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

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ABSTRACT

Lepisosteid fishes are well known from the Upper 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). These remains represent one of the most diverse assemblages of lepisosteid fish material from Upper Cretaceous continental deposits of Europe. Based on tooth morphology, scale-microstructure and the features of the supracleithrum 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 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 studies (Regan, 1923; Hammarberg, 1937; Rayner, 1948; Jollie, 1984; Gottfried and Krause, 1998; Kammerer et al., 2006). Their earliest fossils are from 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 Upper Cretaceous (Fig. 1) to Oligocene deposits of various localities (Wiley and Schultze, 1984). Their Upper 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 Ajka Coal Formation (Ajka, western Hungary, representing a swampy lacustrine environment), has been described as Lepisosteidae indet. (Ősi et al., 2016). The other locality is the Iharkút vertebrate site 25 km northeast of the Ajka site. This assemblage is much more diverse than the one from Ajka, and it originates from the fluvial deposits of the Csehbánya Formation (Ősi et al., 2012).

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 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).

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

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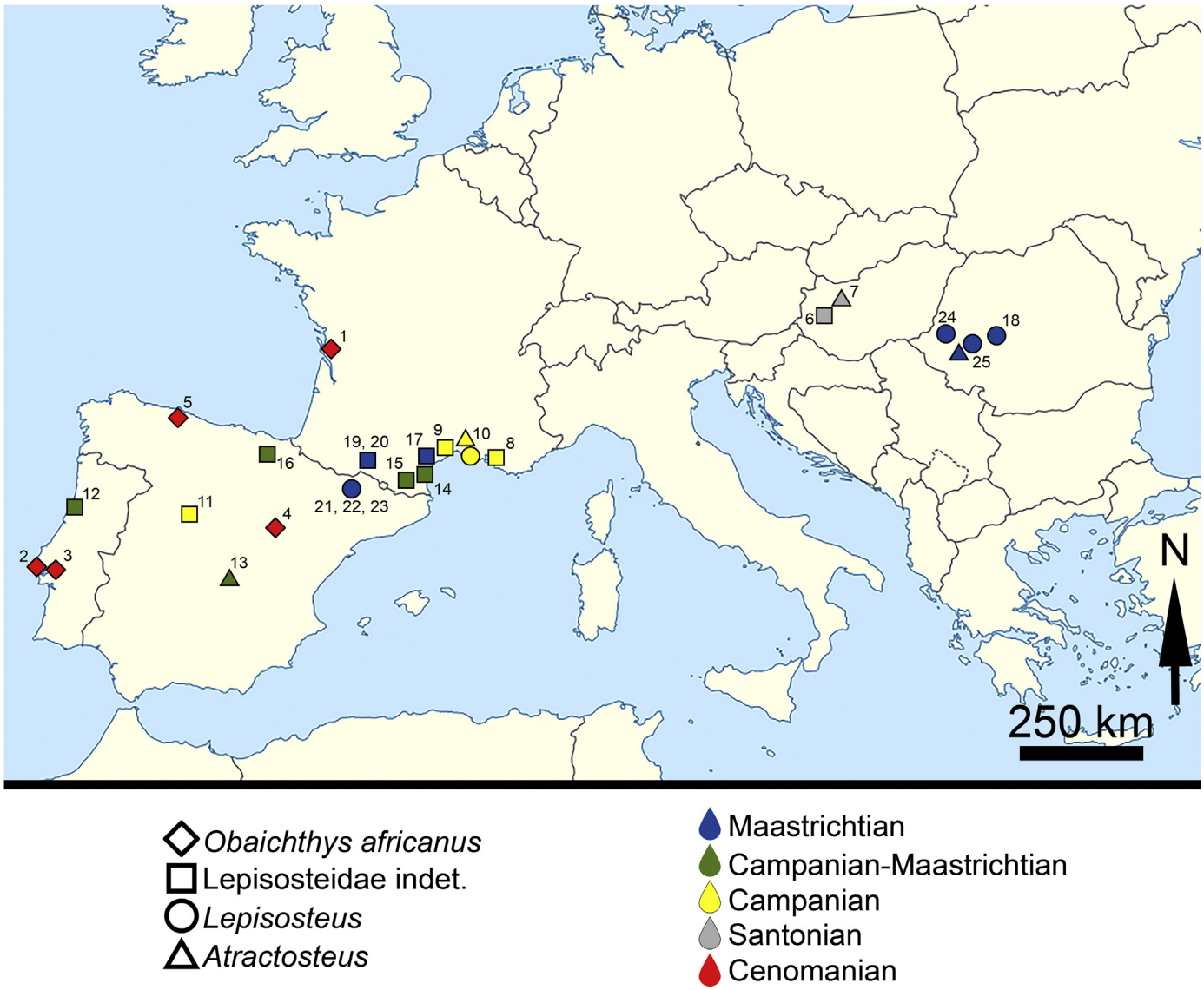


Fig. 1. Paleogeographic distribution of the Late Cretaceous Lepisosteiformes remains in Europe. 1, Les Renardiéres (France) (see Vullo and Néraudeau, 2008). 2, Cacém (Portugal) (see Jonet, 1970–71, 1981). 3, Pendão (Portugal) (see Sauvage, 1897–98). 4, Algora (Spain) (see Torices et al., 2012). 5, Asturias (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 et al., 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 et al., 2002). 20, Lestaillats (France) (Laurent et al., 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 and Néraudeau, 2008) and scales of ?*Dentilepisosteus kemkemensis* from Cacém (Portugal) (see Jonet, 1981). For further data see Table 1.

Europe during the Mesozoic (Csontos and Vörös, 2004). The oldest rock at the Iharkút locality is the Upper Triassic Main Dolomite Formation. Deep (50–90 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, 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 et al., 2015). Palynological studies indicate a Santonian age for this formation (Bodor and Baranyi, 2012). Bone-yielding beds which occur in various stratigraphic horizons in the Csehbánya Formation 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., 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.

