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

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ABSTRACT

LRemains of lepisosteid fishes are well known from the UpperLate Cretaceous of Europe, but only by fragmentary remains fromof some Cenomanian and Campanianо-Maastrichtian deposits. Here we report various cranial and postcranial remains of gars, discovered infrom 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 materialremains 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 and 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-~~well-known group of primitive~~lower~~ neuropterygian fishes, including extant and fossil taxa. Their evolution, historical biogeography, functional anatomy and interrelationships with other actinopterygian fishes have been ~~subjects of interest~~the subject of many ~~papers~~studies ~~for a long time~~ (~~Regan, 1923; Hammarberg, 1937; Rayner, 1948; Jollie, 1984;~~ Gottfried ~~&~~and Krause, 1998; Hammarberg, 1937; Jollie, 1984; Kammerer, Grande, & Westneat ~~et al.,~~ 2006; Rayner, 1948; Regan, 1923). ~~Their fossilized remains going back~~Their earliest fossils ~~to~~ are from ~~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 ~~&~~and 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 Up to now, Santonian gar remains from Europe have been reported only from Hungary.~~the

~~Ganoid scales from the Cenomanien of Portugal identified as remains of *Stromerichthys* (Jonet, 1970-71, 1981) and Paleoniscidae indet. (Sauvage, 1897-98) were reidentified as scales of *Obaichthys africanus* Grande, 2010 (Cavin et al., 2015). However, another obaichthyid taxon seems to be also presented here. Jonet (1981) desribed scales also from the Cenomanian of this locality as '*Paralepidosteus caecemensis*' and '*Lepidotes minimus*', but these remains are very similar to those of ?*Dentilepisosteus* cf. *kemkemensis* (see in Grande, 2010 and Cavin et al., 2015).~~

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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 assingnment to lepisosteid fishes . A ganoid scale assigned to *Stromerichthys* sp. has been reported from Les Renardiéres (Charentes, southwestern France; Vullo, 2005) and from the Cenomanian of Algora and Asturias (Spain; Vullo et al., 2009; Torices et al., 75 2012). These specimens have been reinterpreted as *Obaichthys africanus* (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 reffered 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 africanus* (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) reffered 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 Arazéde (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 (Haţeg 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 Budurone (Haţeg 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 Haţeg Basin (Codrea et al., 2010).~~

~~There is a report of Santonian gars 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~~The other locality is the Iharkút vertebrate site 25 km northeast

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fromof the Ajka site. This assemblage is much more diverse than the remainsone from Ajka, and itthey originates from the fluvial deposits of the Csehbánya Formation (Ősi et al., 2012), the latter being produced the material described h.ere. These tooth remains have lanceolate tips, which feature could refer to *Atractosteus* (Sigé et al., 1997).

Santonian occurence 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 fromof the Santonian Iharkút continental vertebrate site of western Hungary, summarize their morphological features, compare them with other European gar fossilsm, 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).

TIn a tectonical point of view, the Iharkút vertebrate locality is on the Transdanubian Central Range, a tectonic block that was being situated on the northern part of the triangular-shaped Apulian microplate between Africa and Europe during the Mesozoic (Csontos &and

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Vörös, 2004). The oldest rock ~~outeropping~~ at the Iharkút locality is the Upper Triassic Main Dolomite Formation. ~~ in which d~~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) Nagytárkány Bauxite Formation that was mined in the area from the 1970's. The bauxite, together with the karstified paleosurface of Triassic rocks, ~~were~~ was 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 ~~&and~~ Mindszenty, 2009; Botfalvai, Haas, Bodor, Mindszenty, & Ősi, ~~et al.,~~ in press.~~2015~~). Palynological studies indicate a Santonian age for~~of~~ this formation (Bodor ~~&and~~ 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 brow~~au~~nish siltstone that produced 99 percent of the vertebrate remains including the fish fossils described in this paper (Fig. 2B-C). At the locality ~~The~~ the Csehbánya Formation is only partially covered by the m~~M~~iddle 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-

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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 w~~as~~ere 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

