. Most of the remains show *Atractosteus* affinity, but *Lepisosteus* also occurs, at least in the **lower** Early Campanian of western Europe. The **present-current** record indicates the occurrence of the *Atractosteus* from the Santonian to Campanian (perhaps until Maastrichtian) with the Hungarian fossils, being the earliest **record occurrence** of the genus in the European archipelago.

7. **Concluding remarks**

Tooth morphology, scale micro-ornamentation and characters of the supracleithrum revealed the occurrence of the actinopterygian fish *Atractosteus* in the Late Cretaceous Iharkút vertebrate fauna representing the oldest definitive record of this genus in Europe. The relatively diverse skeletal material described here can help the identification of some still unknown lepisosteid skeletal elements in other Late Cretaceous faunas for a better understanding of the taxonomy and European biogeography of these basically freshwater predators. In the light of the Iharkút material and using the work of Cavin et al. (2015) the European Late Cretaceous lepisosteiform (according to Grande, 2010) fauna is at least composed of at least the obaichthyids (*Obaichthys*) during the early Late Cretaceous and lepisosteids (*Atractosteus* and *Lepisosteus*) in the Santonian to Maastrichtian period.

Referring the Iharkút gar material to the genus *Atractosteus* was supported by the tooth morphology, the measurements of the scale microsurfaces and the morphology of the supracleithrum. Based on our results, up to n the occurrence of the genus *Atractosteus* (also the family Lepisosteidae) in the Santonian of Hungary is the oldest in Europe.

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Figure 1. Paleogeographic distribution of the Late Cretaceous Lepisosteiformes remains in Europe: 1, Les Renardiéres (France) (see Vullo and Néraudeau, 2008). 2, Cacém (Portugal) (see Jonet, 1970-71, 1981). 3, Pendão (Portugal) (see Sauvage, 1897-98). 4, Algora (Spain) (see Torices et al., 2012). 5, Asturias (Spain) (see Vullo et al., 2009). 6, Aika (Hungary) (see Ősi et al., 2016). 7, Iharkút (Hungary) (see Ősi et al., 2012). 8, Ventabren (France) (see Cavin et al., 1996). 9, Villeveyrac Basin (France) (see Buffetaut et al., 1996). 10, Champ-Garimond (France) (see Sigé et al., 1997). 11, Armuña and Carbonero el Mayor (Spain) (Pérez-García et al., 2016). 12, Arazéde (Portugal) (see Sauvage, 1897-98). 13, Lo Hueco (Spain) (see Ortega et al., 2015). 14, Monsérét (France) (see Tong, Buffetaut, Le Loeuff, Cavin, & Martin, 1993). 15, Campagne-sur-Aude (France) (see Le Loeuff, 1992). 16, Laño (Spain) (see Astibia et al., 1990; Cavin, 1999). 17, Cruzy (France) (see Buffetaut et al., 1999). 18, Oarda de Jos (Romania) (see Codrea et al., 2010). 19, Cassagnau (France) (Laurent, Bilotte, & La Loeuff, 2002). 20, Lestaillats (France) (Laurent, Cavin, & Bilotte, 1999). 21, Serrat del Pelleu (Spain) (Blanco and Bolet, 2014). 22, l’Espinau (Spain) (Blanco and Bolet, 2014). 23, Camí del Soldat (Spain) (Blanco and Bolet, 2014). 24, Fântânele (Romania) (see Grigorescu et al., 1999). 25, Budurone (Romania) (see Csiki et al., 2008). The map does not include the following uncertain remains: one ?Lepisosteidae indet. tooth from Fouras-Vauban (France) (see Vullo & Néraudeau, 2008) and scales of ?Dentilepisosteus kemkemensis from Cacém (Portugal) (see Jonet, 1981). For further data see Table 1.
2012). 2, Asturias (Spain) (see Vullo et al., 2009). 3, Les Renardières (France) (see Vullo and Néraudeau, 2008). 4, Cacém (Portugal) (see Jonet, 1970-71, 1981). 5, Pendão (Portugal) (see Sauvage, 1897-98). 6, Ajka (Hungary) (see Ósi et al., in press). 7, Iharkút (Hungary) (see Ósi et al., 2012). 8, Ventabren (France) (see Cavin et al., 1996). 9, Villeveyrac Basin (France) (see Buffetaut et al., 1996). 10, Champ-Garimond (France) (see Sigé et al., 1997). 11, Arazéde (Portugal) (see Sauvage, 1897-98). 12, Campagne-sur-Aude (France) (see Le Loeuff, 1992). 13, Monséret (France) (see Tong et al., 1993). 14, Laño (Spain) (see Astibia et al., 1990). 15, Le Hueco (Spain) (see Ortega et al., 2015). 16, Cruzy (France) (see Buffetaut et al., 1999). 17, Făntânele (Romania) (see Grigorescu et al., 1999). 18, Budurone (Romania) (see Csiki et al., 2008). The map does not include the following uncertain remains: one ?Lepisosteidae indet. tooth from Fouras-Vauban (France) (see Vullo & Néraudeau, 2008) and scales of ?Dentilepisosteus cf. kemkemensis from Cacém (Portugal) (see Jonet, 1981). The material from the localities 6, 9 and 11 were considered to *Atractosteus* based on the work of Sigé et al. (1997).