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	Stage	Locality	Reference(s)
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–?upper 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 indet.	Infraorbitals (=lacrimomaxillae), dermopalatine, opercular bone, scales	Lower Campanian	Ventabren, France	Cavin et al., 1996; Grande, 2010
Lepisosteidae indet.	Teeth and scales	Lower 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, teeth, 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 lower Maastrichtian	Cruzy, Hérault, France	Buffetaut et al., 1999
Lepisosteus sp.	Scales	Maastrichtian	Oarda de Jos, Romania	Codrea et al., 2010
Lepisosteidae indet.	Scales, teeth, vertebrae	Upper Maastrichtian	Cassagnau, Petites Pyrénées, France	Laurent et al., 2002; Marmi et al., 2016
Lepisosteidae indet.	Scales	Upper Maastrichtian	Lestaillats, near to village Mauran, Petites Pyrénées, France	Laurent et al., 1999; Marmi et al., 2016
Lepisosteus sp.	Unpublished material	Upper Maastrichtian	Serrat del Pelleu, southern Pyrenees, Spain	Blanco and Bolet, 2014
Lepisosteus sp.	Unpublished material	Upper Maastrichtian	L'Espinau, southern Pyrenees, Spain	Blanco and Bolet, 2014
Lepisosteus sp.	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	Uppermost Maastrichtian	Budurone, Haţeg Basin, western Romania	Csiki et al., 2008
Lepisosteus sp.	Teeth and scales	Uppermost Maastrichtian	Budurone, Haţeg Basin, western Romania	Csiki et al., 2008

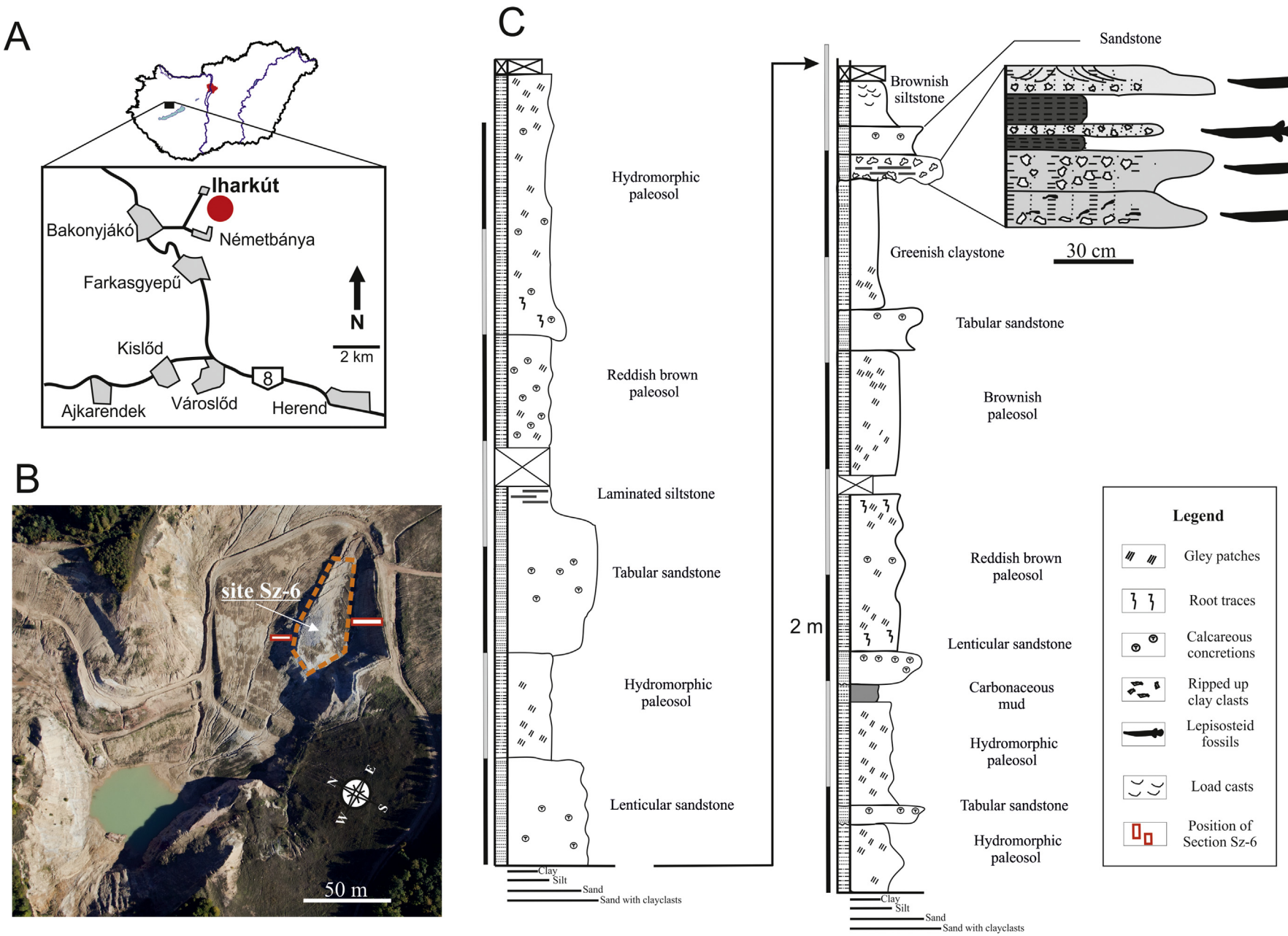


Fig. 2. A, Location map of the Iharkút vertebrate locality. B, Aerial photo of the Iharkút open-pit, showing the position of the SZÁL-6 site. C, Stratigraphic section of site SZÁL-6. (Modified after Botfalvai et al., 2015)

3. Material and methods

Lepisosteid remains from Iharkút have been collected during the summer fieldworks from 2000–2014, also by means of 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., 2015).

