

The continental fish fauna of the Late Cretaceous (Santonian) Iharkút locality (Bakony Mountains, Hungary)

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The Late Cretaceous (Santonian) fish fauna of the Iharkút vertebrate site (Bakony Mountains, Hungary) is described here. The ichthyofauna includes the lepisosteid *Atractosteus* sp., the pycnodontid cf. *Coelodus* sp., Vidalamiinae indet., a non-vidalamiin Amiidae indet., Elopiformes indet., two indeterminate ellimichthyiforms, cf. Salmoniformes indet., Acanthomorpha indet., at least one indeterminate teleostean, and numerous indeterminate actinopterygians (represented by teeth). Among these taxa, the Iharkút remains of Vidalamiinae and the suggested indeterminate Salmoniformes represent their first occurrence in the Late Cretaceous of Europe. The unidentifiable specimens may suggest the presence of further fish taxa. The gar remains described here further support the *Atractosteus* sp. affinity of the Iharkút form. Most of the Iharkút fishes are carnivorous, but durophagous taxa are also represented. Although chondrichthyan remains have not been identified in the Iharkút vertebrate material up to now, the ecological distribution of some local fish taxa presumes the possible vicinity of a marine–deltaic environment. Several Iharkút fish taxa are known from North American localities as well, suggesting that the Late Cretaceous European continental fish might have been more diverse and similar to that of North America than previously thought. The necessity of more intensive screen-washing at other European Late Cretaceous vertebrate sites is also emphasized.

Keywords: Iharkút, Santonian, fish fauna, microvertebrates, Vidalamiinae

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Introduction

Fishes are important faunal elements of Late Cretaceous non-marine paleocommunities. Studies on the diversity and distribution of fish in the Late Cretaceous could provide conclusive informations on understanding the structure and structural changes of continental paleocommunities through this era. Excavations of European Late Cretaceous continental vertebrate localities resulted in a high number of various osteichthyan fish remains referred to at least 11 families (summarized in the paper of Csiki-Sava et al. 2015), but in most cases, these fossils are isolated elements.

The ichthyofauna of the Late Cretaceous (Santonian) Iharkút vertebrate locality (Csehbánya Formation, western Hungary) was partially described (Makádi et al. 2006; Ősi et al. 2012; Szabó et al. 2016a, 2016b), but the excavations and extensive screen-washing in the last 16 years clearly demonstrated that the Iharkút ichthyofauna is much more diverse than previously thought. In addition to lepisosteiforms and pycnodontiforms, remains of at least four additional orders of fish have been unearthed increasing the diversity of the Iharkút fish fauna (Table 1).

In this paper, we describe these new fish remains from Iharkút, compare them with related remains from other European and non-European localities (mostly from Mesozoic eras), and discuss their paleoecological and paleobiogeographical significance.

Locality and geological background

The Iharkút vertebrate fossil site is situated in the southeastern part of an open-pit bauxite mine near the villages of Németsbánya and Bakonyjákó (Bakony Mountains, western Hungary, 47° 13' 52" N, 17° 39' 01" E; Fig. 1). Iharkút is located on the Transdanubian Central Range, a tectonic block that was part of the Apulian microplate located between Africa and Europe during the Mesozoic (Csontos and Vörös 2004). The oldest rock outcropping at the locality is the Upper Triassic Main Dolomite Formation. The Cretaceous (pre-Santonian) bauxite (Nagytárkány Bauxite Formation), mined in the area from the 1970s, was deposited in deep (50–90 m), tectonically controlled and karstified sinkholes within the Triassic dolomite.

The bauxite, together with the karstified paleosurface of Triassic rocks, is overlain by the Csehbánya Formation, an alluvial flood plain deposit consisting of alternating coarse basal breccia, sandstone, siltstone, and paleosol beds deposited in a freshwater environment (Jochá-Edelényi 1988; Ősi and Mindszenty 2009; Botfalvai et al. 2016). The age of this formation is Santonian based on palynological studies (Bodor and Baranyi 2012). In the last 16 years, systematic excavations of the bone-yielding beds, occurring in various stratigraphic horizons in the Csehbánya Formation, resulted in a rich (specimen number > 50.000) and diverse (taxon number > 40) fossil assemblage of isolated and associated bones, teeth, and plant remains. The vertebrate fauna is composed of fishes, amphibians, turtles, mosasaurs and other lizards, pterosaurs, crocodylians, and dinosaurs including birds (Ősi et al. 2012). The most productive sequence (SZ-6 site) is a grayish, coarse basal breccia covered with sandstone and

Table 1
 Ichthyofaunal list of the Late Cretaceous (Santonian) Iharkút vertebrate site

Superclass Osteichthyes
Class, subclass, cohort, order, family, and genus indet.
Class Actinopterygii
Subclass, cohort, order, family, and genus indet.
Subclass Neopterygii
Infraclass Holostei
Order Lepisosteiformes
Family Lepisosteidae
<i>Atractosteus</i> sp.
Order Pycnodontiformes
Family Pycnodontidae
cf. <i>Coelodus</i> sp.
Order Amiiformes
Family Amiidae
Subfamily indet.
Subfamily Vidalamiinae
Infraclass Teleostei
Cohort, order, family, and genus indet.
Cohort Elopomorpha
Order Elopiformes
Family and genus indet.
Cohort Otocephala
Order Ellimmichthyiformes
Family and genus indet. 1
Family and genus indet. 2
Cohort Euteleostei
Subcohort Protacanthopterygii
Order cf. Salmoniformes
Family and genus indet.
Subcohort Neoteleostei
Subsection Acanthomorpha
Order, family, and genus indet.

brownish siltstone that produced 99% of the vertebrate remains including the fish fossils described in this paper.

At the Iharkút locality, the Csehbánya Formation is partially overlain by the Middle Eocene Iharkút Conglomerate Formation and partially by Pleistocene loess.

Materials and methods

All fish remains described here were unearthed from the bone-yielding beds of the Santonian Csehbánya Formation, at the SZÁL-6 site of Iharkút, during the period 2000–2015. The macroscopic material was collected through hand-quarrying, whereas the microscopic material has been sampled by underwater screening processes.

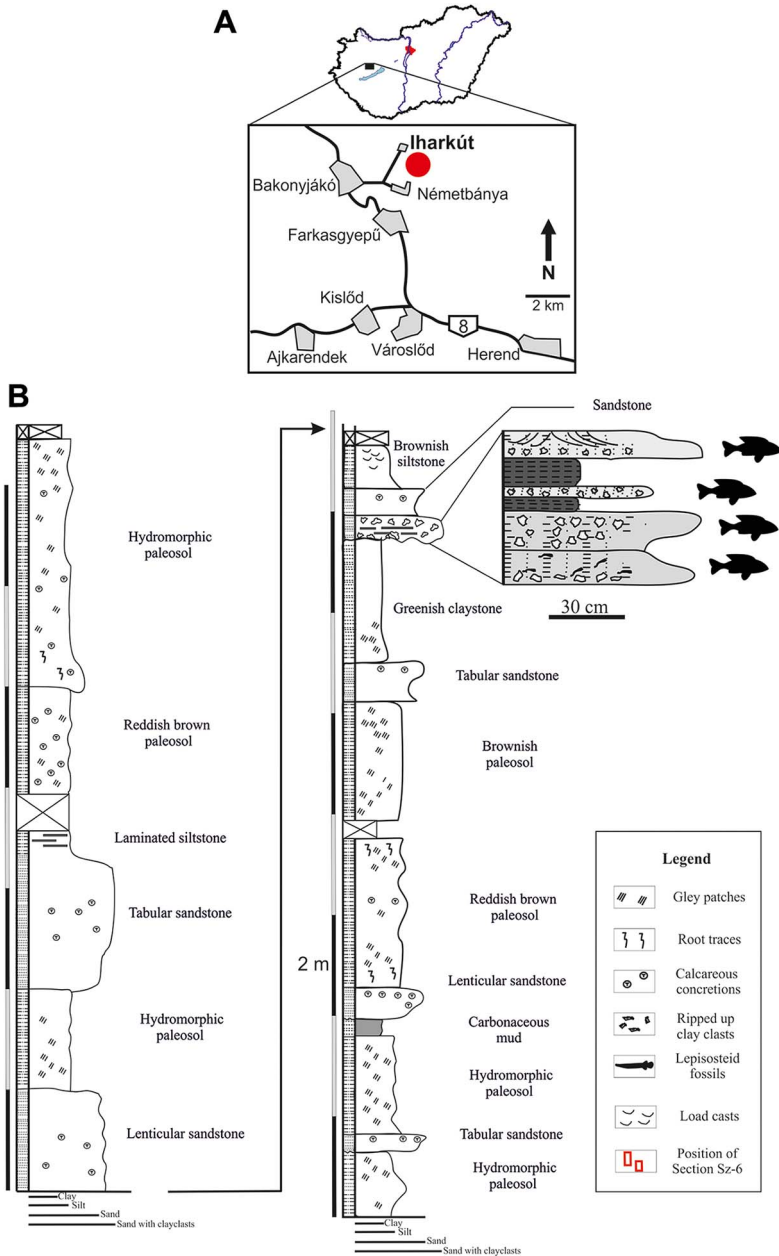


Fig. 1
 (A) Location map of the Iharkút vertebrate locality. (B) Stratigraphic section of site SZÁL-6 (modified after Botfalvai et al. 2016; Szabó et al. 2016a)

All specimens are housed in the vertebrate paleontological collection of the Hungarian Natural History Museum (Magyar Természettudományi Múzeum). For repairing the broken specimens, cyanoacrylate (superglue) was used. Most of the collected material is brownish or black in color. Since the specimens are rich in pyrite, some of the specimens were treated with polyvinyl butyral to stop or at least slow down the oxidization of the pyrite. Specimens VER 2010.130.A-B, VER 2014.111.A-C, and VER 2015.283.A-B got individual, letter-associated numbering.

For scanning electron microscopic photography, we used a Hitachi S-2600N scanning electron microscope. We measured the line drawings of the ganoine microspheres with the free version of ImageJ 1.48v. Photographs of specimen VER 2016.2811. were taken with a QImaging MP5.0 digital microscope camera under a Nikon LV100 polarized light microscope and processed with Image-Pro Insight 8.0 software.

For specimen orientations of VER 2016.2782., we used the work of Grande and Bemis (1998, captions of Figs 54–56). Osteichthyan classification used in this paper follows the works of Nelson (2006) and Wiley and Johnson (2010), in accordance with Grande and Bemis (1998) and Grande (2010).

Systematic paleontology

Superclass Osteichthyes Huxley 1880

Class Actinopterygii Cope 1887

Subclass Neopterygii Regan 1923

Infraclass Holostei Müller 1846

Order Lepisosteiformes Hay 1929

Family Lepisosteidae Cuvier 1825

Genus *Atractosteus* Rafinesque 1820

Atractosteus sp.

(Figs 2–7)

Referred material. Seven hemitrichia (VER 2016.2766., VER 2016.2767., VER 2016.2768., VER 2016.2769.), eight ?fringing fulcræ and/or ?rudimentary fin rays (VER 2015.289., VER 2016.2770., VER 2016.2771., VER 2017.2772., VER 2016.2773., VER 2016.2774.), one ?anal or ?ventral midline scale (VER 2015.294.), 14 unidentified elements (VER 2014.76., VER 2015.271., VER 2015.272., VER 2015.283.A-B, VER 2016.2775., VER 2016.2776., VER 2016.2777., VER 2016.2778., VER 2016.2779., VER 2016.2780., VER 2016.2781.).

Remarks. The Iharkút locality is very rich in lepisosteid fossils, and some of these remains were described as *Atractosteus* sp. (Szabó et al. 2016a). All additional specimens described below have a bony base covered by a layer of ganoine arranged in different patterns. Since there is no sign of the presence of

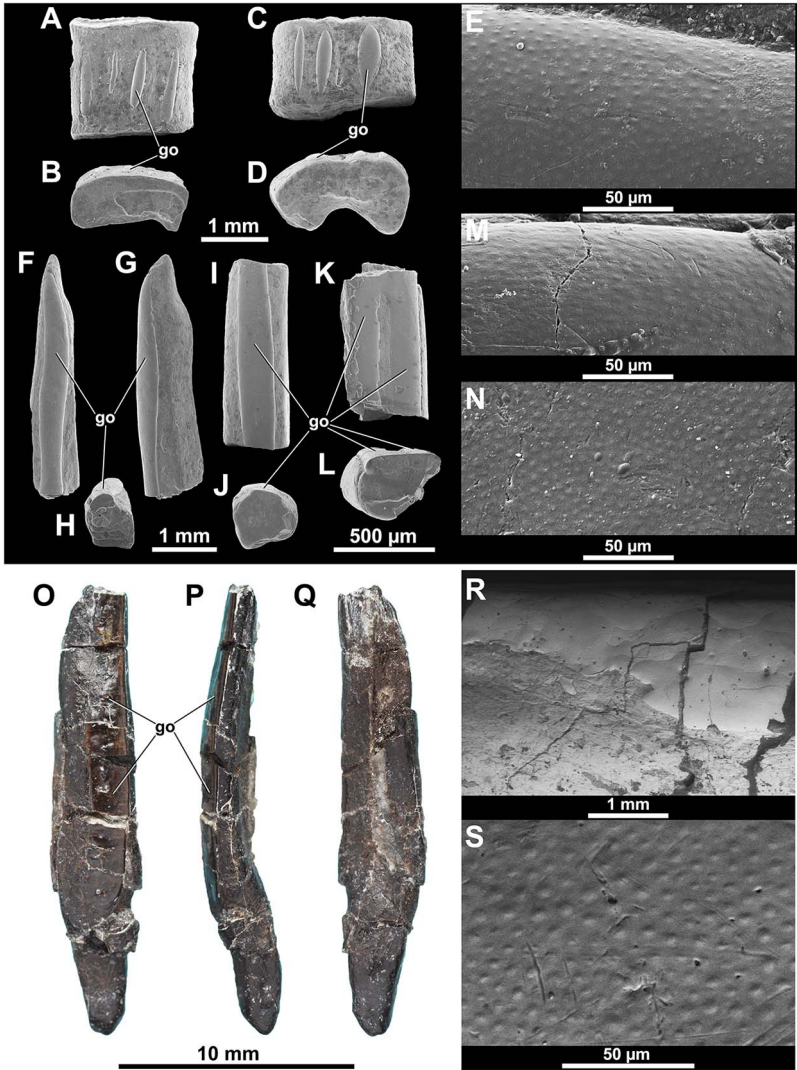


Fig. 2
Atractosteus sp. remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) Hemitrichium (VER 2016.2766.) in outer view; (B) in cross-view. (C) Hemitrichium (VER 2016.2767.) in outer view; (D) in cross-view. (E) Scanning electron photograph of the ganoine ornamentation of specimen VER 2016.2766. (A and B of the current figure). (F) ?Fringing fulcrum or ?rudimentary fin ray (VER 2016.2771.) in outer view; (G) in profile view; (H) in cross-view. (I) ?Fringing fulcrum or ?rudimentary fin ray (VER 2016.2772.) in outer view; (J) in cross-view. (K) ?Fringing fulcrum or ?rudimentary fin ray (VER 2016.2773.) in outer view; (L) in cross-view. (M) Scanning electron photograph of the ganoine ornamentation of specimen VER 2016.2771. (F–H of the current figure). (N) Scanning electron photograph of the ganoine ornamentation of specimen VER 2016.2773. (K and L of the current figure). go – ganoine ornamentation. (O) ?Fringing fulcrum or ?rudimentary fin ray (VER 2015.289.) in outer view; (P) in profile view; (Q) in inner view. (R, S) Scanning electron photographs of the ganoine ornamentation of specimen VER 2015.289. (O–Q of the current figure). go – ganoine ornamentation

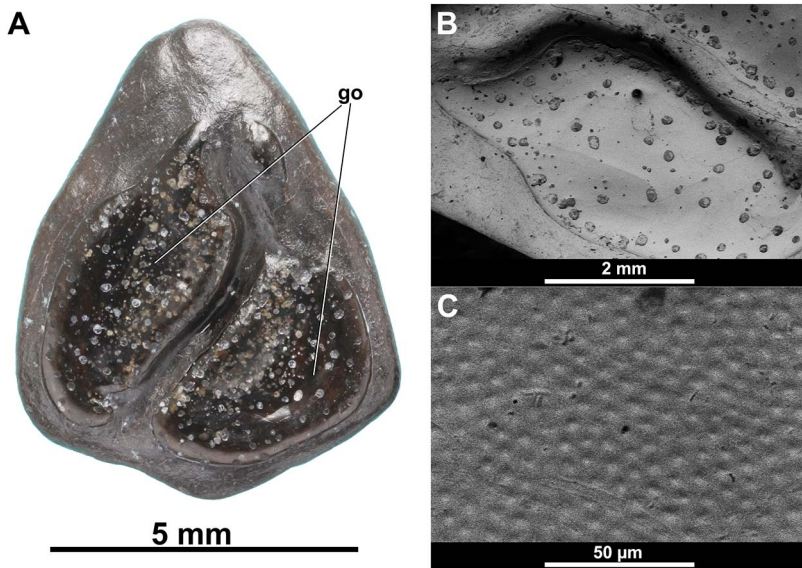


Fig. 3
Atractosteus sp. ?anal or ?ventral midline scale (VER 2015.294.) from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) Outer view. (B, C) Scanning electron micrographs of the ganoine ornamentation

other ganoid fishes at the locality, we refer these fossils to *Atractosteus* sp. until more or better preserved specimens clarify their more precise taxonomic identity. For supporting their *Atractosteus* relationship, distance measurements on the ganoine microsurface of the specimens were taken following the methods of Gayet and Meunier (2001), and Gayet et al. (2002). The results of these measurements are summarized in Table 2.