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dermal bones (VER 2014.74.1-2., VER 2015.1.); 1672474 tooth remains (V.2010.158.1., VER 2014.78., VER 2014.79., VER 2014.80., VER 2014.81., VER 2014.82., VER 2014.83., VER 2014.84., VER 2014.85., VER 2014.86., VER 2014.87., VER 2014.88., VER 2014.89., VER 2014.90.,; VER 2014.91.1-4., VER 2014.92.1-7., VER 2014.93.1-9., VER 2015.4., VER 2015.5., VER 2015.6., VER 2015.7., VER 2015.30., VER 2015.31., VER 2015.32., VER 2015.33., VER 2015.34., VER 2015.35., VER 2015.285., VER 2015.286., VER 2015.287.); 1 right supracleithrum (VER 2015.246.); 453 vertebral remains (V.-2010.156.1., VER 2014.94., VER 2014.95., VER 2014.96., VER 2014.97., VER 2014.98., VER 2014.99., VER 2014.100., VER 2014.101., VER 2014.102., VER 2014.103., VER 2014.104., VER 2014.120., VER 2015.8., VER 2015.9., VER 2015.10., VER 2015.36., VER 2015.37., VER 2015.165., VER 2015.288.); 490399 scale remains (V.2010.158.1., VER 2014.105., VER 2014.106., VER 2014.107., VER 2014.108., VER 2014.109., VER 2014.110., VER 2014.112., VER 2014.113., VER 2014.114., VER 2014.115., VER 2014.116., VER 2014.117., VER 2015.11., VER 2015.12., VER 2015.13., VER 2015.14., VER 2015.15., VER 2015.16., VER 2015.17., VER 2015.38., VER 2015.39., VER 2015.40., VER 2015.41., VER 2015.42., VER 2015.164., VER 2015.289., VER 2015.290., VER 2015.291., VER 2015.292., VER 2015.293., VER 2015.294., VER 2015.295., VER 2015.296.).

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 opened

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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 ~~identify~~ identification of its exact position within the upper jaw.

Frontal: The largest ~~identified~~ recognized cranial element is a partial left frontal (VER 2014.73.; Fig. 3F-G). It is flattened dorsoventrally and elongated anteroposteriorly~~ventrally~~. 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~~Just~~ 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~~ with a clearly visible suture.

Dermal bones: These remains are skull elements, showing diverse size and shape, and they cover~~ing~~ the dorsal and the lateral sides of the head. The extinct ~~species~~ *Lepisosteus indicus* Woodward, 1908 bears~~had~~ unornamented dermal bones making it unique among all the gars (Gottfried &~~and~~ 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 o~~i~~n the skull.

Dentary: Among the four~~six~~ lepisosteid dentaries from Iharkút (VER 2014.75.1-2., VER 2014.77., VER 2015.2.~~, VER 2015.3.~~) three~~wo~~ specimens ~~have~~ preserve teeth, or ~~preserved~~ alveoli ~~sometimes~~ occasionally containing~~with~~ 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 ~~among which~~ contain teeth. A ~~well~~ 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 de~~a~~void of ganoin (unlike most of the

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bones of the gar skull)~~,~~ but it has a smooth, longitudinal striation. An~~-~~other specimen (VER 2015.2.; Fig. 4G-H)~~, with~~has~~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 dentary-fragment 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~~Teeth 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~~hardly~~ striated longitudinally starting from their base towards the tip (these striae are the outer expressions of the dentine-folds). ~~The~~ S~~st~~triation vanishes around the half of the apicobasal h~~ig~~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~~

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~~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-García et al. (2016), and Grigorescu, Venczel, Csiki and Limberea (1999), and the pointed *in situ* fangs published by Cavin, Martin and Valentin (1996). The ap~~ex~~ices 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: ~~1~~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~~an anteroposteriorly extending lateral

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line canal~~ runs through this bone element anteroposteriorly, it~~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 is present. ~~The supracleithrum~~It has a dorsal and a ventral process, although only the base of the ventral process is preserved~~not preservedonly fragmentary?????~~. The ~~of the~~ dorsal process ~~for what? 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~~e-~~ ornamentation consisting of relatively extended surfaces of ganoine, instead of a pattern of small, dot-like spots of ganoine. However, this ornamentation is also much less complex than those seen in ~~„~~*Atractosteus*~~”~~ *turanensis* (see Nessov ~~&and~~ Panteleeva, 1999), *Lepisosteus osseus* (see Grande, 2010), and all *Atractosteus* and *Lepisosteus* supracleithra pu~~s~~blished by Wiley (1976).