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

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.
(Figs. 3–8)

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 dermal bones (VER 2014.74.1-2., VER 2015.1.); 1672 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 2014.91.1-4., 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.); 45 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.); 490 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.,

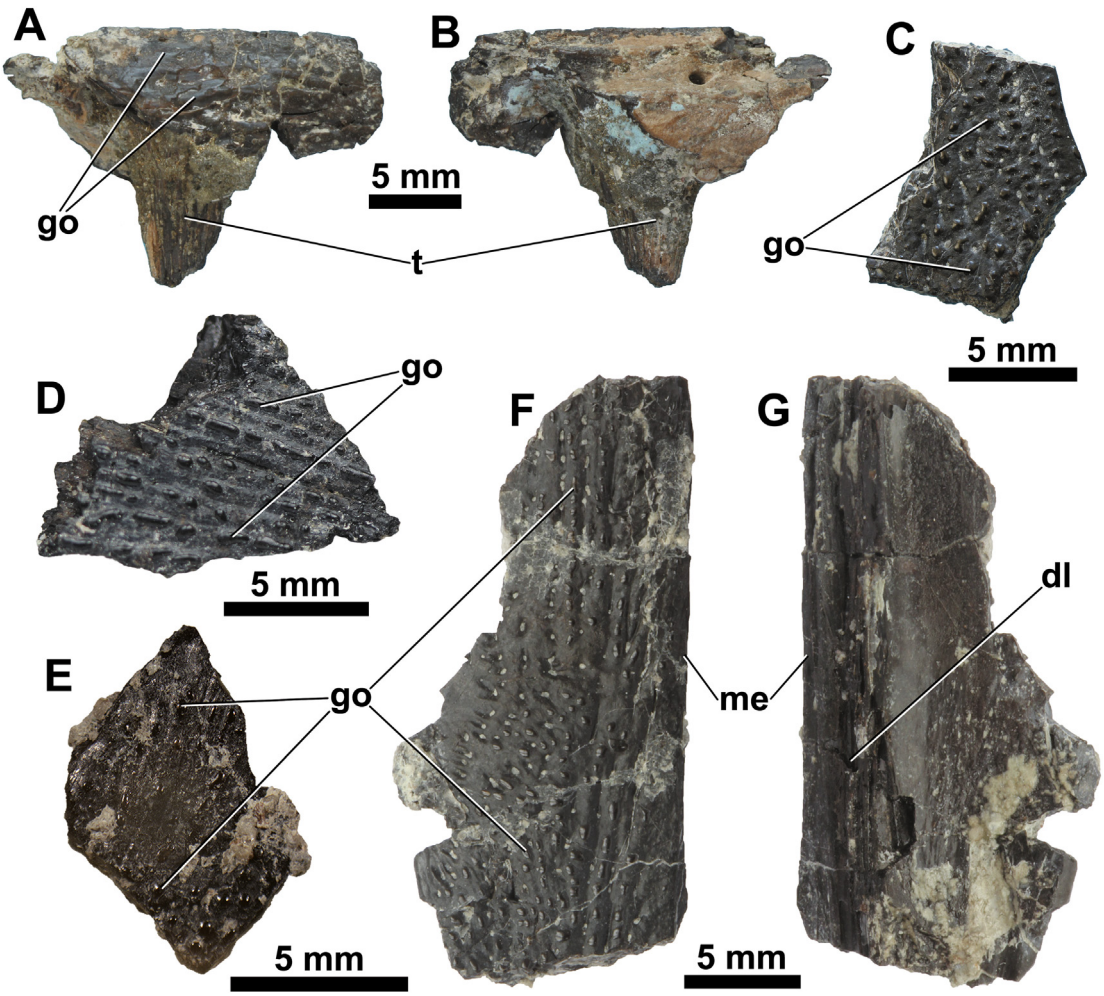


Fig. 3. *Atractosteus* sp. cranial remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, Lacrimomaxilla (V.2010.155.1.) in labial view; B, in lingual view. C–E, Unidentified dermal bones (VER 2014.74.1-2., VER 2015.1.) in outer view. F, Left frontal (VER 2014.73.) in dorsal view; G, in ventral view. Abbreviations: dl, descending lamina; go, ganoin ornamentation; me, medial margin; t, tooth.

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 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 recognized 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 with 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 *Lepisosteus indicus* Woodward, 1908 bears 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 on the skull.

Dentary: Among the four lepisosteid dentaries from Iharkút (VER 2014.75.1-2., VER 2014.77., VER 2015.2.) three specimens preserve teeth, or alveoli occasionally 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 is clearly visible along the medial side of the dentary. The preserved fragment is straight with the lateral