Fin elements. The hemitrichia are small, half tube-like elements showing a “C”-shaped contour in cross section (Fig. 2A–E). The ganoine ornamentation is arranged in 3–6 narrow, linear, elongated oval to stripe-like ridges, running subparallel on the outer surface of the specimens. Lepisosteid principal fin rays are made up by closely similar elements (Figs 127, 148, 169, 317, 338, 361, 420, and 445 in Grande 2010). Lepisosteid lepidotrichia are made up by sectionally arranged pairs of hemitrichia. These hemitrichia are “C”-shaped cross section and made up by a bony base with ganoine ridges on their outer surface. Each pair of hemitrichia are joined along their length, forming a tube-like structure. Morphologically identical remains were reported from the Lower Cretaceous (Barremian) Wessex Formation of the Isle of Wight, England as *Scheenstia* sp. scales (Fig. 13H, J in Sweetman et al. 2014). Identical remains are known from the Maastrichtian of the Iberian Peninsula (Blanco et al. 2017). A lepisosteid hemitrichium from the

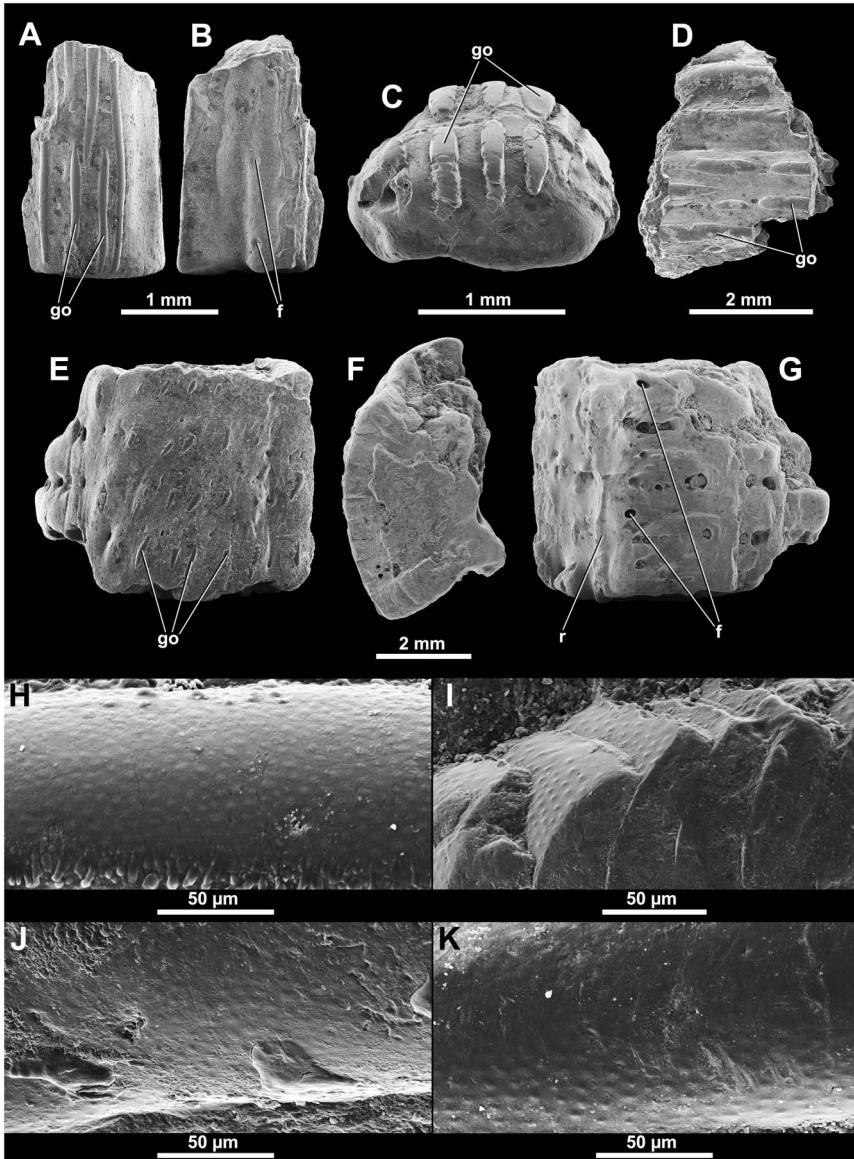


Fig. 4
Atractosteus sp. indeterminate elements from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A, B) VER 2016.2777. (C) VER 2016.2778. (D) VER 2016.2780. (E–G) VER 2016.2779. (H) Scanning electron photograph of the ganoine ornamentation of specimen VER 2016.2777. (A and B of the current figure). (I) Scanning electron photograph of the ganoine ornamentation of specimen VER 2016.2778. (C of the current figure). (J) Scanning electron photograph of the ganoine ornamentation of specimen VER 2016.2780. (D of the current figure). (K) Scanning electron photograph of the ganoine ornamentation of specimen VER 2016.2779. (E–G of the current figure). f – foramen; go – ganoine ornamentation; r – ridge

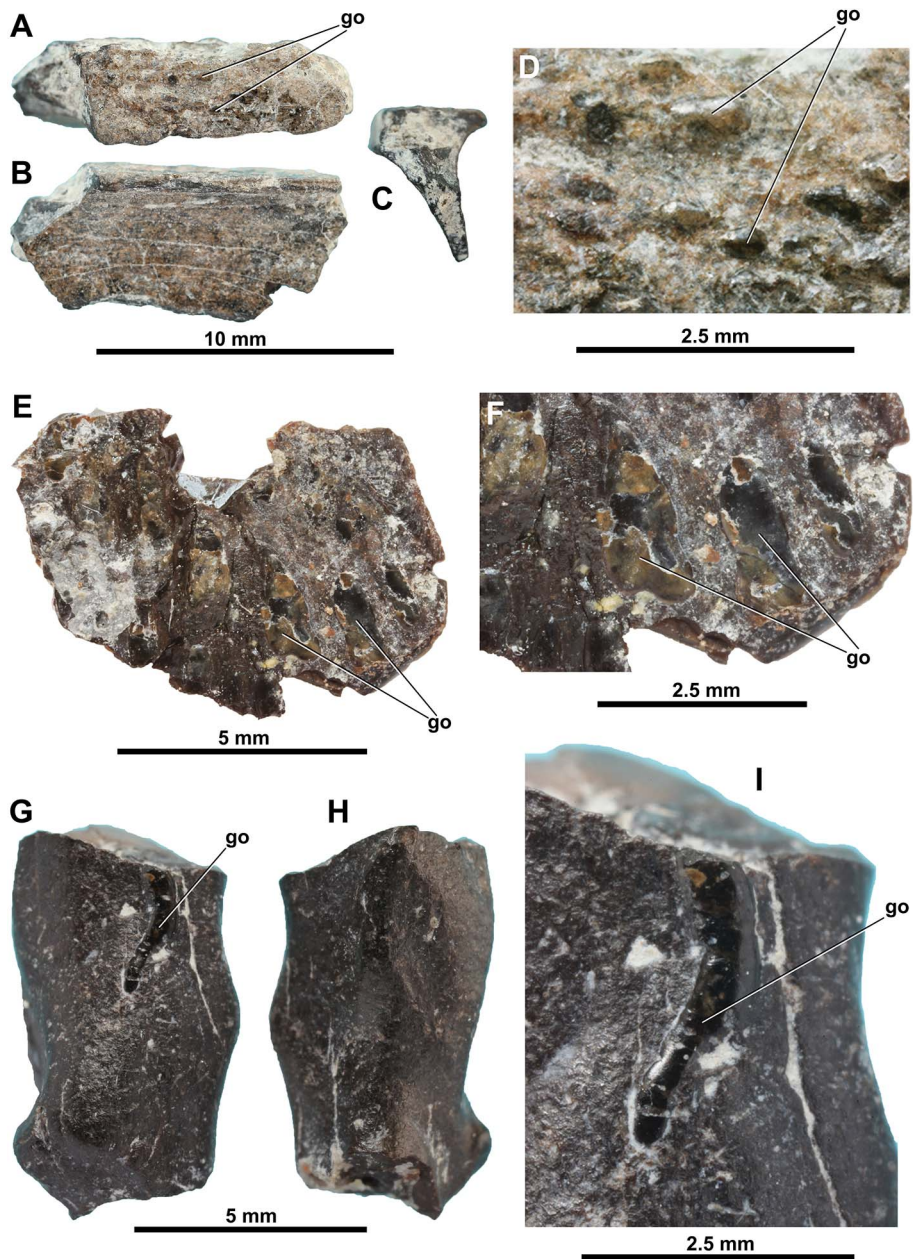


Fig. 5
Atractosteus sp. indeterminate elements from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A–C) VER 2015.283.A in three different views; (D) close-up of the ganoine ornamentation. (E) VER 2015.283.B; (F) close-up of the ganoine ornamentation. (G, H) VER 2016.2781.1; (I) close-up of the ganoine ornamentation. go – ganoine ornamentation

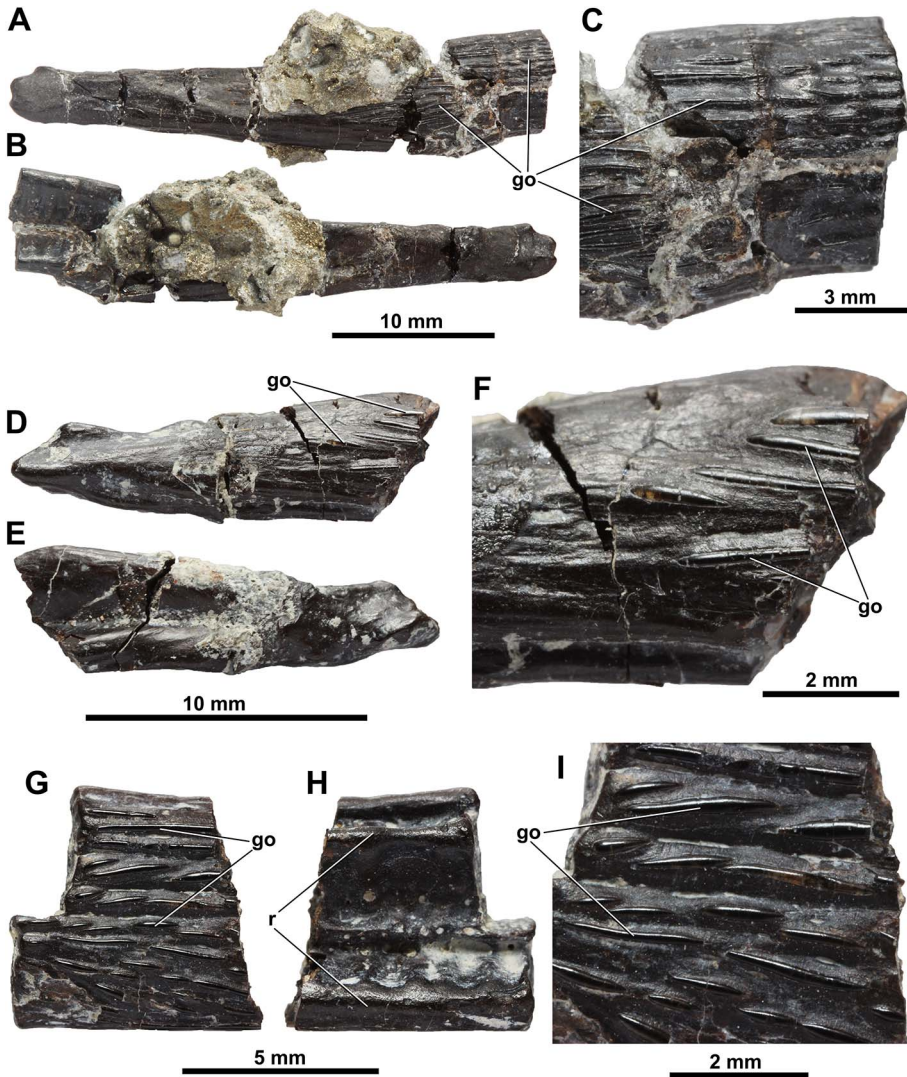


Fig. 6
Atractosteus sp. indeterminate elements from the Upper Cretaceous (Santonian) Csehánya Formation (Iharkút, Hungary). (A) VER 2015.271. in outer view; (B) in inner view; (C) close-up of the ganoine ornamentation. (D) VER 2015.272. in outer view; (E) in inner view; (F) close-up of the ganoine ornamentation. (G) VER 2014.76. in outer view; (H) in inner view; (I) close-up of the ganoine ornamentation. go – ganoine ornamentation; r – ridge

Late Cretaceous of Madagascar was published by Gottfried and Krause (1998, Fig. 1D) showing different ornamentation, size, and shape compared with those of the Iharkút specimens.