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

Vertebrae: 4~~5~~3 opisthocoelous vertebrae are known from the bone-yielding beds of the Csehbánya Formation at Iharkút. Most specimens are only vertebral centra, but on some specimens the lateral parapophyses ~~on the lateral side~~, and dorsally the bases of the paired neural spines are also preserved. The vertebrae are variable in size and shape (Fig. 7~~6~~). Anterior abdominal vertebrae are much lower dorsoventrally than the other abdominal

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vertebrae??? (Fig. 7A-B). ~~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. 7~~6~~C-D) is 13 mm, ~~the~~ its dorsoventral height is 9 mm, and ~~the~~ its 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 vetebrae are much lower dorsiventrally (Fig. 6A-B).~~ The caudal vertebrae are more elongated anteroposteriorly (Fig. 7~~6~~E-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 ~~marcomorphologically~~ macromorphologically identical.

Scales: 490~~399~~ ganoid scales referred to lepisosteid fishes are known from Iharkút, ~~referred to lepisosteid fishes. These~~They ~~ganoid scale fossils scale remains~~ are thick dorsoventrally and rhomboidal in shape (Fig. 8~~7~~A-F). A haft-like, anterodorsal process is present for their attachment to the body. On some lateral line scales (Fig. 8~~7~~F) 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.

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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-García 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 ganoine layer on the bony base of the scales.~~

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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 trib~~us~~ 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 verify~~ies~~ this theory (see Grande, 2010; Kammerer et al., 2006). Most of the gar teeth from Iharkút have lanceolate tip~~, which~~ refersing them to *Atractosteus*.

Wiley (1976) di~~ffers~~ stinguishes *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~~ strenghtening~~hows~~ ~~an~~the *Atractosteus* affinity.

Furthermore, other authors (e.g. Gayet ~~&and~~ 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 an~~each~~ other. Measurements were taken on the lateral surface of ~~a~~ two ~~well~~ 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~~ (430~~146~~ 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.~~ D~~The d~~istances 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 (1078~~379~~ measurement~~s~~s 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~~se~~ our results with measurements on

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other lepisosteid scales ~~we can conclude~~indicates that the parameters of the micro-ornamentation of the Iharkút gar scales are close~~belong~~ to that of ~~genus~~ *Atractosteus* (Fig. 9 and Table 2.~~8~~).

A~~To sum up, a~~mong 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 species~~belive that they belong to the same genus,~~ until more complete material justifies ~~the oppositotherwisee~~.

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 help~~s~~ in further~~a 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 referred to lepisosteiforms (~~e.g.~~ Vullo &~~and~~ Néraudeau, 2008) may suggest at least a~~the~~ mid-Cretaceous occurrence of lepisosteids in the western part of the European archipelago. This can be a possible scenario since *Oniichthys* (regarded as

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Atractosteus in~~by~~ Grande, ~~[~~2010~~]~~) from the Cenomanian of Morocco (Cavin ~~&and~~ Brito, 2001) definitely indicates the occurrence of the family in the southern region~~neighbourhood~~ 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 precis~~z~~e taxonomical identification. *Atractosteus* has been described from the c~~E~~arly 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 excange 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 resembles~~is much closer~~ ~~to~~ 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 o~~fn~~ 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 ~~form~~ from Europe, teeth and scales have been described from the l~~L~~ower 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~~refer to~~ 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~~ were later referred to Lepisosteidae indet. (Pereda-Suberbiola et al., 2015). In