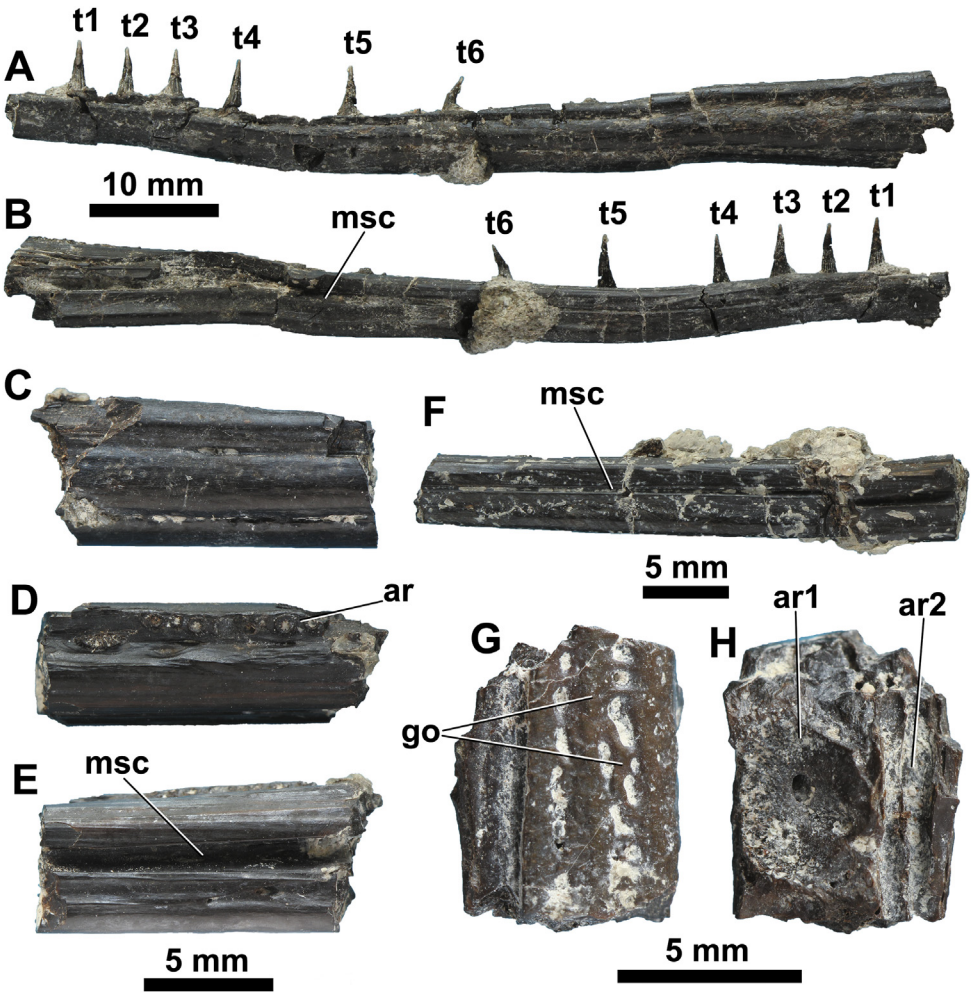


Fig. 4. *Atractosteus* sp. lower jaw remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, Left dentary (VER 2014.75.1.) in labial view; B, in lingual view. C, Dentary fragment (VER 2014.77.) in labial view; D, in occlusal view; E, in lingual view. F, Dentary fragment (VER 2014.75.2.) in lingual view. G, Dentary fragment (VER 2015.2.) in ventral view; H, in dorsal view. Abbreviations: ar, alveolar row; msc; mandibular sensory canal.

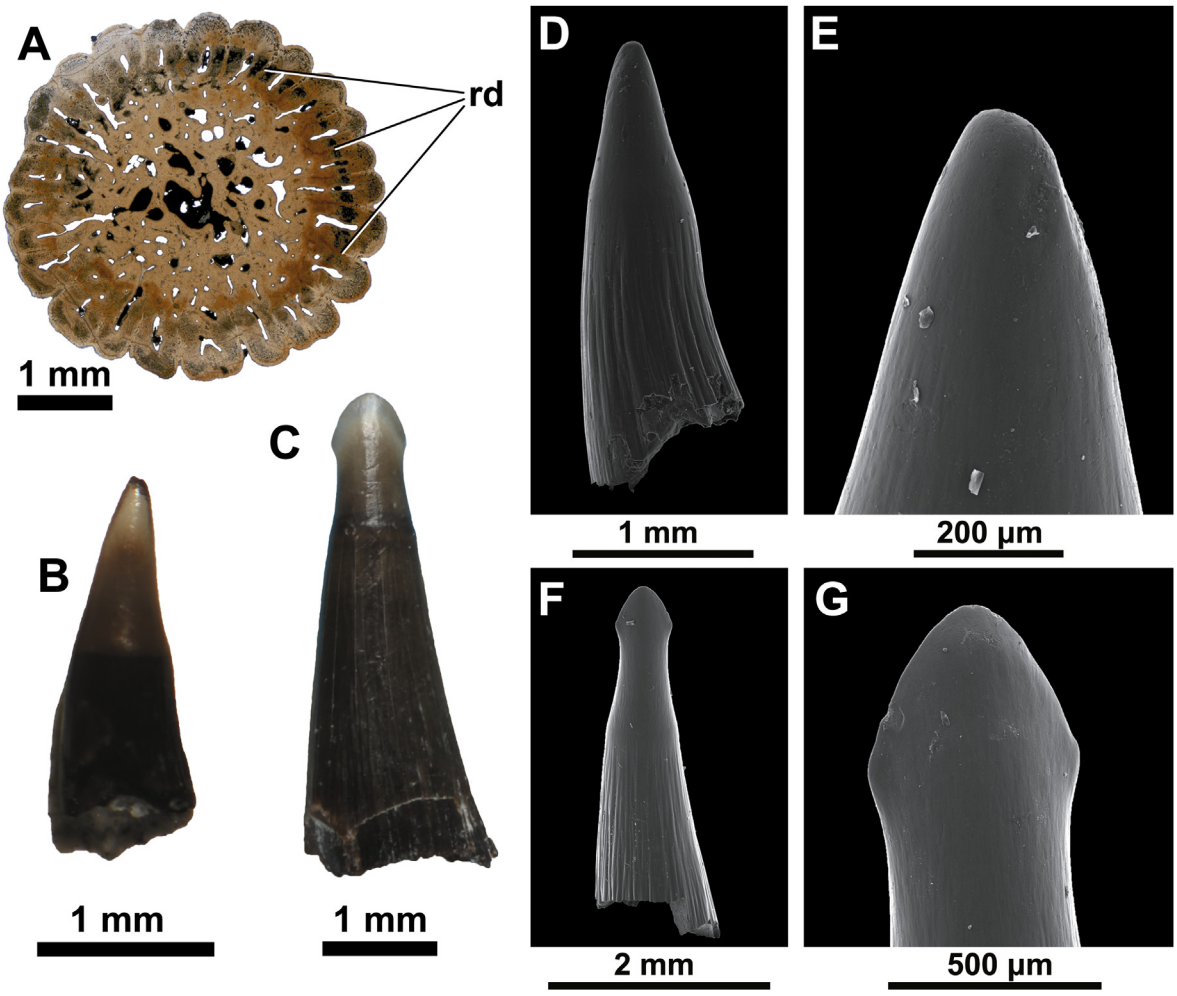


Fig. 5. *Atractosteus* sp. tooth remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, Cross-section of a tooth (VER 2014.91.3.). B, Conical tooth (VER 2015.32.). C, Lanceolate tooth (VER 2014.92.3.). D, Scanning electron micrograph of a conical tooth (VER. 2015. 33). 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.

surface devoid of ganoin (unlike most of the bones of the gar skull) but it has a smooth, longitudinal striation. Another specimen (VER 2015.2.; Fig. 4G–H) has ornamented ventral surface, and is 6 mm long and dorsoventrally flattened, 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: 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. They show the characteristic plicidentine structure (Grande, 2010) well seen in the external 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). 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). A few teeth have simple, conical tip (VER 2014.85., VER 2015.33., VER 2015.35.; Fig. 5D–E), and based on their size and apical morphology, they could have been part of the outer 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 lanceolate teeth (referable to *Atractosteus*) from Iharkút are similar to the teeth published from several Upper 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 et al. (1999), and the pointed *in situ* fangs published by Cavin et al. (1996). The apices 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.