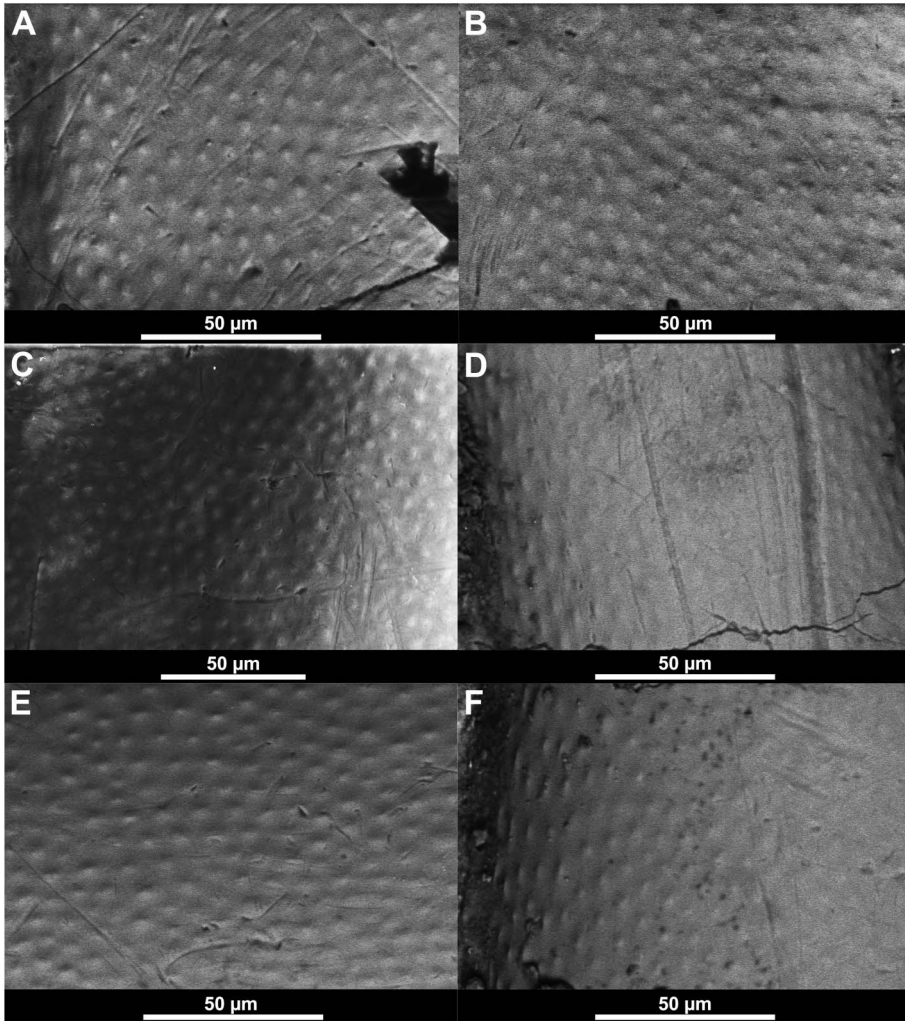


Fig. 7
 Scanning electron photographs of *Atractosteus* sp. indeterminate elements from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) VER 2015.283.A (same specimen on Fig. 5A–D). (B) VER 2015.283.B (same specimen on Fig. 5E, F). (C) VER 2016.2781. (same specimen on Fig. 5G–I). (D) VER 2015.271. (same specimen on Fig. 6A–C). (E) VER 2015.272. (same specimen on Fig. 6D–F). (F) VER 2014.76. (same specimen on Fig. 6G–I)

The suggested fringing fulcræ or rudimentary fin rays have an elongated, rod- to knife-like contour, while they are irregular, drop-like, or oval to circular in cross section. The ganoine ornamentation is arranged in one (Fig. 2F–J, O) or two

Table 2
Measurements of the parameters on the microornamentation of the ganoine on the Iharkút gar remains (including the results of Szabó et al. 2016a; Table 2)

Specimen		Measured tubercles	Measured inter-tubercular spaces	Average tubercle diameter (μm)	Average inter-tubercular space (μm)
Hemitrichia	VER 2016.2766.	58	122	6.96	1.63
	VER 2016.2767.	52	110	6.76	1.45
	VER 2016.2768.	48	83	6.42	1.88
Fin ray	VER 2015.289.	40	92	6.38	2.14
	VER 2016.2770.	32	66	8.36	1.79
	VER 2016.2771.	32	69	7.33	1.84
	VER 2016.2772.	49	100	7.79	1.62
	VER 2016.2773.	49	101	6.2	1.04
Scales in Szabó et al. (2016a)	VER 2015.39.	430	1,078	5.85	2.09
	VER 2015.116.	166	314	5.99	1.64
Anal scale	VER 2015.294.	46	101	6.4	1.4
Indeterminate elements	VER 2015.272.	45	104	6.3	2.15
	VER 2015.271.	23	42	6.21	1.67
	VER 2014.76.	47	91	6.29	2.11
	VER 2015.283.A	59	121	6.72	2.01
	VER 2015.283.B	49	107	6.75	1.5
	VER 2016.2776.	52	93	5.86	1.4
	VER 2016.2777.	49	107	6.07	1.3
	VER 2016.2778.	20	39	5.2	2.16
	VER 2016.2779.	39	82	6.8	2.14
	VER 2016.2780.	30	53	5.97	1.27
	VER 2016.2781.	56	131	6.76	1.59
Total		1,471	3,206		
Averages (μm)				6.52	1.72

(Fig. 2K, L) linear stripes along the full length of the specimens. Specimen VER 2015.289. (Fig. 2O–Q) is much bigger, more flattened, and weakly bent in cross section than the other specimens. These features suggest a lepisosteid affinity (Figs 89, 148, 169, 191, 280, 317, 338, 361, 420, 445, and 464 in Grande 2010) and we tentatively refer these specimens to *Atractosteus* sp. well known from the locality, but since they are isolated elements, this cannot be certainly proved until more complete material is discovered. A similar specimen of fringing fulcræ has been reported by Sweetman et al. (2014, Fig. 13M) as *Scheenstia* sp. scale.

Scales. The here reported anal or ventral midline scale (VER 2015.294.; Fig. 3) has a very thin bony base, with a yellowish–brownish, slightly translucent, glossy layer of ganoine on it. Its symmetrical, deltoid shape resembles to the anterior anal scale of *Atractosteus spatula* and *Atractosteus tropicus* reported by Grande (2010, Figs 290C, D and 340C, D). The ventral midline scales of some recent lepisosteids also are similar in contour (Figs 173 and 342 in Grande 2010). Various gar scales of other positions from Iharkút were reported by Szabó et al. (2016a, Figs 8 and 10).

The anatomically unidentifiable elements (Figs 4–7) are asymmetrical or irregular in shape, mostly broken or worn. All referred specimens bear ganoine substantiated ornamentation, arranged in units similar to that of the hemitrichial elements (described above). They could be dermal elements (or fin ray- and scale fragments) according to this kind of ornamentation, but the preserved morphological features do not allow us to identify their in-life anatomical position. Specimen VER 2016.2777. (Fig. 4A, B, H) is fragmentary on both ends, there is a well-observable ganoine ornamentation on its outer surface, whereas its inner surface bears a few small foramina. Specimen VER 2016.2778. (Fig. 4C, I) also has a well-developed ganoine ornamentation, arranged in numerous layers overlapping each other (Fig. 4I). Specimen VER 2016.2780. (Fig. 4D, J) and VER 2016.2779. (Fig. 4E–G, K) are also fragmentary, and they bear foramina on their inner side, with visual ridges extending along their long axis. Specimen VER 2015.283.A (Figs 5A–D and 7A) is “T”-shaped cross section, and is very fragmentary. It bears rounded units of ganoine only on a small part of its surface. VER 2015.283.B (Figs 5E, F and 7B) is flattened and fragmentary, its ganoine ornamentation is arranged in oval- to drop-like shaped units. Specimen VER 2016.2781. (Figs 5G–I and 7C) is asymmetrical in shape from any view, it bears one well-developed, glossy ridge of ganoine. Specimen VER 2015.271. (Figs 6A–C and 7D) is elongated and narrow, ornamented with ganoine on the outer side and ridges squarely to the long axis of the bone on the inner side. Here, the ganoine ornamentation (Fig. 6C) is made up by elongated, linear, stripe-, drop-, or spool-like units (similar to that of the hemitrichial elements; see above). Specimen VER 2015.272. (Figs 6D–F and 7E) is very similar to specimen VER 2015.251. in its shape and ganoine pattern (Fig. 6F); however, it is more fragmentary, and the section-bearing ridges on the inner side is missing. Specimen VER 2014.76.

(Figs 6G–I and 7F) has also a pattern of ganoine on the outer side, comparable to that of specimen VER 2015.251. and VER 2015.252., while it bears ridges and two rows of alveolar-like structures on the inner side (Fig. 6H). This makes specimen VER 2014.76. similar to a fin ray- or a jaw fragment [but plicidentine tooth bases (typical for lepisosteid fishes) cannot be observed on the inner side].

Division Halecostomi [Regan 1923 sensu Patterson 1973](#)

Order Amiiformes [Hay 1929 sensu Grande and Bemis 1998](#)

Family Amiidae [Bonaparte 1838](#)

Subfamily Vidalamiinae [Grande and Bemis 1998](#)

Vidalamiinae indet.

(Figs 8 and 9)

Referred material. Two vertebrae (VER 2010.130.A-B).

The Iharkút vidalamiin vertebrae are the biggest known fish vertebrae from the locality. The centra are short and wider than high. The lateral, dorsal, and ventral surfaces of the centra are dominated by a network of thin, bony, fiber-like structures. The better preserved specimen (VER 2010.130.A; Fig. 8) is nearly complete. It has two, oval to slightly hourglass-shaped neural arch articular pits. The articular surfaces show circular annuli with large notochord foramen. A pair of closely spaced, elongated ventral pits are visible on the ventral side, typical for amiid vertebrae ([Brinkman et al. 2013](#)). Ventral to the notochordal foramen a massive bulge can be seen both on the posterior articular surface. The corresponding part of the anterior articular surface is covered by a relatively thick layer of pyrite, therefore, it is not informative in this view.

The less complete specimen (VER 2010.130.B; Fig. 9) has one hourglass-shaped neural arch articular pit preserved. It also bears visible, circular annuli on the articular surfaces, with a massive bulge on the posterior articular surface. This matching part of the anterior articular surface shows signs of bearing a similar bulge, but this surface is worn and partially covered by pyritized sediment. The ventral side of the specimen is damaged, so the ventral pits are not preserved.

The parapophyseal articular pits of both specimens bear anteroposteriorly broad, posteriorly located, large ridges that extend across the ventrolateral surface of the vertebrae. No large, well-developed parapophyses are fused to the centra. This indicates that these specimens do not belong to the subfamily Amiinae ([Grande and Bemis 1998](#)). Based on their general morphology and their size, we refer them to the subfamily Vidalamiinae ([Grande and Bemis 1998](#)). Except for the bulge on their articular surface, the Iharkút amiid vertebrae are similar to the Vidalamiinae centra published by [Martinelli et al. \(2013, Fig. 7\)](#) and [Vullo and Courville \(2014, Fig. 4B, D\)](#). An abdominal vertebra of the vidalamiin *Pachyamia mexicana* with a similar, but less-defined bulge on its anterior side was reported by [Grande and Bemis \(1998, Fig. 283B\)](#). Vidalamiin fishes, which are known from the early Cretaceous to the early Eocene are a diverse, monophyletic subfamily of amiids, several of which reaching 1.4–2 m in total length making them the largest known amiid fishes

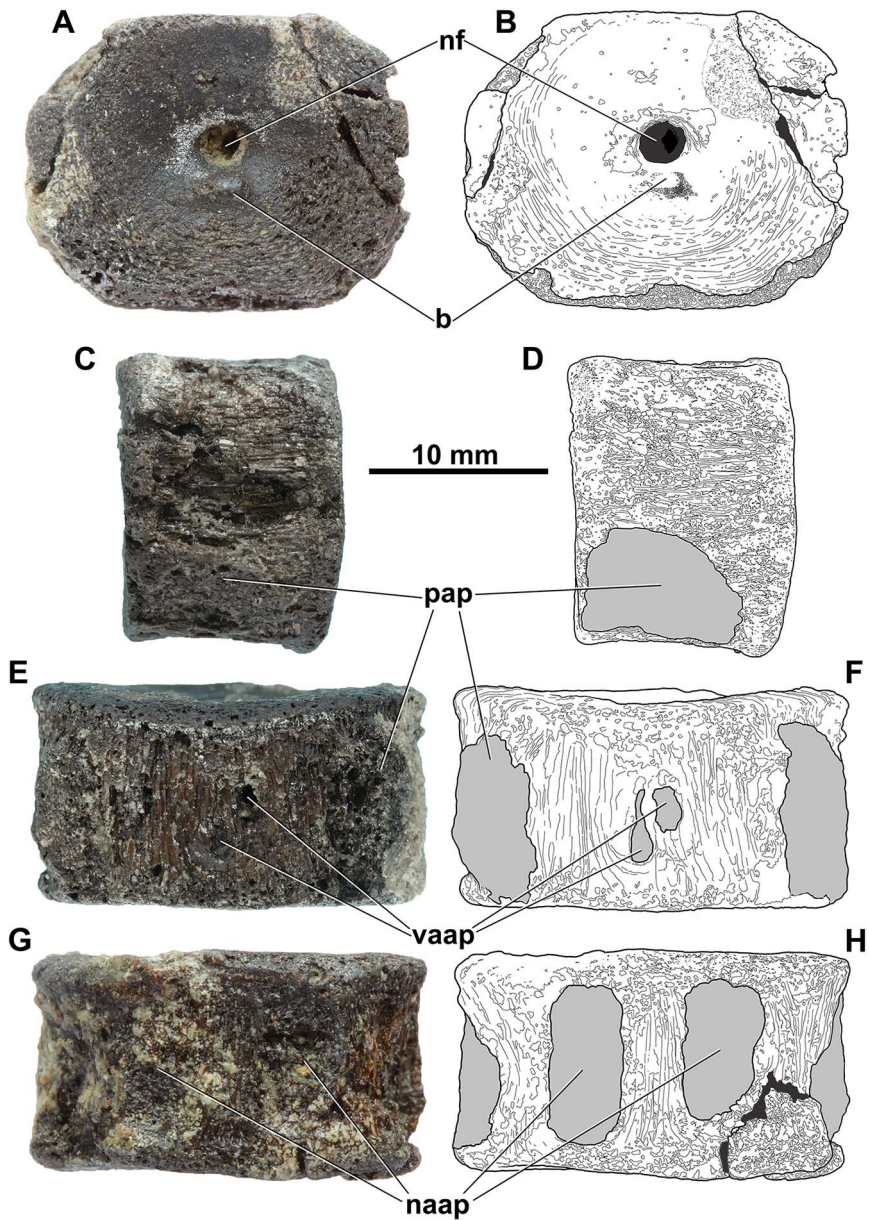


Fig. 8
 Vidalamiinae indet. vertebra (VER 2010.130.A) from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary) (A) in posterior view; (B) line drawing of the posterior view; (C) in right lateral view; (D) line drawing of the right lateral view; (E) in dorsal view; (F) line drawing of the dorsal view; (G) in ventral view; (H) line drawing of the ventral view. b – bulge ventrally to the notochordal foramen; naap – neural arch articular pit; nf – notochord foramen; pap – region of the parapophyseal articular pit; vp – ventral pit