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addition, some skull bones, teeth, ~~opisthocoelic~~ opisthocoelous vertebrae and scales are known from the Campanian~~o~~-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 ~~&~~and 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~~s~~ ~~their~~ 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 remains 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~~ was ~~known~~ described from different localites (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, Ionescu, & Grigorescu ~~et al.~~, 2008) their detailed description is still to be done. The lepisosteid material of the ~~Santonain~~ Santonian of Ajka (Hungary) (Ősi et al., 2016~~in press~~), and the Campanian~~o~~-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~~Late~~ Cretaceous record it ~~can be~~is 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

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recorded so far. Most of the remains show *Atractosteus* affinity, but *Lepisosteus* also occurs, at least in the lowerEarly 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 remarkssions

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 occurence of the genus *Atractosteus* (also the family Lepisosteidae) in the Santonian of Hungary is the oldest in Europe.

Acknowledgements

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Figure captions

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, Ajka (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, Monséret (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.~~Paleogeographic distribution of the Late Cretaceous Lepisosteoidea remains in Europe. 1, Algora (Spain) (see Torices et al.,~~

~~2012). 2, Asturias (Spain) (see Vullo et al., 2009). 3, Les Renardiéres (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 Ősi et al., in press). 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, 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, Lo Hueco (Spain) (see Ortega et al., 2015). 16, Cruzy (France) (see Buffetaut et al., 1999). 17, Fântânele (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, ~~ganione~~ganoin- ornamentation; me, medial margin; t, tooth

[M7] megjegyzést írt: This caption was rewritten according to the redone Figure 1..

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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; mscg; ~~Meckelian groove~~mandibular 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, ganioin e- ornamentation; pfsc, posterior foramen of the sensory canal

Figure 76. *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

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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 8~~7~~. *Atractosteus* sp. postcranial (scale) remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, postcleithral scale. B, dorsal precaudal midline scale (VER 2015.40.). C, ?ventral scale (VER 2015.41.). D-F, lateral line scales (VER 2015.42, VER 2014.112., VER 2015.13). G-I, scanning electron micrographs of the surface of a lateral line scale (VER 2015.39). J, line-drawing of the fig. I (used for measuring the ganoin tubercles and the space between them). Abbreviations: ap, anterodorsal process; dp, dorsal process; go, ganoin- ornamentation

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Figure 9~~8~~. 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 10~~9~~. 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

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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

Name	Material	Age	Locality	Reference(s)

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Obaichthys africanus	Scale	Lower Cenomanian	Les Renardiéres, Charentes, southwestern France	Cavin et al., 2015; Vullo, 2005; Vullo and Néraudeau, 2008
?Lepisosteidae indet.	Tooth	Lower Cenomanian	Fouras-Vauban, Charentes, southwestern France	Vullo, 2005; Vullo and Néraudeau, 2008
?*Dentilepisosteus kemkemensis*	Scales	Cenomanian	Cacém, Portugal	Cavin et al., 2015; Jonet, 1981; Grande, 2010
Obaichthys africanus	Scales	Cenomanian	Cacém, Portugal	Cavin et al., 2015; Jonet, 1970-71, 1981; Grande, 2010
Obaichthys africanus	Scales	Cenomanian	Pendão, Portugal	Cavin et al., 2015; Sauvage, 1897-98
Obaichthys africanus	Scales	Cenomanian	Algora, Spain	Cavin et al., 2015; Torices et al., 2012
Obaichthys africanus	Scale	middle-?late Cenomanian	Asturias, Spain	Cavin et al., 2015; Vullo et al., 2009
Lepisosteidae indet.	Teeth and vertebra	Santonian	Ajka, southwestern Hungary	Ősi et al., 2016
Atractosteus sp.	Frontal, lacrimomaxilla, other skull elements, dentaries, teeth, supracleithrum, vertebrae, scales	Santonian	Iharkút, southwestern Hungary	this paper
Lepisosteidae	Infraorbitals (=lacrimomaxillae),	early	Ventabren,	Cavin et al., 1996; Grande,