5.2. Postcranial elements

Supracleithrum: A single, nearly complete right supracleithrum (VER 2015.246., Fig. 6) has an anteroposteriorly extending lateral line canal that enters the bone anterolaterally (near the dorsal process), and exits it posteromedially. A ganoin ornamentation on the dorsolateral surface of the bone is present. It has a dorsal and a ventral process, although only the base of the ventral process is preserved. The dorsal process bears no projecting ridges (see Wiley, 1976).

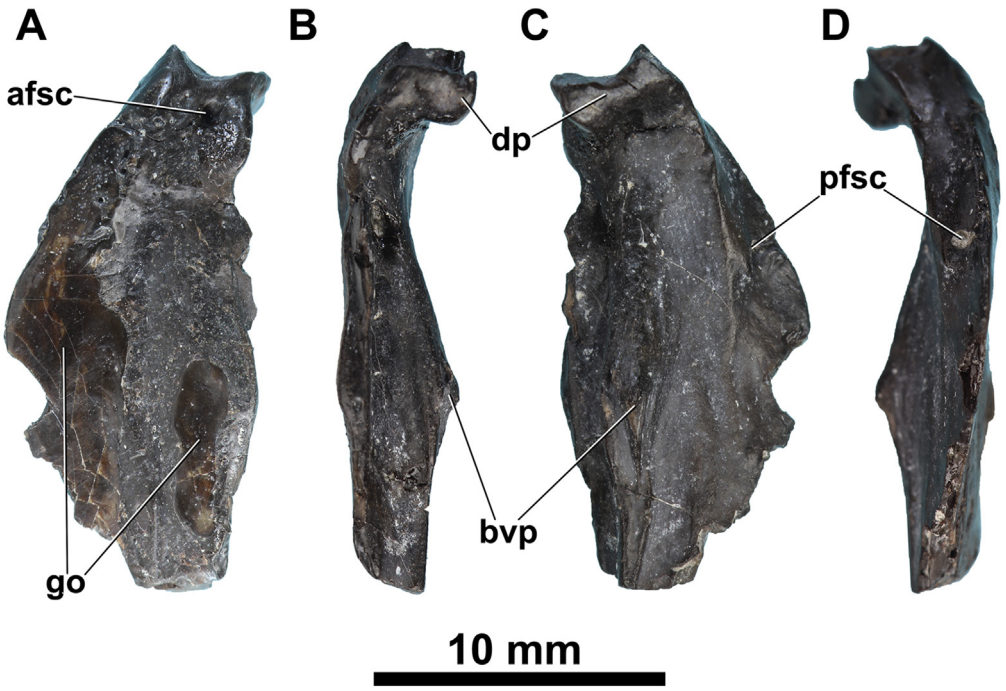


Fig. 6. *Atractosteus* sp. right supracleithrum (VER 2015.246.). A, In lateral view; B, in ventral view, C, in medial view; D, in dorsal view. Abbreviations: afsc, anterior foramen of the sensory canal; bvp, base of the ventral process; dp, dorsal process; go, ganoin ornamentation; pfsc, posterior foramen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

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 and Panteleeva, 1999), *Lepisosteus osseus* (see Grande, 2010), and all *Atractosteus* and *Lepisosteus* supracleithra published by Wiley (1976).

Vertebrae: 45 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

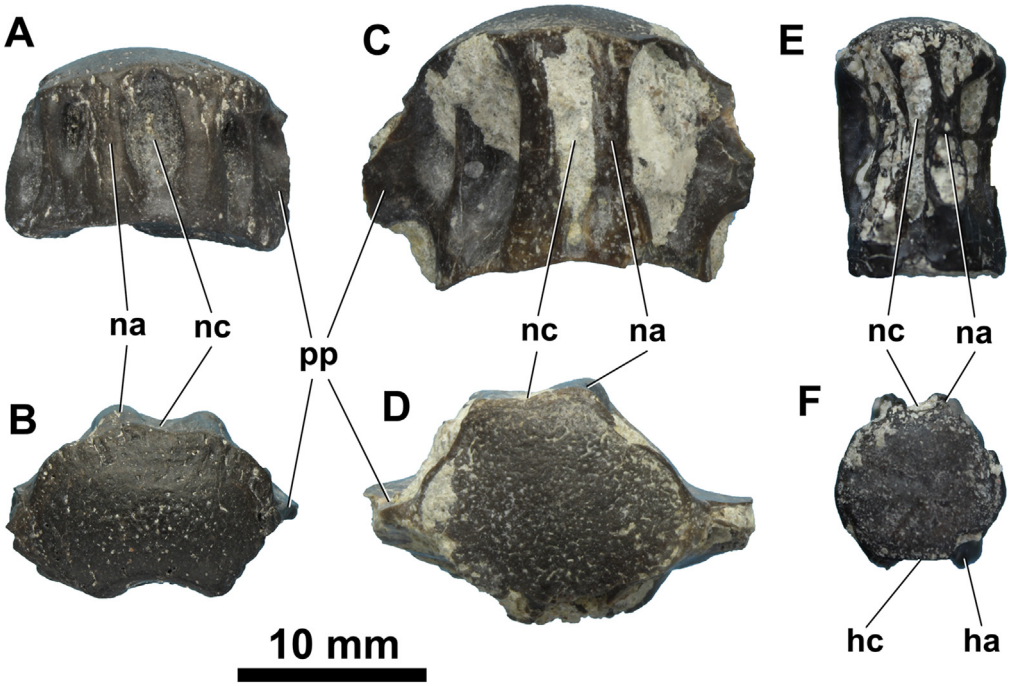


Fig. 7. *Atractosteus* sp. postcranial (vertebral) remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, Anterior abdominal vertebra (VER 2014.102.) in dorsal view; B, in anterior view. C, Abdominal vertebra (VER 2014.94., VER 2014.97.) in dorsal view; D, in anterior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