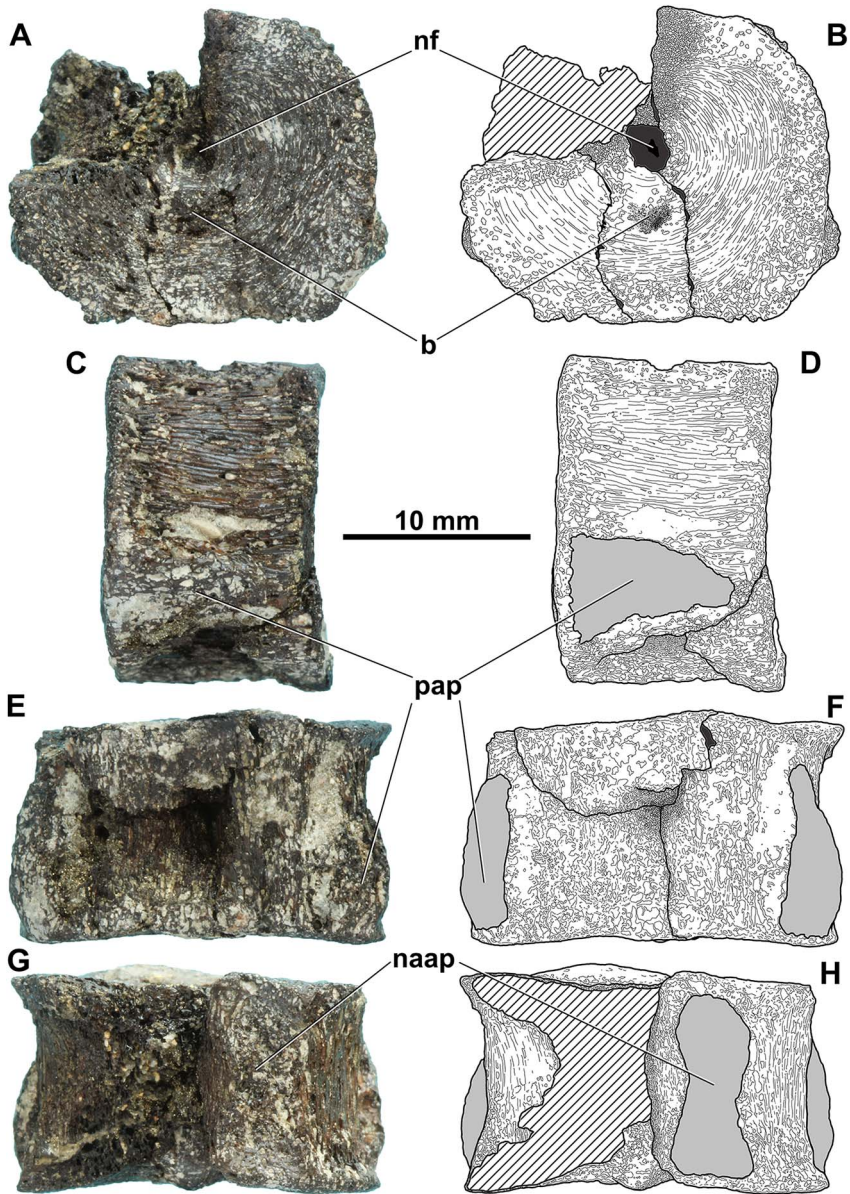


Fig. 9
 Vidalamiinae indet. vertebra (VER 2010.130.B) from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary) (A) in anterior view; (B) line drawing of the anterior view; (C) in left lateral view; (D) line drawing of the left lateral view; (E) in dorsal view; (F) line drawing of the dorsal view; (G) in ventral view; (H) line drawing of the ventral view. b – bulge ventrally to the notochordal foramen; naap – neural arch articular pit; nf – notochord foramen; pap – region of the parapophyseal articular pit

(Grande and Bemis 1998). Amiid fishes have one extant genus with one living species, *Amia calva* (bowfin or mudfish).

Amiidae indet.

(Fig. 10)

Referred material. One left anterior ceratohyal (VER 2016.2782.), one vertebra (VER 2016.2783.).

The left anterior ceratohyal (VER 2016.2782.; Fig. 10A, B) is in a relatively good condition, showing the characteristic morphology of an amiid anterior ceratohyal. Posteriorly from the knob-like, anterior articulation surface the bone narrows to a “neck,” then widens, and turns to a wide but still flat, spatulate portion, which continuously widens posteriorly. In dorsoventral view, the posterolateral edge shows a rectangularly angled margin. The long posterior margin is concave, whereas the anterior margin is convex in dorsoventral view. The spatulate portion is weakly convex in dorsal view, bearing a massive, narrow ridge, positioned near to the anterior margin (Fig. 10A). The ventral surface is concave, having a narrow, visual ridge along its anterior margin, and a weaker developed ridge on the posterior margin. These ridges and the concave surface between them create a widening pit along the long axis of the element (Fig. 10B). The anterior ceratohyal of the extant *Amia calva* attaches anteriorly to the hypohyal, and posteriorly to the smaller posterior ceratohyal (Grande and Bemis 1998). However, the strongly concave dorsal surface (following Friedman et al. 2003), and the large size might suggest a vidalamiini affinity but better preserved specimens are needed for a more accurate taxonomic identification.

Similarly, isolated amiid anterior ceratohyals were reported by Friedman et al. (2003, Fig. 3H) and Yabumoto and Grande (2013, Fig. 7.1–7.2).

Centrum VER 2016.2783. (Fig. 10C–L) is wider than high, the notochordal foramen is clearly visible. The neural arch articular pits are large- and hourglass-shaped, and a mid-dorsal pit is preserved. The ventral pits are oval and a mid-ventral pit is present between them. The centrum has a large foramen on both lateral sides (Fig. 10E, F). The ventral, dorsal, and lateral sides are ornamented by a pattern of pores. No parapophyseal articular pits are present. This amiid centrum is different from the two local Vidalamiinae vertebrae described above in being shorter, and smaller in diameter, and having clearly observable mid-dorsal and mid-ventral pits, enlarged lateral foramina, and in the absence of the parapophyseal articular pits and of the massive bulge ventrally to the notochordal foramen. Although some of these features could be related to variation, following these differences we exclude this specimen from the subfamily Vidalamiinae, but, on the other hand, we do not place it unambiguously to Amiinae, thus we refer it to Amiidae indet. In addition, the differences between the two amiid vertebra types suggest that they represent two amiid taxa.

Infraclass Teleostei Müller 1846 *sensu* Patterson and Rosen 1977

Cohort Elopomorpha Greenwood et al. 1966

Order Elopiformes Sauvage 1875

Elopiformes indet.

(Fig. 11)

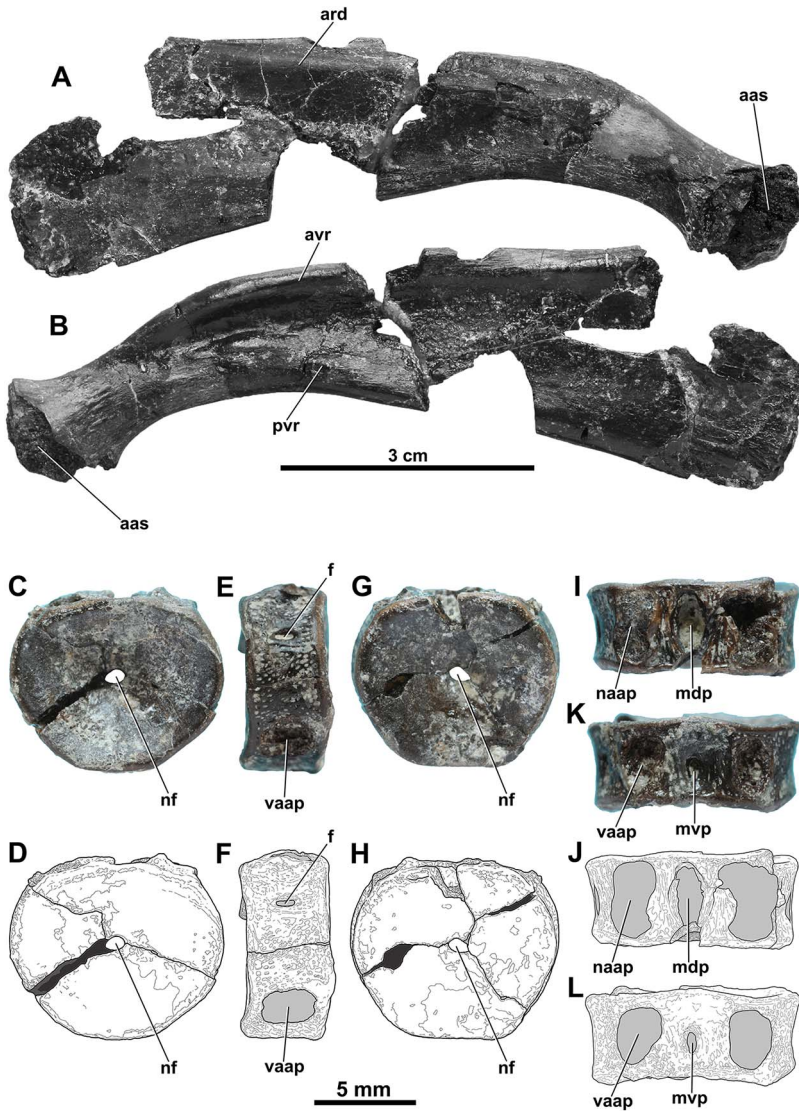


Fig. 10
 Amiidae indet. remains from the Upper Cretaceous (Santonian) Csehánya Formation (Iharkút, Hungary). (A) Left anterior ceratohyal (VER 2016.2782.) in dorsal view; (B) in ventral view. (C) Vertebra (VER 2016.2783.) in anterior view; (D) line drawing of the anterior view; (E) in lateral view; (F) line drawing of the lateral view; (G) in posterior view; (H) line drawing of the posterior view; (I) dorsal view; (J) line drawing of the dorsal view; (K) ventral view; (L) line drawing of the ventral view. aas – anterior articular surface; ard – anterior ridge on the dorsal surface; avr – anterior ridge on the ventral surface; mdp – mid-dorsal pit; mvp – mid-ventral pit; naap – neural arch articular pit; nf – notochordal foramen; pvr – posterior ridge of the ventral surface; vaap – ventral arch articular pit

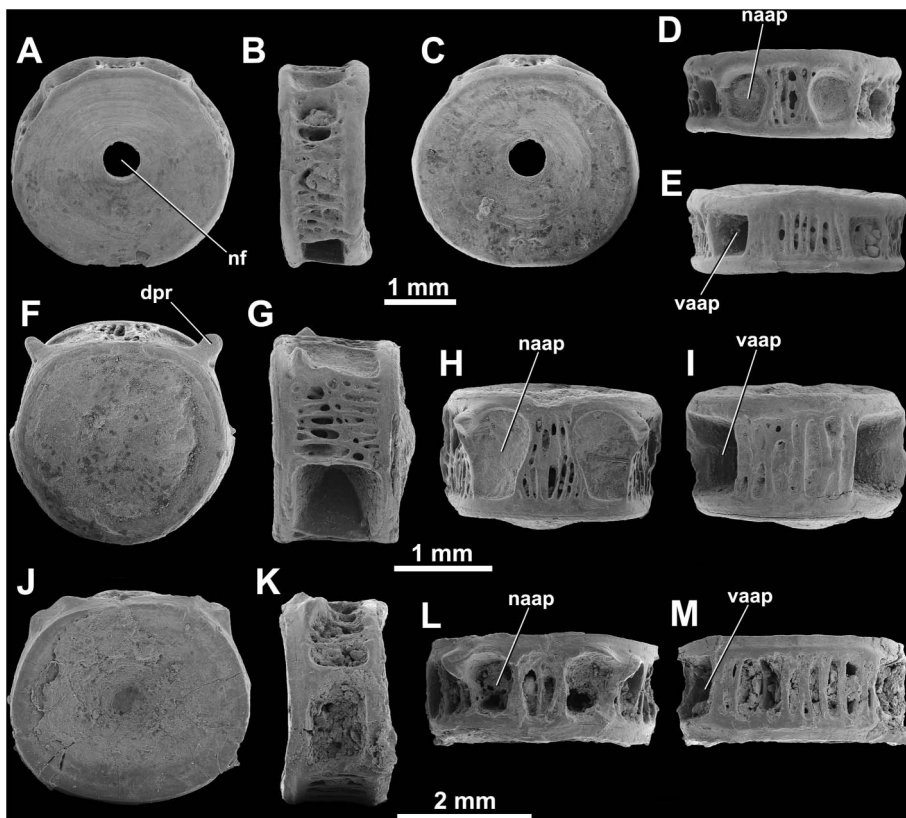


Fig. 11
 Elopiform remains from the Upper Cretaceous (Santonian) Cschbánya Formation (Iharkút, Hungary). (A) *Elopiformes* indet. vertebra (VER 2016.2785.) in anterior view; (B) in lateral view; (C) in posterior view; (D) in dorsal view; (E) in ventral view. (F) *Elopiformes* indet. vertebra (VER 2016.2786.) in anterior view; (G) in lateral view; (H) in dorsal view; (I) in ventral view. (J) *Elopiformes* indet. vertebra (VER 2015.266.) in anterior view; (K) in lateral view; (L) in dorsal view; (M) in ventral view. dpr – dorsal process; naap – neural arch articular pit; nf – notochordal foramen; vaap – ventral arch articular pit

Referred material. 13 vertebrae (VER 2015.266., VER 2016.2785., VER 2016.2786., VER 2016.2787., VER 2016.2788.).

Elopomorph centra are distinctive in being short and septate (numerous bars of bone are extending between the anterior and the posterior ends of the centra), and having widely spaced parapophyseal arch pits and neural articular pits. The two, relatively large, oval parapophyseal arch pits are placed more far from each other than the two neural articular pits, being similar in size and shape. The small morphological differences (e.g., the shape of the neural arch articular pits; Fig. 11D, H, L) suggest that the vertebrae belong to different parts of the vertebral column.

Very similar elopiform vertebrae were published by Brinkman et al. (2013, Fig. 10.14.C) from the Late Cretaceous of Utah, and vertebrae morphologically almost identical with the Iharkút specimens were published by Brinkman and Neuman (2002, Fig. 1.19–1.27) and Brinkman (2014, pp. 34–35) from Upper Cretaceous beds of the Dinosaur Provincial Park (Alberta, Canada). A similar vertebra was also reported by Sweetman et al. (2014, Fig. 12A) from the Barremian of the Isle of Wight. It is worth mentioning that specimen VER 2016.2786. (Fig. 11J–M) shows close affinities with the mid-precaudal centra of the extant *Elops saurus* reported also by Brinkman et al. (2013, Fig. 10.14E).

Cohort Otocephala Johnson and Patterson 1996

Superorder Clupeomorpha Greenwood et al. 1966

Order Ellimmichthyiformes Grande 1985

Ellimmichthyiformes indet. 1

(Fig. 12A–M)

Referred material. Four vertebrae (VER 2016.2789., VER 2016.2790., VER 2016.2791., VER 2016.2792.).

Centrum VER 2016.2789. (Fig. 12A–E) is oval, and slightly wider than high in articular views, while it is anteroposteriorly short. Two, large, oval, shallow neural arch articular pits are visible on the dorsal surface. Two large transversal processes are fused to the centrum. The transversal processes are anteroposteriorly flattened, long and laterally directed. A mid-dorsal and a mid-ventral ridge is present. Specimen VER 2016.2789. is similar to the *Diplomystus* sp. anterior precaudal centrum reported by Brinkman (2014, p. 39, Fig. 1 – same specimen in Brinkman and Neuman 2002, Fig. 7.1–7.4).

Specimen VER 2016.2790. (Fig. 12F–H) is fragmentary with the dorsal portion of the centrum preserved. The neural arch articular pits are shallow and are restricted to the anterior portion of the centrum. The neural arch articular pits are about half the length of the centrum, and are separated by a mid-dorsal pit. A dorsal process is present on the posterior part of the centrum. The specimen is identical with the *Diplomystus* sp. anterior precaudal centrum reported by Brinkman (2014, p. 39, Fig. 2 – same specimen in Brinkman and Neuman 2002, Fig. 7.5–7.8).

Specimen VER 2016.2791. (Fig. 12I–M) is hardly pyritized and is relatively high in anteroposterior view. The neural arch articular pits are located anteriorly (unlike those of the other two Ellimmichthyiformes indet. 1 centra described above), they are widely separated and are filled with pyrite crystals. This specimen strongly resembles to the *Diplomystus* sp. posterior precaudal centrum reported by Brinkman (2014, p. 39, Fig. 5 – same specimen in Brinkman and Neuman 2002, Fig. 7.9–7.12).