**Figure 2.** A, Location map of the Iharkút vertebrate locality. B (A), Aerial photo of the Iharkút open-pit, showing the position of the SZÁL-6 site. C and geology (B) of the Iharkút vertebrate fossil site, Stratigraphic section of site SZÁL-6 (Modified after Botfalvai et al., in press.).

**Figure 3.** *Atractosteus* sp. cranial remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, lacrimomaxilla (V.2010.155.1.) in labial view; B, in lingual view. C-E, unidentified dermal bones (VER 2014.74.1-2., VER 2015.1.) in outer view. F, left frontal (VER 2014.73.) in dorsal view; G, in ventral view. Abbreviations: dl, descending lamina; go, ganioneganor ornamentation; me, medial margin; t, tooth.
**Figure 4.** *Atractosteus* sp. lower jaw remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, left dentary (VER 2014.75.1.) in labial view; B, in lingual view. C, dentary-fragment (VER 2014.77.) in labial view; D, in occlusal view; E, in lingual view. F, dentary-fragment (VER 2014.75.2.) in lingual view. G, dentary-fragment (VER 2015.2.) in ventral view; H, in dorsal view. Abbreviations: ar, alveolar row; mg: Meckelian-groovemandibular sensory canal.

**Figure 5.** *Atractosteus* sp. tooth remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, cross-section of a tooth (VER 2014.91.3.). B, conical tooth (VER 2015.32.). C, lanceolate tooth (VER 2014.92.3.). D, scanning electron micrograph of a conical tooth (VER. 2015. 33). E, scanning electron micrograph of the tip of the tooth on fig. D. F, scanning electron micrograph of a lanceolate tooth (VER. 2015. 34). G, scanning electron micrograph of the tip of the tooth on fig. F. Abbreviations: rd, radial foldings of the dentine.

**Figure 6.** *Atractosteus* sp. right supracleithrum (VER 2015.246.). A, in lateral view; B, in ventral view, C, in medial view; D, in dorsal view. Abbreviations: afsc, anterior foramen of the sensory canal; bvp, base of the ventral process; dp, dorsal process; go, ganoin e-ornamentation; ppsc, posterior foramen of the sensory canal.

**Figure 7.** *Atractosteus* sp. postcranial (vertebral) remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, anterior abdominal vertebra (VER 2014.102.) in dorsal view; B, in anterior view. C, abdominal vertebra (VER 2014.94., VER 2014.102.) in dorsal view; D, in anterior view.
2014.97.) in dorsal view; D, in anterior view. E, caudal vertebra (VER 2015.36.) in dorsal view; F, in anterior view. Abbreviations: ha, haemal arch; hc, haemal canal; na, neural arch; nc, neural canal; pp, parapophysis


**Figure 98.** Measurements of the diameter of the ganoin tubercles and the inter-tubercular distances on the scales of extant and extinct lepisosteid fishes, including the Iharkút *Atractosteus* sp.. Abbreviations: F, fossil; K, Cretaceous; T, Tertiary; Q, Quaternary; R, Recent (after Gayet et al., 2002)

**Figure 109.** Anatomical summary of the identified remains of the Iharkút *Atractosteus* sp.. A, skull line-drawing with identified cranial elements in dorsal view; B, in lateral view. C, full body line-drawing with identified postcranial elements in lateral view. Line-drawings are modified after Grande, 2010. Scale bars: 5 mm. Bone elements on figures A and B were figured with scale bars on Fig. 3 and 4. Abbreviations: aav, anterior abdominal vertebra (close to the basioccipital region); av, abdominal vertebra; cv, caudal vertebra d, dentary (including teeth); dpms, dorsal precaudal midline scale; fr, frontal; lls, lateral line scale; lm, lacrimomaxillary bone; pcls, postcleithral scale; scl, supracleithrum
Table 1. Late Cretaceous lepisosteiform fish remains from Europe listed in chronostratigraphical order. Papers of Csiki et al., 2008 and Sigé et al., 1997 do not list which specimens are referred to which taxon.

<table>
<thead>
<tr>
<th>Name</th>
<th>Material</th>
<th>Age</th>
<th>Locality</th>
<th>Reference(s)</th>
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<td>Scale</td>
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<td>Tooth</td>
<td>Lower</td>
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<td>Cacém, Portugal</td>
<td>Cavin et al., 2015; Jonet, 1981; Grande, 2010</td>
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<td>Cacém, Portugal</td>
<td>Cavin et al., 2015; Jonet, 1970-71, 1981; Grande, 2010</td>
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Table 2. Measurements of the parameters on the micro-ornamentation of the Iharkút ganoid gar scales

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<th>Average intertubercular space (µm)</th>
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