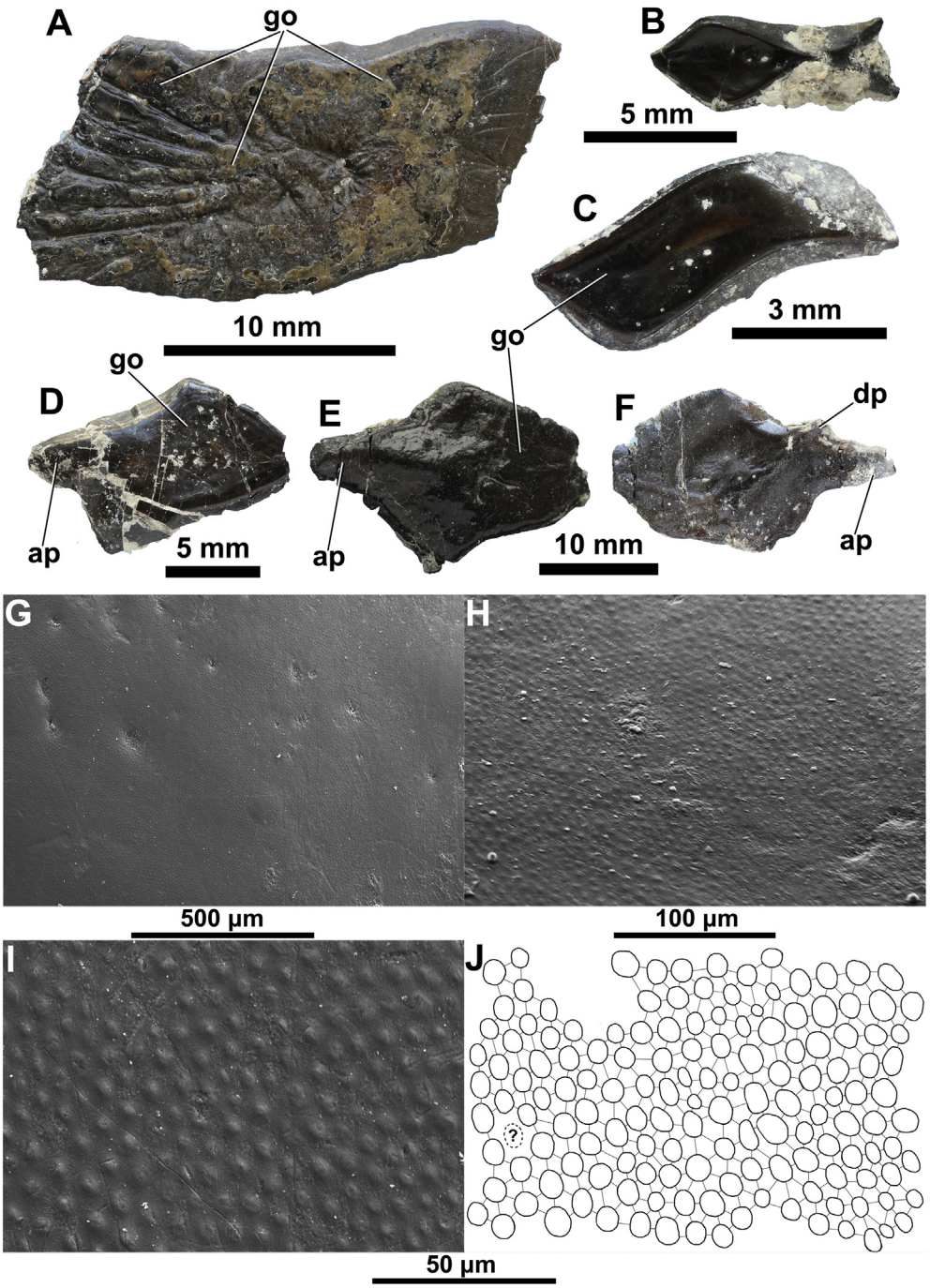
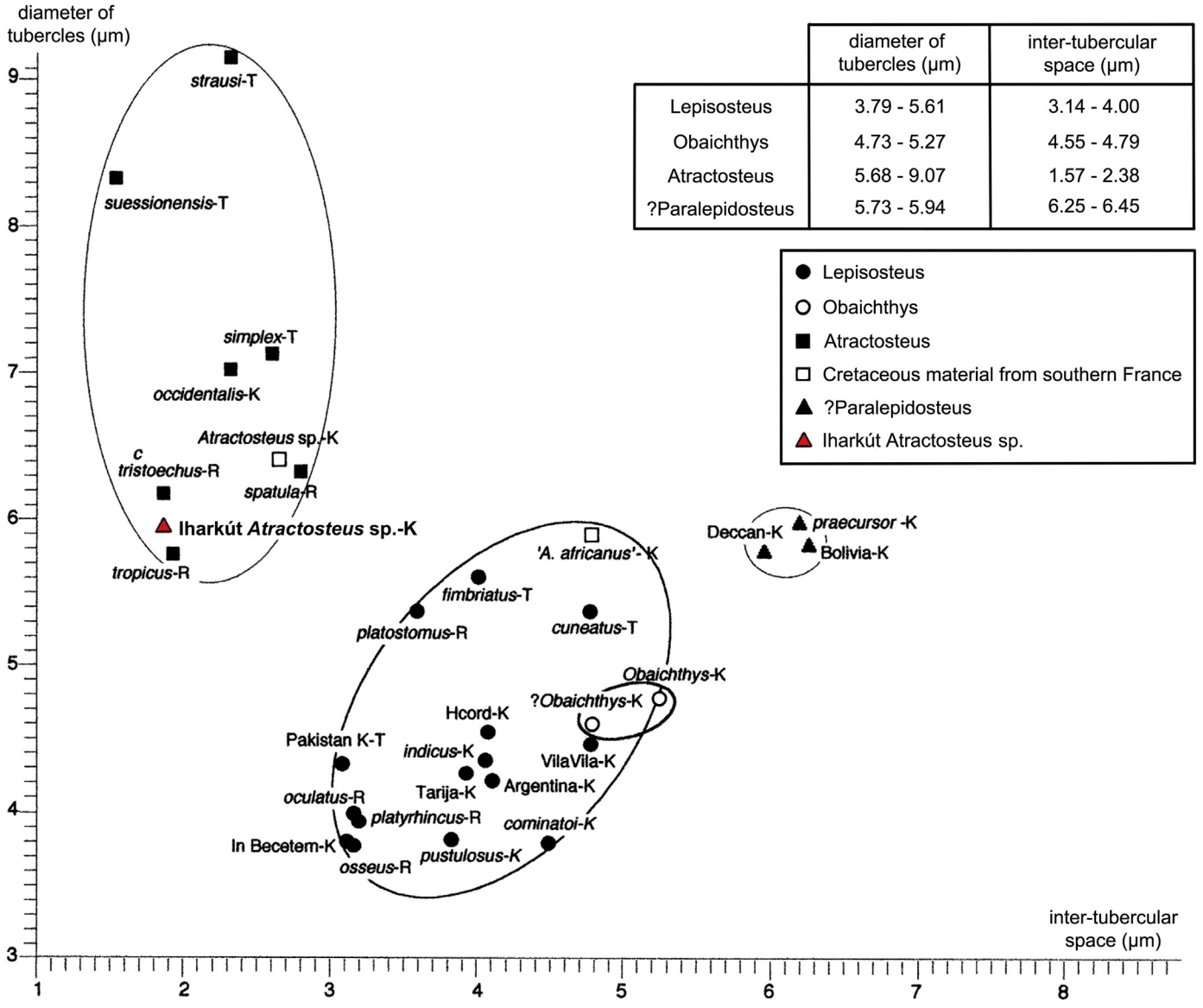