Although all Iharkút Ellimmichthyiformes indet. 1 centra are comparable to centra of *Diplomystus*, here we refer them only as indeterminate ellimmichthyiform remains, until more remains (e.g., cranial elements) are unearthed. It is worth mentioning that Diedrich (2012) reported *Diplomystus brevissimus* from the Upper Cretaceous (Cenomanian–Turonian) of northwestern Germany; however, Grande (1982) assigned this species to *Armigatus*.

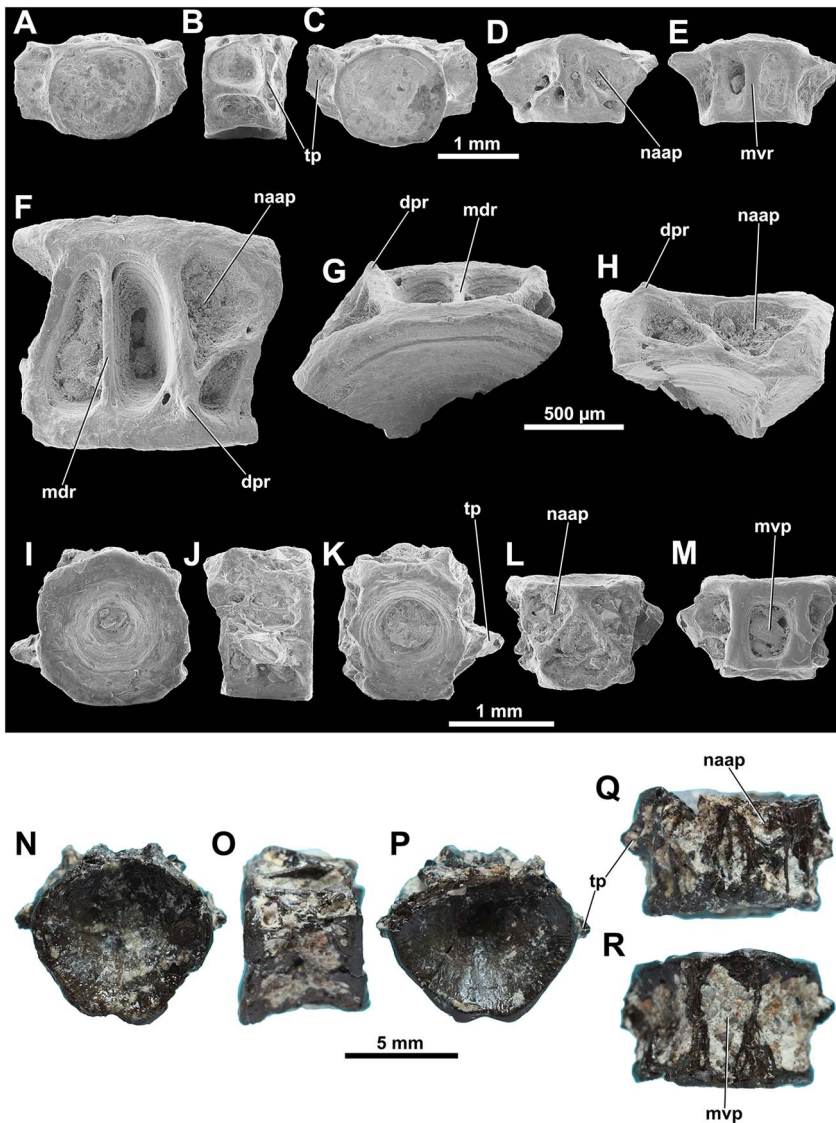


Fig. 12
 Ellimmichthyiform remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) Ellimmichthyiformes indet. 1 anterior precaudal vertebra (VER 2016.2789.) in anterior view; (B) in lateral view; (C) in posterior view; (D) in dorsal view; (E) in ventral view. (F) Ellimmichthyiformes indet. 1 anterior precaudal vertebra (VER 2016.2790.) in dorsal view; (G) in anterior view; (H) in lateral view. (I) Ellimmichthyiformes indet. 1 posterior precaudal vertebra (VER 2016.2791.) in anterior view; (J) in lateral view; (K) in posterior view; (L) in dorsal view; (M) ventral view. (N) Ellimmichthyiformes indet. 2 vertebra (VER 2016.2793.) in anterior view; (O) in lateral view; (P) in posterior view; (Q) in dorsal view; (R) in ventral view. dpr – dorsal process; mdr – mid-dorsal ridge;.mvp – mid-ventral pit; naap – neural arch articular pit; tp – transversal process

Ellimmichthyiform fishes are among the most widely cited teleosts in the literature. To date, the earliest fossil record of ellimmichthyiform fishes is *Scutatuspinosus itapagipensis* from the Neocomian of Brazil, originally described by Silva Santos and Silva Corr ea (1985) as Clupeidae incertae sedis. The youngest ellimmichthyiform fossils are from the Eocene of China and North America (Grande 1985; Alvarado-Ortega et al. 2008).

Ellimmichthyiformes indet. 2

(Fig. 12N–R)

Referred material. One vertebra (VER 2016.2793.).

The single vertebra is very similar to those of Ellimmichthyiformes indet. 1 in having anteriorly positioned neural arch articular pits and a well-developed mid-dorsal ridge, however, it is almost six times bigger than any Ihark t Ellimmichthyiformes indet. 1 vertebra.

Specimen VER 2016.2793. is taller than long and nearly as wide as tall. The neural arch articular pits are filled with pyritized sediment, therefore their shape cannot be determined, but their length is nearly the half of that of the centrum. A pair of narrow dorsal fossae is visible being constricted anteriorly. Prominent longitudinal ridges fill the lateral surfaces of the centrum. A wide mid-ventral pit is present. The dorsoventral contour of specimen VER 2016.2793. is closely similar to the *Horseshoeichthys armaserratus* vertebra described by Newbrey et al. (2010, Fig. 5E). Since specimen VER 2016.2793. is very similar to the centra of *Horseshoeichthys* (Newbrey et al. 2010), but is strongly different in size, and in having an apple-like contour in anteroposterior view, we refer it as an indeterminate ellimmichthyiform centrum, until more complete material will be available.

Cohort Euteleostei *sensu* Arratia 1999

Subcohort Protacanthopterygii Greenwood et al. 1966

Order Salmoniformes Bleeker 1859

cf. Salmoniformes indet.

(Fig. 13)

Referred material. Two vertebrae (VER 2016.2794., VER 2016.2895.).

Centrum VER 2016.2794. is simple, spool-like in shape with large neural arch, and rib articular pits close to each other. The neural arch and rib articular pits are separated by a pair of narrow ridges. The centrum lacks parapophyses or fused neural arch (a typical feature of salmoniform centra; also mentioned by Brinkman 2014; Brinkman et al. 2014). Unlike the Salmoniform centra reported by Brinkman (2014, pp. 61, 65) and Brinkman et al. (2014, Fig. 9), this specimen is nearly twice as wide as long. The other specimen (VER 2016.2895.) is fragmentary (ca. 50% is preserved) and does not give any additional features. Unfortunately, the Ihark t salmoniform centra cannot be associated with any other local teleost element. These specimens differ from the elopomorph centra in the absence of the numerous bars of bone extending between the anterior and the posterior surfaces of the centra, and in having mid-dorsal articular pits. We refer them tentatively as cf. Salmoniformes centra, until more, better preserved specimen lead us to a different conclusion.

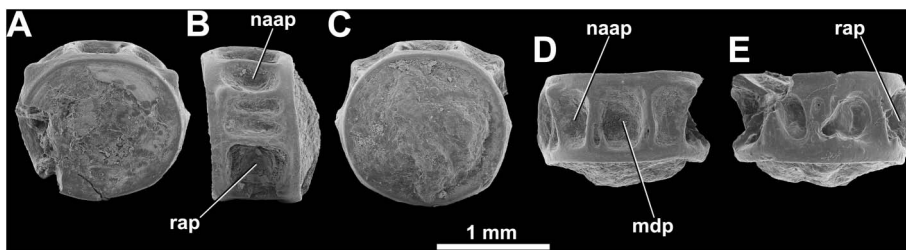


Fig. 13
cf. Salmoniformes vertebra remain (VER 2016.2794.) from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary) (A) in anterior view; (B) in lateral view; (C) in posterior view; (D) in dorsal view; (E) in ventral view. mdp – mid-dorsal pit; naap – neural arch articular pit; rap – rib articular pit

Fossils of salmoniform fishes are mostly known from North American and European localities (Romero 2003). Salmoniform fishes are known by unambiguously identified fossils from the Late Cretaceous with the oldest otolith-based record of salmoniform relatives reported from the Campanian of Mississippi (Nolf and Dockery 1990). Recent salmoniforms are one of the most abundant freshwater fishes of the Northern Hemisphere.

Subcohort Neoteleostei *sensu* Arratia 1999

Subsection Acanthomorpha Rosen 1973 *sensu* Stiassny 1986

Acanthomorpha indet.

(Fig. 14)

Referred material. Three vertebrae (VER 2016.2800., VER 2016.2801., VER 2016.2802.), 18 fin spines (VER 2016.2796., VER 2016.2797., VER 2016.2798., VER 2016.2799.).

Acanthomorph fish vertebrae are distinctive in having well-developed zygapophyseal articulations (Brinkman 2014; Brinkman et al. 2014). The parapophyses are missing on the first 3–6 vertebrae. The acanthomorph fish atlas centra have tripartite anterior surfaces, and the neural arch is not fused together with the centrum (Brinkman et al. 2014). The most anterior vertebrae have rib articulations on the lateral surface of the neural arch, rather than low on the centrum. The following, still anterior centra mostly bear ventrolateral articulations of ribs (Rosen and Patterson 1969; Grande 1988; Brinkman et al. 2014).

The Iharkút acanthomorph fish centra are posteriorly wider than anteriorly, therefore they have a trapezoid shape in dorsal (and ventral) view. The lateral and dorsal surfaces are filled in by a network of bone. Large zygapophyses and mid-ventral pits are present on all specimens (Fig. 14D, E, I, J, N, O). Based on the preserved morphological features, these vertebrae could belong to the precaudal section of the vertebral column. The Iharkút specimens are almost identical with the centra published by Brinkman (2008, p. 65, Fig. 5), by Brinkman and Neuman (2002, Fig. 9.11–9.20), and by Brinkman et al. (2013, Fig. 10.28E and 2014, Fig. 15B). Since they are only

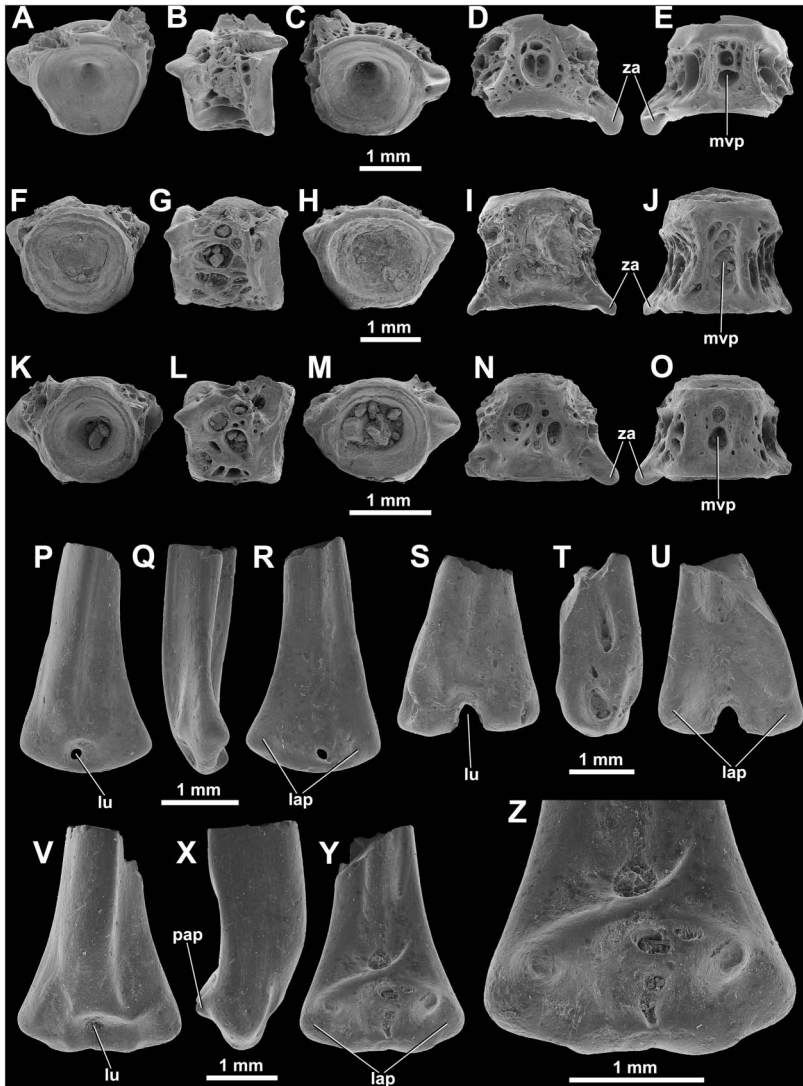


Fig. 14

Acanthomorpha indet. remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) Precaudal vertebra (VER 2016.2800.) in anterior view; (B) in lateral view; (C) in posterior view; (D) in dorsal view; (E) in ventral view. (F) Precaudal vertebra (VER 2016.2801.) in anterior view; (G) in lateral view; (H) in posterior view; (I) in dorsal view; (J) in ventral view. (K) Precaudal vertebra (VER 2016.2802.) in anterior view; (L) in lateral view; (M) in posterior view; (N) in dorsal view; (O) in ventral view. (P) Fin ray (VER 2016.2796.) in outer view; (Q) in profile view; (R) in inner view. (S) Fin ray (VER 2016.2797.) in outer view; (T) in profile view; (U) in inner view. (V) Fin ray (VER 2016.2798.) in outer view; (X) in profile view; (Y) in inner view; (Z) close-up of the articulation surface in inner view (Y of the current figure). lap – lateral articulation process; lu – lumen; mvp – mid-ventral pit; pap – posterior articulation process; za – zygapophysis

isolated finds, without referable dentaries, we refer them only as indeterminate acanthomorph precaudal centra.

The fin spines are small, and none of them is completely preserved. The surface of the specimens is smooth, no striation is present. Two main morphotypes can be distinguished. The first morphotype bears a tight lumen, which is subtended by a bar of bone and/or other structures extending between the two lateral articular processes (also called as articular limbs; Fig. 14P–R, V–Z). These features are typical for many derived acanthomorph fishes (Larson et al. 2010). The second morphotype lacks the aforementioned bone bars between the two articular processes (Fig. 14S–U) and this is not the result of preservation (for a comparable acanthomorph spine, see Fig. 7C, D in Larson et al. 2010).

In the view of symmetry, the acanthomorph fin spines have been grouped in two groups. One group includes generally symmetrical specimens; they were most probably parts of median fins. Similar acanthomorph fin spines have been reported from the early Maastrichtian of the upper Horseshoe Canyon Formation in Alberta (Fig. 7A, B in Larson et al. 2010), from the Cenomanian of Bainbridge River bonebed in Saskatchewan (Fig. 5S in Cumbaa et al. 2013), and from the Maastrichtian of Albaina (Spain; Fig. 5C in Poyato-Ariza et al. 1999). The other morphogroup includes strongly asymmetrical specimens. However, asymmetry is present in some dorsal fin spines (which allows them to array in an alternating pattern when the dorsal fin is depressed; see Fig. 2.5 in Becker 2009), but the degree of asymmetry could suggest that some of these Itharkút fin spines might have been associated with paired fins.