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indet.	dermopalatine, opercular bone, scales	Campanian	France	2010
Lepisosteidae indet.	Teeth and scales	early Campanian	Villeveyrac Basin, France	Buffetaut et al., 1996
Atractosteus sp.,	Teeth, scales, vertebrae, cranial fragment	Campanian	Champ-Garimond, Gard, France	Sigé et al., 1997
Lepisosteus sp.	Teeth, scales, vertebrae, cranial fragment	Campanian	Champ-Garimond, Gard, France	Sigé et al., 1997
Lepisosteidae indet.	Dentary- fragment, scales, teeth	upper Campanian	Armuña and Carbonero el Mayor, Spain	Pérez-García et al., 2016
Lepisosteidae indet.	Scales, teeth, vertebrae	Campanian-Maastrichtian	Arazéde, Portugal	Grande, 2010; Sauvage, 1897-98
Atractosteus sp.	Skull bones, Tteeth, scales, vertebrae	Campanian-Maastrichtian	Lo Hueco, Spain	Ortega et al., 2015
Lepisosteidae indet.	Scales and teeth	Campanian-lower Maastrichtian	Monséret, Aude, southern France	Tong et al., 1993
Lepisosteidae indet.	Scales and teeth	Campanian-lower Maastrichtian	Campagne-sur-Aude, southern France	Buffetaut et al., 1997; Le Loeuff, 1992;
Lepisosteidae indet.	Supracleithrum, scales, vertebrae	Upper Campanian-Lower Maastrichtian	Laño, Basque County, Spain	Astibia et al., 1990; Cavin, 1999; Pereda-Suberbiola et al., 2015
Lepisosteidae indet.	Scales	probably early Maastrichtian	Cruzy, Hérault, France	Buffetaut et al., 1999
Lepisosteus sp.	Scales	Maastrichtian	Oarda de Jos, Romania	Codrea et al., 2010
Lepisosteidae	Scales, teeth,	Late	Cassagnau, Petites Pyrénées,	Laurent et al., 2002; Marmi et

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indet.	vertebrae	Maastrichtian	France	al., 2016
Lepisosteidae indet.	Scales	Late Maastrichtian	Lestaillats, near to village Mauran, Petites Pyrénées, France	Laurent et al., 1999; Marmi et al., 2016
Lepisosteus sp.	~~u~~Unpublished material	Upper Maastrichtian	Serrat del Pelleu, southern Pyrenees, Spain	Blanco and Bolet, 2014
Lepisosteus sp.	~~u~~Unpublished material	Upper Maastrichtian	l'Espinau, southern Pyrenees, Spain	Blanco and Bolet, 2014
Lepisosteus sp.	~~u~~Unpublished material	Upper Maastrichtian	Camí del Soldat, southern Pyrenees, Spain	Blanco and Bolet, 2014
Lepisosteus sp.	Tooth, scales	Upper Maastrichtian	Fântânele, Haţeg Basin, western Romania	Grigorescu et al. 1999
Atractosteus sp.,	Teeth and scales	Latest Maastrichtian	Budurone, Haţeg Basin, western Romania	Csiki et al., 2008
Lepisosteus sp.	Teeth and scales	Latest Maastrichtian	Budurone, Haţeg Basin, western Romania	Csiki et al., 2008

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Table 2. Measurements of the parameters on the micro-ornamentation of the Iharkút ganoid gar scales

	Average diameter of tubercles								Average intertubercular space							
Scale specimen	VER 2015.39.				VER 2015.116.				VER 2015.39.				VER 2015.116.			
Measuring points	P1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4
Number of measured tubercles or intertubercular spaces/ Measuring point	146	148	40	96	47	43	33	43	379	377	90	232	89	80	63	82
Average tubercle-diameter or intertubercular space/ Measuring point (µm)	5.65	6.13	5.49	6.11	5.25	6.38	6.1	6.22	2.09	2.61	1.72	1.93	1.4	1.2	1.88	2.08
Averages of the average results of the measuring points/ Scale specimen (µm)	5.85				5.99				2.09				1.64			
Final averages/ Scale specimen (µm)	5.92								1.87							

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