Fig. 8. *Atractosteus* sp. postcranial (scale) remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, Postcleithral scale. B, Dorsal precaudal midline scale (VER 2015.40.). C, ?Ventral scale (VER 2015.41.). D–F, Lateral scales (VER 2015.42, VER 2014.112., VER 2015.13). G–I, Scanning electron micrographs of the surface of a lateral 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.

lateral parapophyses, and dorsally the bases of the paired neural spines are also preserved. The vertebrae are variable in size and shape (Fig. 7). Anterior abdominal vertebrae are much lower dorsoventrally than the other abdominal vertebrae (Fig. 7A–B). The anteroposterior length of the vertebral centrum of the largest specimen (VER 2014.97.; Fig. 7C–D) is 13 mm, its dorsoventral height is 9 mm, and its mediolateral width is 15 mm. 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 of the genera *Lepisosteus* and *Atractosteus* are macromorphologically identical.

Scales: 490 ganoid scales referred to lepisosteid fishes are known from Iharkút. They 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 scales (Fig. 8F)



	diameter of tubercles (μm)	inter-tubercular space (μm)
Lepisosteus	3.79 - 5.61	3.14 - 4.00
Obaichthys	4.73 - 5.27	4.55 - 4.79
Atractosteus	5.68 - 9.07	1.57 - 2.38
?Paralepidosteus	5.73 - 5.94	6.25 - 6.45

Fig. 9. Measurements of the diameter of the ganoin tubercles and the intertubercular 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).

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 showing a typical tuberculated surface (Fig. 8G–J). The size of the scales varies from 2 × 3 mm to 19 × 25 mm.

The scales from Iharkút are similar in outer morphology to some published scales from other localities (Sauvage, 1897–98; Grigorescu et al., 1999; Becker et al., 2009; Pérez-García et al., 2016), 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.

5.3. Taxonomic assignment

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 of Grande, 2010) and the

Table 2
Measurements of the parameters on the microornamentation 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							