Acanthomorph fishes represent the largest group of bony fish, with more than 60% of the modern species (Chen et al. 2003; Nelson 2006; Murray 2016). Acanthomorph fishes occur in all aquatic habitats and dominate most marine ecosystems (Chen et al. 2014). Their oldest record extends back into the Late Cretaceous (Cenomanian; González-Rodríguez and Fielitz 2008).

Teleostei indet.

(Figs 15–18)

Referred material. Two ?pharyngeal teeth: morphotype 1: one specimen (VER 2016.2834.); morphotype 2: one specimen (VER 2016.2835.), 24 vertebrae as subtypes of “A” (type A1: VER 2016.2804., VER 2016.2805.; type A2: VER 2016.2806., VER 2016.2807.; type A3: VER 2015.267., VER 2016.2808.; type A4: VER 2016.2809., VER 2016.2810.; type A5: VER 2016.2811.), 112 fragmentary vertebrae (VER 2015.265., VER 2015.268., VER 2015.269., VER 2015.270., VER 2016.2803.), three cycloid scales (VER 2014.111.A-C).

Two specimens represent the two morphotypes of the assumed teleostean pharyngeal teeth. One specimen VER 2016.2834. (Fig. 15A, B) belongs to the first morphotype. It is flattened and asymmetrical, square to subsquare in shape. The dorsal margin is concave, whereas the ventral margin is convex. The suggested dorsal margin is sinuous-like and smooth (Fig. 15B). Pharyngeal teeth of some cyprinid species are highly similar to this specimen in contour and in general features (e.g., Text-Fig. 7C, E, F and Pl. 1, Figs 9, 10, and 12 in Hierholzer and Mörs 2003).

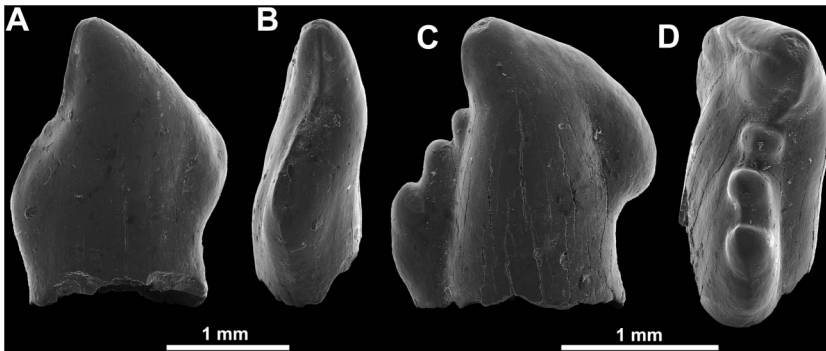


Fig. 15
Teleostei indet. suggested pharyngeal teeth from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) ?Pharyngeal tooth morphotype 1 (VER 2016.2834.) in suggested medial view; (B) in suggested ventral view. (C) ?Pharyngeal tooth morphotype 2 (VER 2016.2835.) in suggested medial view; (D) in suggested ventral view

Specimen VER 2016.2835. represents the second morphotype (Fig. 15C, D). It is very similar to the assumed teleostean pharyngeal tooth morphotype 1 (see above) in the general characters of contour and symmetry, but important differences can be observed as well. This tooth is much more concave on the presumed ventral side (Fig. 15C), while the presumed dorsal side bears three cusplets, similar in shape and decreasing in size to the main tip, however, all are smaller than the rounded main tip itself (Fig. 15D). Cyprinid pharyngeals with similar morphology were published by Hierholzer and Mörs (2003, Text-Fig. 10 and Pl. 3).

The teleost vertebrae are highly variable in contour and small details of the ridges, pits and foramina of the dorsal and lateral surfaces. However, they all have large, anteriorly located neural arch articular pits oval in shape, which are nearly as long as the half of the length of the centrum. The neural arch articular pits are separated by a relatively wide bone-ridge. On the better preserved specimens the large neural arch articular pits are posteriorly followed by large, narrow, or drop-like foramina. In some specimens, these foramina are asymmetrical in size or position. Based on their general morphology, they are grouped in four morphotypes. All morphotypes (see below) are strongly concave both anteriorly and posteriorly, but only the first two morphotypes bear fused parapophyses. The neural arches do not appear to be fused to the centra. Foramina are present posteriolaterally on both lateral sides of the centra.

Morphotype A1 (Fig. 16A–D) is represented by two, fragmentary specimens (VER 2016.2804., VER 2016.2805.), nearly of the same conditions. They are shorter than wide, with one, ventrally bent parapophysis being preserved. Their ventral side is simple, without ridges or pits. Morphotype A2 (Fig. 16E–H) includes centra nearly as long as wide, with short, dorsoventrally flattened parapophyses. In dorsoventral view, these centra are wider posteriorly than anteriorly. They bear large foramina on their

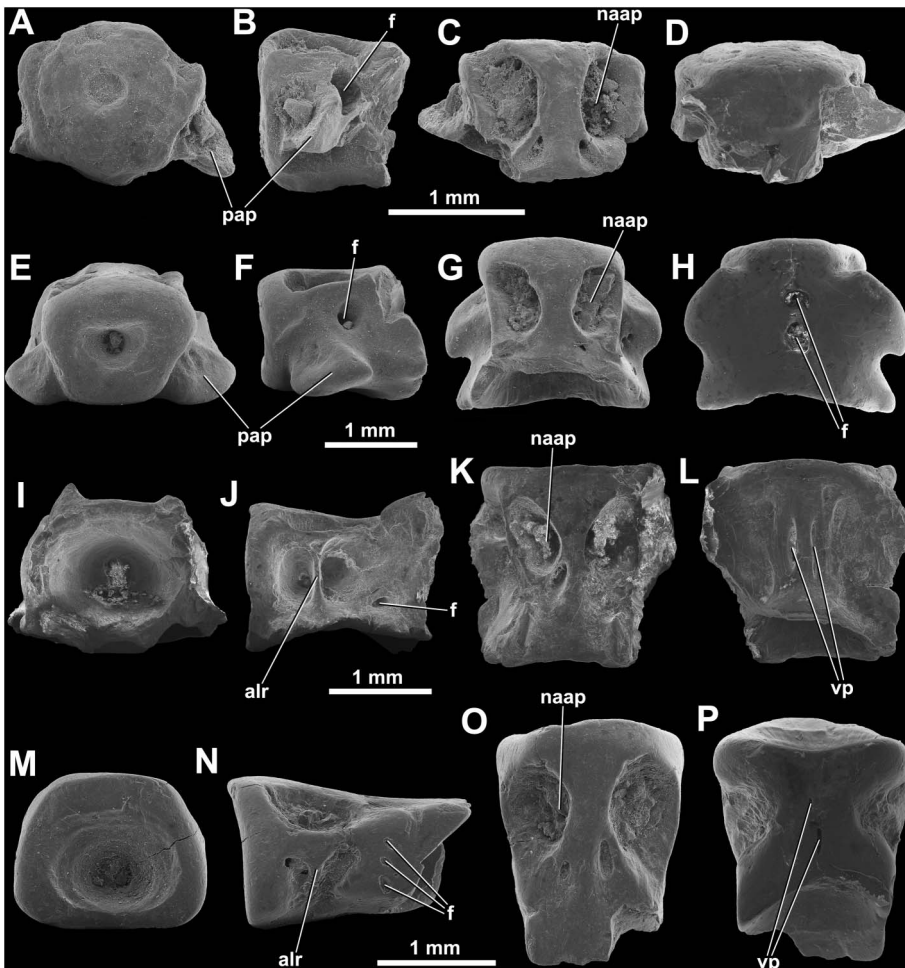


Fig. 16
 Teleostei indet. vertebra morphogroup A1–A4 remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) Vertebra type A1 (VER 2016.2804.) in anterior view; (B) in lateral view; (C) in dorsal view; (D) in ventral view. (E) Vertebra type A2 (VER 2016.2806.) in anterior view; (F) in lateral view; (G) in dorsal view; (H) in ventral view. (I) Vertebra type A3 (VER 2015.267.) in posterior view; (J) in lateral view; (K) in dorsal view; (L) in ventral view. (M) Vertebra type A4 (VER 2016.2809.) in anterior view; (N) in lateral view; (O) in dorsal view; (P) in ventral view. pap – parapophysis; f – foramen (posteriorly to the parapophyseal region); naap – neural arch articular pit; alr – anterolateral ridge; vp – ventral pit

ventral side. Morphotype A3 (Fig. 16I–L) is the most informative among all indeterminate teleostean centra. Posteriorly to the lateral ridge a foramen is present. The lateroventral regions are convex, whereas the ventromedial part is weakly

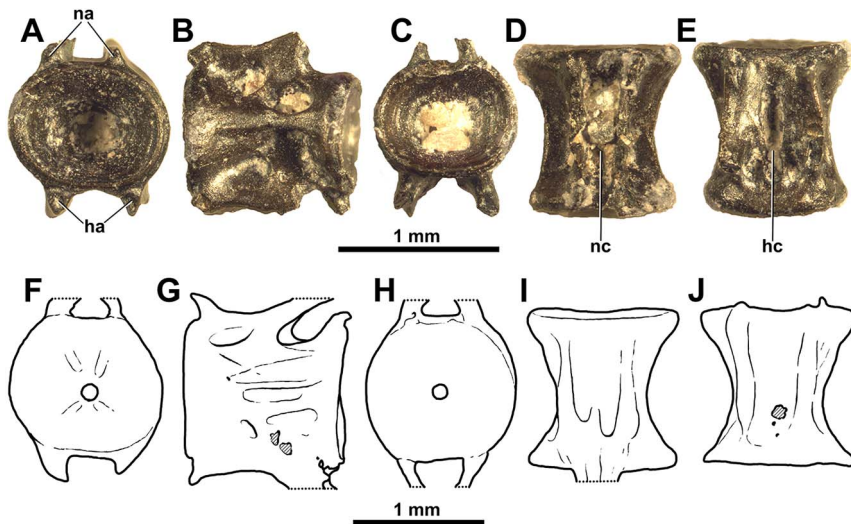


Fig. 17

Teleostei indet. morphogroup A5 caudal vertebra remain (VER 2016.2811.) from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary) with comparing material (A) in anterior view; (B) in lateral view; (C) in posterior view; (D) in dorsal view; (E) in ventral view. (F) *Percopsis omiscomaycus* caudal vertebra (for compare, re-drawn after Fig. 7C in Divay and Murray 2015) in anterior view; (G) in lateral view; (H) in posterior view; (I) in dorsal view; (J) in ventral view. ha – hemal arch; hc – hemal canal; na – neural arch; nc – neural canal

concave. Specimen VER 2015.267. bears two narrow, parallel pits, positioned on the midline of the ventral side, running anteroposteriorly, whereas the ventral surface of specimen VER 2016.2808. is smooth, and pits are absent. Both VER 2015.267. and VER 2016.2808. have subrectangular contour in anteroposterior view. In specimen VER 2015.267., a narrow ridge extends from the lateral surfaces of the arch onto the anterolateral half of the centrum on both lateral sides (Fig. 16J). This ridge separates the large lateral pit into two smaller pits. In specimen VER 2016.2808., the posterior separated lateral pit is also segmented by ridges. Two massive, posteriorly positioned dorsal processes are present. Ventral pits are missing on specimen VER 2016.2808. Morphotype A4 (Fig. 16M–P) is similar to A3 in general shape, in bearing signs of extending, narrow, anterolateral ridges, in the lack of parapophyses, in the position of the neural arch articular pits, and in having lateral foramina. However, the two specimens of this morphotype weakly narrow posteriorly, they bear no dorsal processes, both specimens have narrow ventral pits, and they have 2–3 posterolateral foramina on both sides. The dorsal surface is craniocaudally longer than the ventral one, which is the most visible in lateral view.

Type A5 is represented only by one vertebra (VER 2016.2811.; Fig. 17A–E), being obviously different from types A1–A4. However, similar to the teleost centrum

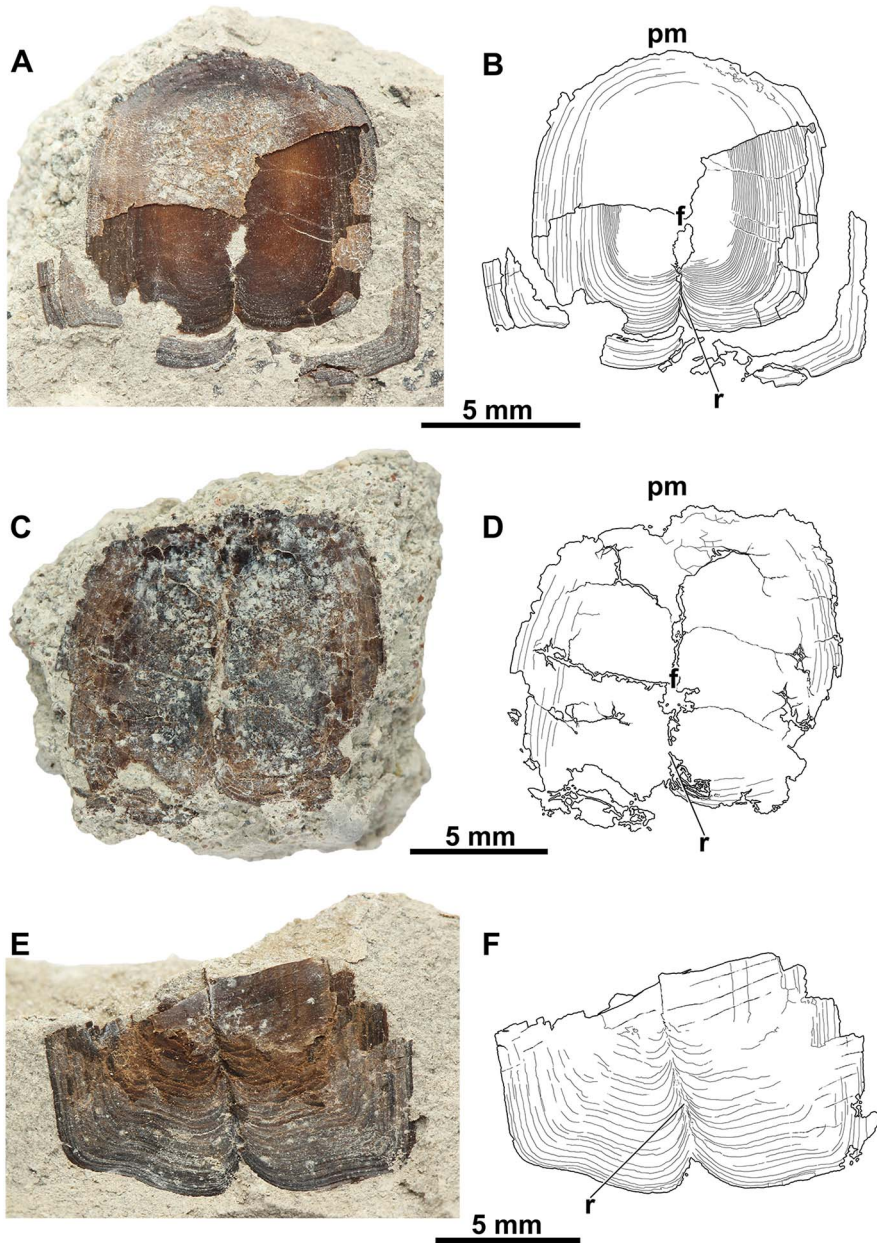


Fig. 18
Teleostei indet. cycloid scales from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) Cycloid scale (VER 2014.111.A); (B) line drawing of the same specimen. (C) Cycloid scale (VER 2014.111.B); (D) line drawing of the same specimen. (E) Cycloid scale (VER 2014.111.C); (F) line drawing of the same specimen. f – focus of the scale; pm – posterior margin of the scale; r – radial ridge

morphotype A3, specimen VER 2016.2811. also has an hourglass-like contour in dorsoventral view, but differs in almost all other features. It is higher than wide but longer than high. The centrum is wider and higher anteriorly than posteriorly (Fig. 17A, C). In lateral view several bony struts are visible, among which a distinct one is placed on the lateral midline, and extends anteroposteriorly (Fig. 17B). Altogether, all struts extend radially from the cone-like anterior region of the centrum. Specimen VER 2016.2811. has fused neural and hemal arches, the bases of them are still preserved.