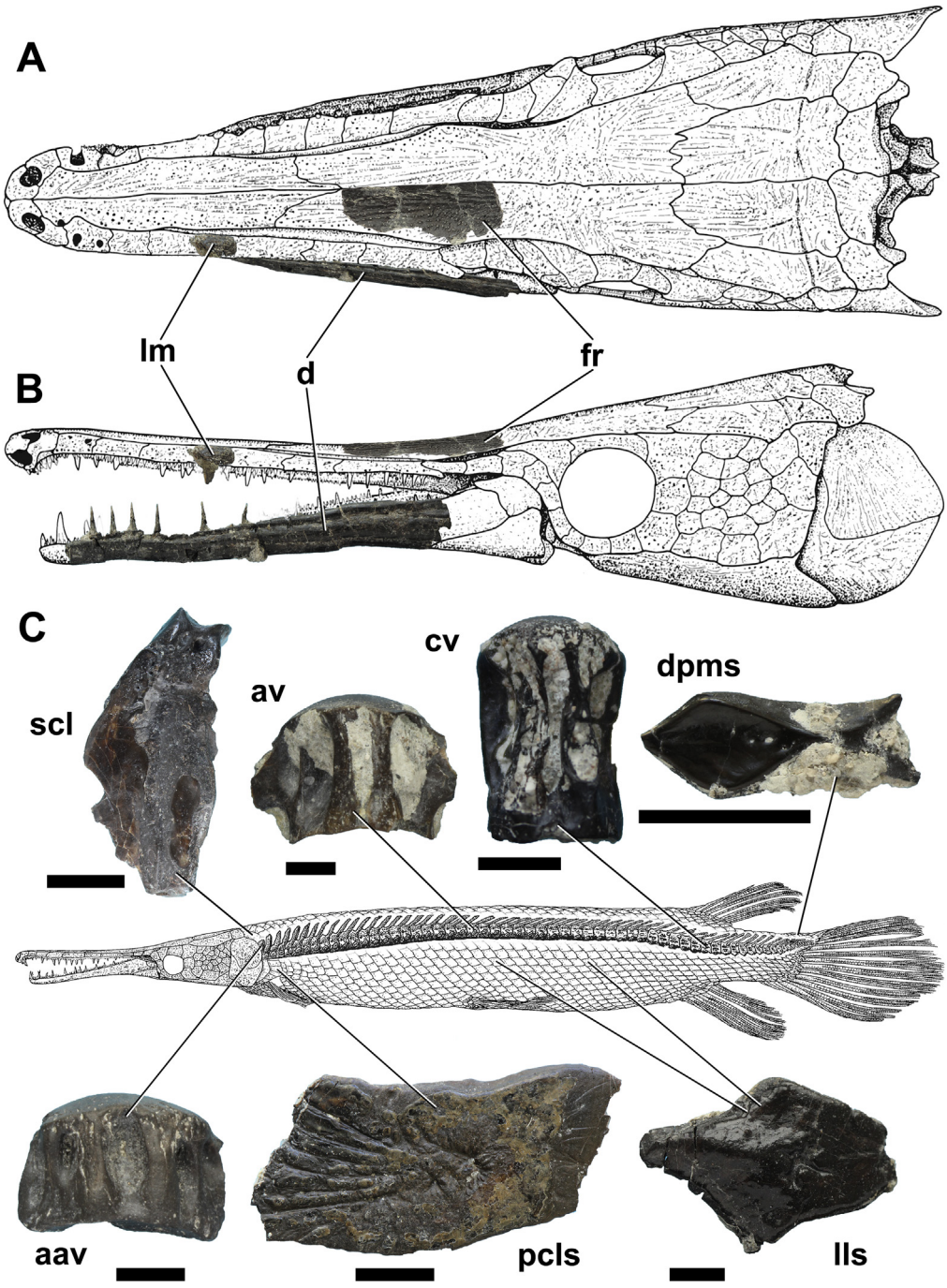


Fig. 10. Anatomical summary of the identified remains of the Iharkút *Atractosteus* sp. A, Skull line drawing with identified cranial elements in dorsal view; B, in lateral view. C, Full body line drawing with identified postcranial elements in lateral view. Line drawings are modified after Grande, 2010. Scale bars: 5 mm. Bone elements on figures A and B were figured with scale bars on Figs. 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 scale; lm, lacrimomaxillary bone; pcls, postcleithral scale; scl, supracleithrum.

supracleithrum has a concave dorsal articular facet (ch. 93 of Grande, 2010). The Iharkút form is a member of Lepisosteinae, since lacrimomaxillary bones are present (ch. 42 of Grande, 2010), and they can be referred to the tribe Lepisosteini because the dentary teeth are arranged as an outer row of small, similar sized conical teeth and an inner row of greatly enlarged fangs (ch. 39 of Grande, 2010).

Unfortunately, neither the single character (ch. 54 of 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 Grande, 2010: collective shape of laterally expanded part of vomerine heads, ch. 80 of Grande, 2010: tooth plates associated with second and third hypobranchials, ch. 104 of Grande, 2010: anterior end of first coronoid curves medially and expands broadly to a flat symphysis) described in *Atractosteus* can 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 Kammerer et al., 2006; Grande, 2010). Most of the gar teeth from Iharkút have lanceolate tip referring them to *Atractosteus*. Wiley (1976) distinguishes *Atractosteus* from *Lepisosteus* in having no projecting ridges on the supracleithrum. The single known Iharkút lepisosteid supracleithrum does not bear projecting ridges, strengthening the *Atractosteus* affinity.

Furthermore, other authors (e.g. Gayet and Meunier, 1986, 2001; Gayet et al., 2002) pointed out that the arrangement of ganoin tubercles on the external surface of the scales clearly distinguishes the extant lepisosteid genera from one another. Measurements were taken on the lateral surface of two well-preserved scales (VER 2015.39. and VER 2015.116.) having a shiny, thick ganoin layer The diameter of the ganoin tubercles was measured on 4–4 points on the examined scales, altogether on 596 tubercles (430 measured tubercles on specimen VER 2015.39., and 166 measured tubercles on specimen VER 2015.116.). Distances between the tubercles were also measured on the same 4–4 points on both scales. Altogether 1392 intertubercular distances have been measured (1078 measurements on specimen VER 2015.39., and 314 measurements on specimen VER 2015.116.). Comparison of our results with measurements on other lepisosteid scales indicates that the parameters of the microornamentation of the Iharkút gar scales are close to that of *Atractosteus* (Fig. 9 and Table 2).

Among the lepisosteid remains from Iharkút the teeth, the scales and the supracleithrum 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, until more complete material justifies otherwise.

6. Discussion

The *Atractosteus* material of Iharkút is of great importance, since these remains are not only teeth, scales and vertebrae, but various other cranial and mandibular elements and a supracleithrum that help in further 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) 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 (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 *Oniichthys* (regarded as *Atractosteus* in 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 Upper 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 lower Campanian of southern France (Cavin et al., 1996), where the authors concluded that this material belongs to *A. africanus* previously described as '*Paralepidosteus*' *africanus* (Arambourg and Joleaud, 1943) from the Upper Cretaceous 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 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 were later referred to Lepisosteidae indet. (Pereda-Suberbiola et al., 2015). In addition, some skull bones, teeth, opisthocoelous vertebrae and scales are known from the Campanian–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), France (Vullo and Néraudeau, 2008) and Spain (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* (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 Grande, 2010; Cavin et al., 2015).

Concerning the Maastrichtian remains from the Haţeg Basin, Romania, additional material was described from different localities (Codrea et al., 2010; Weishampel et al., 2010) since the publication of the first remains (Grigorescu et al., 1999), but with a few exceptions (e.g. Csiki et al., 2008) their detailed description is still to be done. The lepisosteid material of the Santonian of Ajka (Hungary) (Ősi et al., 2016), and the Campanian–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 Cretaceous record is well supported, based on tooth morphology, 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 Campanian of western Europe. The current record indicates the occurrence of *Atractosteus* from the Santonian to Campanian (perhaps up to the Maastrichtian) with the Hungarian fossils being the earliest occurrence of the genus in the European archipelago.

7. Conclusions

Tooth morphology, scale microornamentation 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 composed of at least the obaichthyids (*Obaichthys*) during the early Late Cretaceous and lepisosteids (*Atractosteus* and *Lepisosteus*) in the Santonian to Maastrichtian period.

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