There are reports of teleost centra, comparable with teleost centrum morphotype A3. Brinkman et al. (2013) reported a teleost centrum morphotype (Fig. 10.26 as Teleost centra type HvB) similar to the Iharkút teleost centrum morphotype A3 in having a narrow ridge on the anterolateral surfaces, in being anteroposteriorly elongated, hourglass-shape in dorsoventral view, closely as tall as wide (but being still much longer than tall or wide), and in having large, oval neural arch articular pits separated by a narrow bar of bone. However, the narrow ventral pits and the massive dorsal processes are missing on all specimens of Teleost centra type HvB (Fig. 10.26 in Brinkman et al. 2013). Centra of morphoserries IIIA-1, reported by Brinkman et al. (2013, Fig. 10.26C) are also similar to the Iharkút Teleost centra of morphotype A3 in general contour, but different in having distinct parapophyseal pits. Brinkman et al. (2013) interpreted these differences as representing different sections of the vertebral column and the morphological variation. Divay and Murray (2016, Fig. 4A, B) reported an Eocene gonorynchiform centra exceptionally similar to the Iharkút teleost centra A3 in general shape in dorsal (and ventral) and lateral view, in having large, oval, separated neural arch articular pits, posteriorly located dorsal processes, and fused neural arches. Important differences are also visible in the centra published by Divay and Murray (2016), like the missing anterolateral ridges, the anteroposteriorly middle-positioned neural arch articular pits, and the more like circular than subrectangular shape in anterior (and posterior view).

Based on the similar dorsal features (e.g., position and proportions of the neural arch articular pits, having secondary pits posteriorly to the neural arch articular pits), the presence of foramina caudal to the parapophyseal region (which is a laterally positioned, dorsoventral ridge on the third and fourth morphotypes), and the fused neural arches, we suggest a close taxonomical relation of all these centra (Teleostei indet. centra morphotype A1–A4), and note their variability as the consequence of belonging to different sections of the vertebral column.

The only specimen of type A5 is morphologically similar to a caudal vertebra of *Percopsis omiscomaycus* (e.g., Fig. 7C in Divay and Murray 2015) in general contour (in all views; see the details on Fig. 17), and in having fused neural and hemal arches. Although many other fish taxa could have caudal centra looking very similar, thus we refer the Iharkút specimen tentatively as an indeterminate teleost centrum, until more specimens are discovered.

In addition, various, fragmentary indeterminate teleost vertebrae were found, but they are extremely poorly preserved, thus they are not referable to any indeterminate teleostean centrum morphotypes above, or to any other teleost taxon from Iharkút.

The outer surface of teleost cycloid scales shows various types of ornamentation. Often, concentrically arranged, circular ridges (circuli) and radial grooves (radii), radiating from the center (focus) of the scale, are present in variable number. In some taxa, various superficial structures are also present (e.g., sharp or smooth, tooth-like ornamentation; Meunier and Brito 2004).

Up to now three scale fossils with typical cycloid scale morphology have been unearthed at Iharkút (Fig. 18). All specimens are very thin and fragmentary. No ordinary radii, but one radial ridge (median line or plica) extends from the focus to the anterior margin. Of the two better preserved specimens the posterior margin (or exposed portion) bears no ctenii (the remains are distinguished from ctenoid scales by this feature). Specimens VER 2014.111.A (Fig. 18A, B) and VER 2014.111.B (Fig. 18C, D) are more complete, whereas specimens VER.2014.111.A (Fig. 18A, B) and VER 2014.111.C (Fig. 18E, F) are better preserved in quality. The better preserved specimens show two, angled edge on their anterior margin.

The morphology of the Iharkút cycloid scales is very similar to that of cycloid scales of various teleosts, e.g., to that of the elopiform *Chicolepis punctatus*, reported from the Upper Cretaceous of California (Pl. 34, Fig. 1 in Cockerell 1915). An isolated, indeterminate teleost cycloid scale was published by Callapez et al. (2014, Fig. 3G) from the Cenomanian of Nazaré (Portugal).

Although cycloid scales are present in some local fish taxa, since they are isolated and badly preserved scale remains and cycloid scales are typical for teleost fishes (Nelson 2006; Kardong 2012), we refer the Iharkút cycloid scales only as *Teleostei indet.*

Actinopterygii indet.

(Figs 19–22)

Referred material. Tooth morphotype 1: seven teeth (VER 2016.2812., VER 2016.2813., VER 2016.2814., VER 2016.2815., VER 2016.2816.); tooth morphotype 2: 18 teeth (VER 2016.2817., VER 2016.2818., VER 2016.2819., VER 2016.2820., VER 2016.2821.); tooth morphotype 3: one tooth (VER 2016.2822.); tooth morphotype 4: one tooth (VER 2016.2823.); tooth morphotype 5: one tooth (VER 2016.2824.); tooth morphotype 6: one tooth (VER 2016.2825.); tooth morphotype 7: one tooth (VER 2016.2826.); tooth morphotype 8: one tooth (VER 2016.2827.), tooth morphotype 9: one tooth (VER 2016.2784.), 12 indeterminate tooth-bearing elements (VER 2016.2828., VER 2016.2829., VER 2016.2830., VER 2016.2831., VER 2016.2832., VER 2016.2833., VER 2016.2844.).

Teeth. Teeth of the first morphotype are small, and simple in morphology (Fig. 19A–H). They are more or less conical, the better preserved specimens are pointed. All teeth are circular in cross section, and have a smooth and shiny outer surface. All specimens are deeply hollow in basal view. These remains could be only the apex of the teeth, although their outer morphology represents a distinctive morphotype.

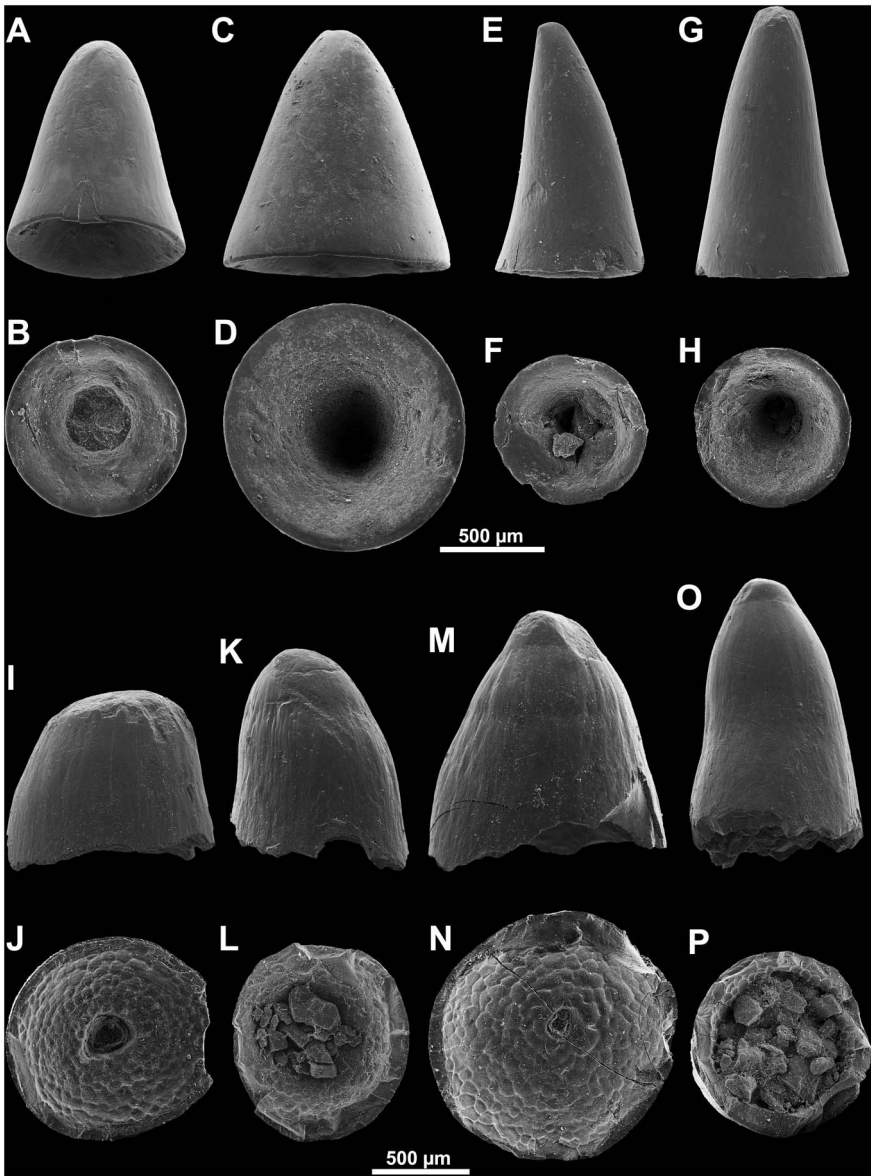


Fig. 19

Actinopterygii indet. tooth remains (morphotypes 1–2) from the Upper Cretaceous (Santonian) Csehánya Formation (Iharkút, Hungary). (A) Tooth morphotype 1 (VER 2016.2812.) in profile view; (B) in basal view. (C) Tooth morphotype 1 (VER 2016.2813.) in profile view; (D) in basal view. (E) Tooth morphotype 1 (VER 2016.2814.) in profile view; (F) in basal view. (G) Tooth morphotype 1 (VER 2016.2815.) in profile view; (H) in basal view. (I) Tooth morphotype 2 (VER 2016.2817.) in profile view; (J) in basal view. (K) Tooth morphotype 2 (VER 2016.2818.) in profile view; (L) in basal view. (M) Tooth morphotype 2 (VER 2016.2819.) in profile view; (N) in basal view. (O) Tooth morphotype 2 (VER 2016.2820.) in profile view; (P) in basal view

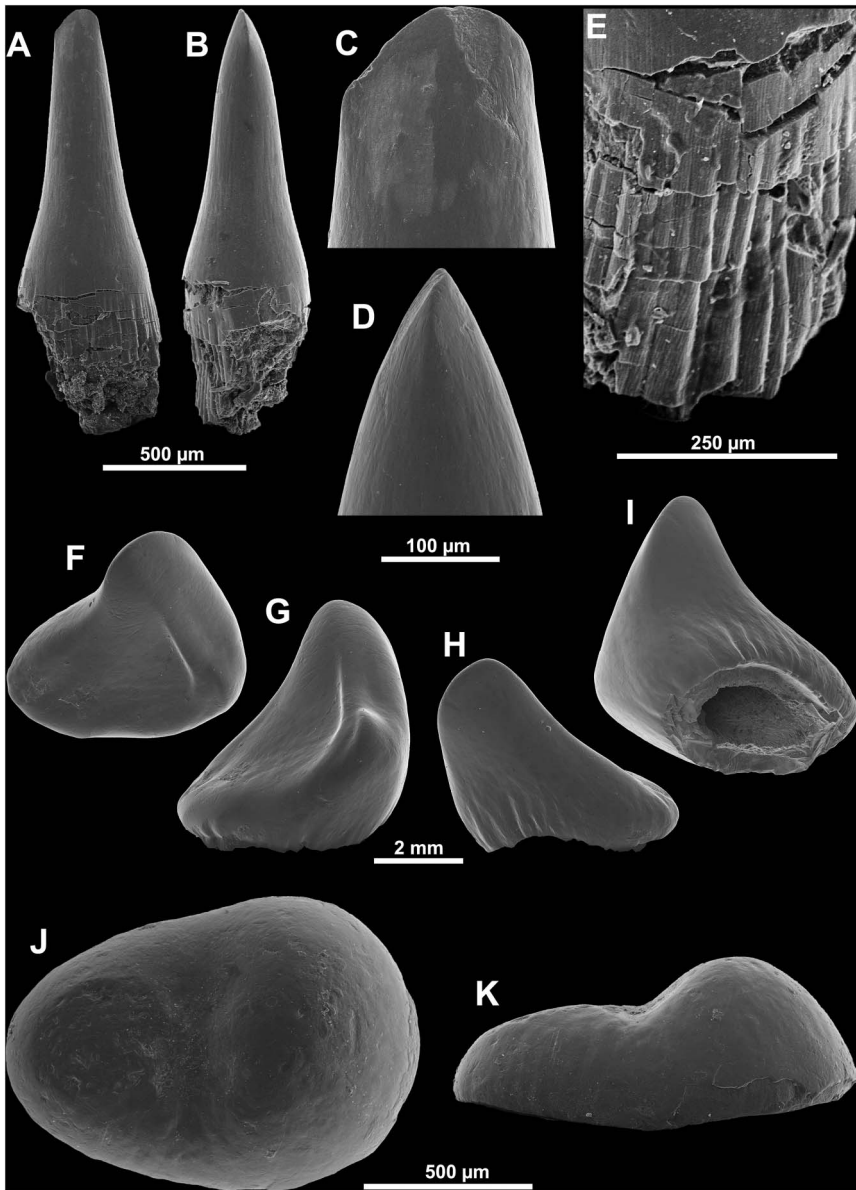


Fig. 20
 Actinopterygii indet. tooth remains (morphotypes 3–5) from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) Tooth morphotype 3 (VER 2016.2822.) in suggested labiolingual view; (B) in suggested anteroposterior view; (C) close-up of the tip in suggested labiolingual view; (D) close-up of the tip in suggested labiolingual view; (E) close-up of the tooth base. (F) Tooth morphotype 4 (VER 2016.2823.) in apical view; (G, H) in lateral views; (I) in basal view. (J) Tooth morphotype 5 (VER 2016.2824.) in apical (occlusal) view; (K) in lateral view

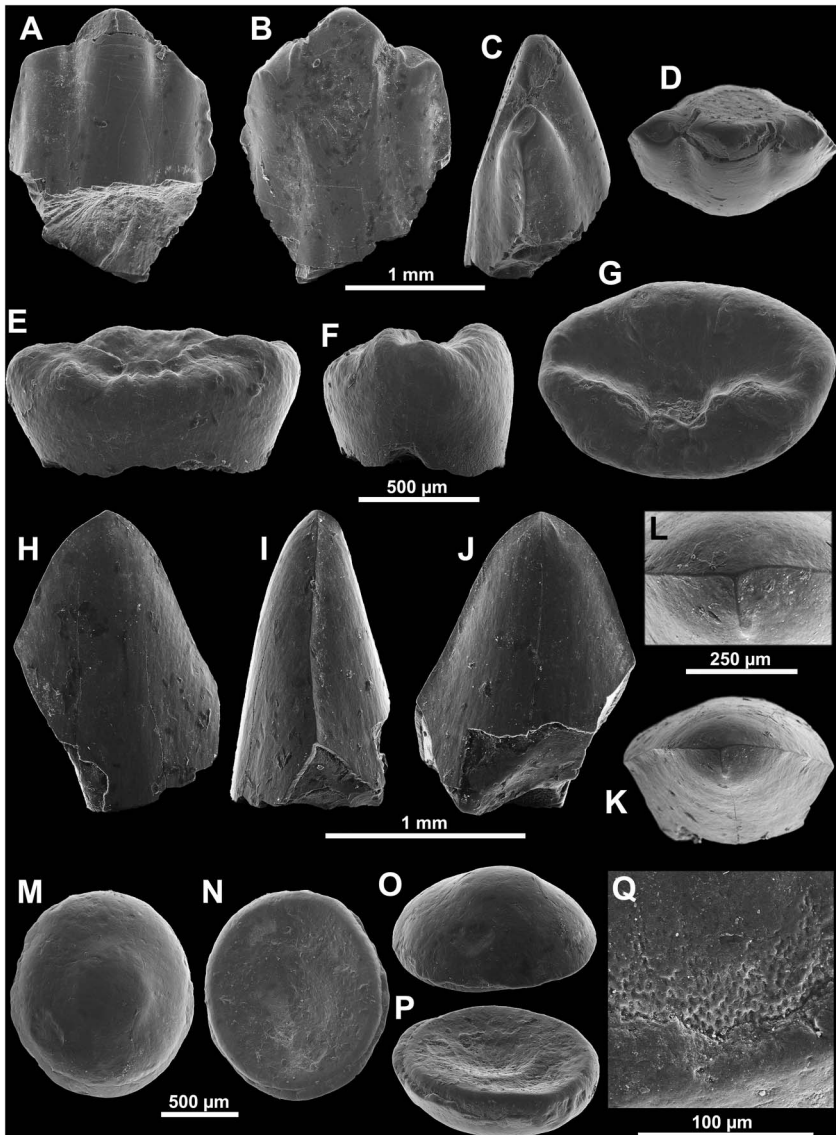


Fig. 21
Actinopterygii indet. tooth remains (morphotypes 6–9) from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) Tooth morphotype 6 (VER 2016.2825.) in suggested labial view; (B) in suggested lingual view; (C) in anteroposterior view; (D) in apical view. (E) Tooth morphotype 7 (VER 2016.2826.) in labiolingual view; (F) in anteroposterior view; (G) in apical (occlusal) view. (H) Tooth morphotype 8 (VER 2016.2827.) in suggested labial view; (I) in anteroposterior view; (J) in suggested lingual view; (K) in apical view; (L) close-up of the tip in apical view (K of the current figure). (M) Tooth morphotype 9 (VER 2016.2784.) in occlusal view; (N) in basal view; (O) in latero-occlusal view; (P) in latero-basal view; (Q) close-up of the pattern of the enameloid base

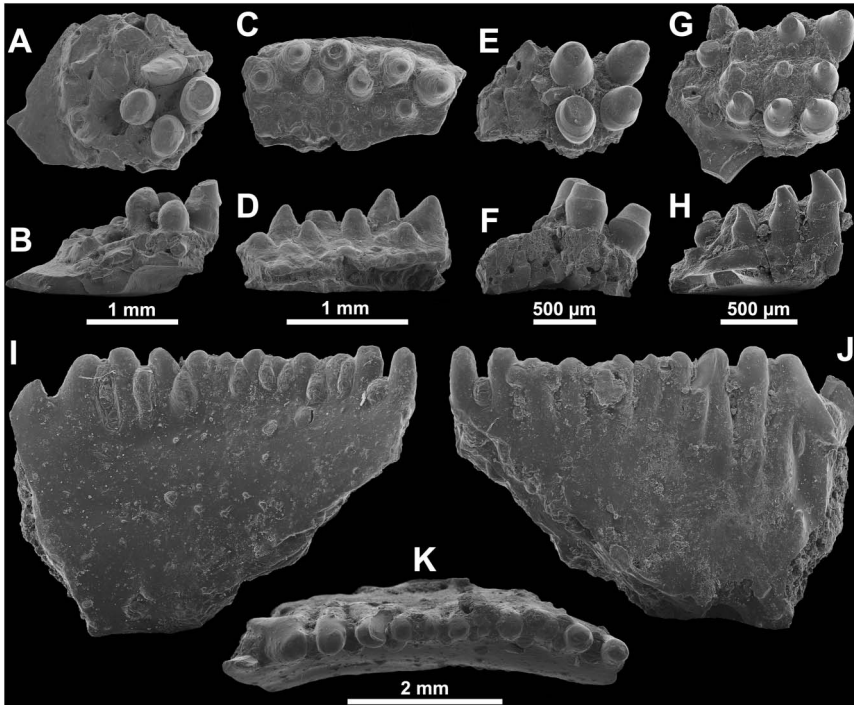


Fig. 22

Actinopterygii indet. tooth-bearing elements from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A) Tooth-bearing element (VER 2016.2828.) in apical view; (B) in profile view. (C) Tooth-bearing element (VER 2016.2829.) in apical view; (D) in profile view. (E) Tooth-bearing element (VER 2016.2830.) in apical view; (F) in profile view. (G) Tooth-bearing element (VER 2016.2831.) in apical view; (H) in profile view. (I) Tooth-bearing element (VER 2016.2832.) in lingual view; (J) in labial view; (K) in apical view

All teeth belonging to morphotype 2 (Fig. 19I–P) are blunt, which could have caused by wearing. The best preserved specimens (e.g., VER 2016.2820., Fig. 19O, P) are relatively high apicobasally. The outer surface is ornamented by small ridges. Teeth are circular in cross section, the basal surface is convex, consisting of smaller, also convex units with small pores, and a large, central pulp cavity (unlike that of morphotype 1). This morphotype is similar to the vomeral and coronoid teeth of *Cyclurus* (e.g., Fig. 3E, F in Gaudant et al. 2005; Figs 206A, B and 207 in Grande and Bemis 1998). A *Caturus* sp. tooth has been reported by Sweetman et al. (2014, Fig. 11C) with a similar basal surface, which could also suggest an amiiform affinity for this morphotype.

The only tooth referred to the third morphotype (VER 2016.2822.) is apicobasally straight, narrow, and relatively high (Fig. 20A, B). The acrodine cap is slightly

translucent, the very tip is flattened (Fig. 20C, D). The basal part of the tooth is only partially preserved, but the preserved portions bear fine apicobasal striations. The main features of this morphotype resembles to those of teeth of lepisosteids, but the basal rupture of specimen VER 2016.2822. does not show a plicidentine structure, the tip is also different in being not pointed or lanceolated, the tooth cap is much more elongated than those of *Atractosteus* (Fig. 5 in Szabó et al. 2016a), and basally the apicobasal ridges are also shorter (Fig. 20E).

Tooth VER 2016.2823. represents morphotype 4 (Fig. 20F–I), which has a robust, massive crown with thick, and shiny enameloid. It is hollow in basal view (exposing a pulp cavity), and asymmetric in all other views. The crown shows a smooth, extended convex surface on its lingual side, possibly caused by wear. The crown base bears well-developed but short apicobasal ridges, vanishing in the direction of the rounded grinding surface. The tooth could have belonged to a durophagous animal, feeding on hard-shelled preys (e.g., molluscs and crustaceans). In general, the tooth is slightly similar to the incisiform teeth of pycnodont fishes.

The fifth morphotype represented by one tooth (VER 2016.2824.; Fig. 20J, K) is similar to pycnodont molariforms in being bean shape in occlusal view, and having an ornamented occlusal surface. However, it differs from any other Iharkút pycnodont molariforms in being more flattened, and having a different surface pattern than any of the tooth positions in any ontogenetic stage of the local pycnodontids (Figs 3–5 in Szabó et al. 2016b). It does not bear any transversal groove or crenulations, but two main protrusions, one being higher than the other (Fig. 20K). The tooth is smoothly convex in basal view, similar to the teeth of Phyllodontidae, however, it has no protruding margin around the base of the occlusal surface. A morphologically very similar tooth was identified as a pycnodontid tooth by Estes and Sanchíz (1982, Fig. 4C).

Morphotype 6 is represented by specimen VER 2016.2825. (Fig. 21A–D). The tooth crown is relatively high, symmetrical, tricuspidate (Fig. 20A, B), and slightly compressed labiolingually (Fig. 21C). The middle cusplet is slightly bigger than the mesial and distal ones, all cusplets are flattened with rounded apical margin. The specimen bears visible occlusal marks on the suggested lingual side. This tooth is closely similar to the tooth published by Otero and Gayet (2001, Fig. 4C, D) as Characidae Alestinae tribe indet. from the Oligocene sediments of Oman, and to a tooth reported by Sharma and Patnaik (2014, Pl. 6, Fig. 18) as Characidae Alestinae trib. indet. from the Miocene of Baripada Beds (Orissa, India), in having a symmetrical, tricuspidate contour. It is worth mentioning that agamid lizard teeth with tricuspid contour are also similar (Figs 4 and 5 in Smith et al. 2009). Since characiforms were reported from the Late Cretaceous of Europe (Grigorsecu et al. 1985; Taverne 2003; Otero et al. 2008; Csiki-Sava et al. 2015), we attribute a possible characiform affinity to this specimen, until more and better preserved remains are unearthed.

The only tooth of the seventh morphotype (VER 2016.2826.) is apicobasally compressed, with an ornamented occlusal surface (Fig. 21E–G). The specimen is oval in occlusal view, and bears a groove-like transversal depression on the longer diameter

of the occlusal surface (Fig. 21G). Flattened cusps (main cusps and accessory cusps) are positioned around the depression in symmetrical ordering. This morphotype is weakly similar to the “*Alestes/Brycinus* sp.” teeth from the Pliocene of Kolla, central Africa (Fig. 9c–f in Otero et al. 2009, p. 67), to the Serrasalmiinae indet. teeth from the Middle Maastrichtian of Pajcha Pata, Bolivia (Fig. 7d, e in Gayet et al. 2001), and to the teeth of *Alestoides eocaenicus* from the Eocene of southern France (Fig. 4 in Monod and Gaudant 1998; Fig. 3d in Gaudant and Smith 2008), all being members of the order Characiformes.

Morphotype 8, represented by specimen VER 2016.2827., is fragmentary, consisting mainly of the apical part of the tooth (Fig. 21H–L). The preserved portion is triangular in labiolingual view, and bears smooth carinae both mesially and distally along the whole apicobasal height of the cap. The apex is rather blunt, with a contour that is formed by the weakly sinuous-like carinae. The very tip is three-bladed in apical view (Fig. 21L). Both the lingual and labial faces are smooth and they do not bear any ornamentation. Teeth with a weakly similar apical portion, referred to amiiform fishes were reported from several Cretaceous European localities (e.g., Fig. 2M–P in Vullo et al. 2009; Fig. 6B in Martin-Abad and Poyato-Ariza 2013).

Morphotype 9 is represented by only one specimen (VER 2016.2784.). The tooth has a hemispherical shape with circular contour in apical (and basal; Fig. 21M, N) view, and a smooth and shiny enamel covering the entire tooth surface. There is a central, bulge-like papilla on the apical face (Fig. 21O). In basal view, the tooth is smooth and slightly concave near to the center, with absent central cavity (Fig. 21N, P). A protruding margin runs around halfway the enameloid base (it is more visible in basal and lateral view; Fig. 21P). A pattern made up by a network of small pores can be seen near to this margin (Fig. 21Q). In general morphology, this remain is identical to the teeth reported by Cuny et al. (1998, Fig. 5E, F) as *Perleidiformes* indet. or *Paralepidotus*, and Godefroit et al. (1998, Fig. 7.5) as ?*Paralepidotus* or ?*Heterolepidotus* (however, these remains are both from Triassic deposits). The genus *Paralepidotus* is a member of Semionotiformes (Bermúdez-Rochas and Poyato-Ariza 2015), whereas *Heterolepidotus* is an ionoscopiform genus (Grande and Bemis 1998). According to Nelson (2006), perleidiform fishes are known from the Triassic to Jurassic, therefore, their presence in the Upper Cretaceous is unlikely. Semionotiforms (members of Ginglymodi) are represented only by Macrosemiidae in the Cretaceous (López-Arbarello 2012, Fig. 25). Papillae are uncommon in the teeth of ginglymodians, however, there are exceptionable reports (e.g., Fig. 5 in Forey et al. 2011; Fig. 8 in Bermúdez-Rochas and Poyato-Ariza 2015). Phyllodontid fishes (members of the order Elopiformes) have a similar tooth morphology and were reported from the Late Cretaceous of Europe (e.g., Laurent et al. 1999, 2002; Pereda-Suberbiola et al. 2015). Although elopiform fishes are represented at the Iharkút locality by vertebrae (see above), specimen VER 2016.2784. differs from the teeth of Phyllodontidae (Elopiformes) in having a central papilla, and having an incomplete, protruding margin around the tooth base (this margin of Phyllodontids

goes fully around the enameloid base). Until better preserved or more specimens are found, we refer specimen VER 2016.2784. as *Actinopterygii* indet.

Tooth-bearing elements. The indeterminate tooth-bearing elements are small, and all of them were sampled by screen-washing process. They consist of a basal, tooth-bearing portion on which all teeth are placed in different arrangements, in several numbers of rows. The teeth of the different specimens show morphological variability suggesting taxonomical variety. From another point of view, teeth of all of these elements refer to a non-durophageous, carnivorous diet. Non-durophageous neopterygian fishes are represented in the Iharkút fish fauna by lepisosteiformes and amiiforms. Numerous cranial elements of these fishes bear teeth with various morphologies. Depending on taxa, these elements could be vomers, parasphenoids, palatals, bones of the pterygoid region, premaxillae, maxillae, lacrimomaxillae, dermopalatines, ectopterygoids, endopterygoid, and various positions of coronoid elements (for further details, see [Grande and Bemis 1998](#); [Grande 2010](#)). Teeth and any potentially tooth-bearing elements of all carnivorous Iharkút teleost taxa (identified at least to ordinal rank) are unknown. Since their closer anatomical and taxonomical affinities are uncertain, we identify these elements here, as indeterminate actinopterygian tooth-bearing elements until associated or better preserved specimens are discovered.

Specimen VER 2016.2828. (Fig. 22A, B) is the largest of the tooth-bearing elements. It bears two styliform teeth with rounded tips, one of them being broken or worn, and the other one with signs of a belt-like incrustation of the enamel. Specimen VER 2016.2829. (Fig. 22C, D) is bent in occlusal view, and bears simple, conical teeth. Specimen VER 2016.2830. (Fig. 22E, F) has four preserved teeth, circular in cross section, with bulbous shape, and having an incrustated belt around on their apicobasal midline (similar to a tooth of specimen VER 2016.2828.; A and B of the same figure). Specimen VER 2016.2831. (Fig. 22G, H) bears pointed teeth. The teeth are convex anteriorly and concave posteriorly, increasing in size anteriorly, and arranged in parallel rows. Specimen VER 2016.2832. (Fig. 22I–K) is labiolingually flattened, and weakly bent in occlusal view. It is hardly fragmentary on both ends, and it bears blunt, styliform teeth, similar to indeterminate actinopterygian tooth morphotype 2 (see above).

Osteichthyes indet.

(Figs 23 and 24)

Referred material. Nine indeterminate elements (VER 2015.281A–B, VER 2016.2836., VER 2016.2837., VER 2016.2838., VER 2016.2839., VER 2016.2840., VER 2016.2841., VER 2016.2842., VER 2016.2843.).

These elements are not diagnostic, too badly preserved in quality or too fragmentary for confident taxonomic or anatomical determination. However, all the here described specimens show some similarity to various osteichthyan elements.

VER 2016.2836. (Fig. 23A, B) is flattened and ornamented by a central ridge, and also by smaller, concave pits in both directions to the central ridge. The other side bears foramina, without ridges. This specimen is somewhat similar to dermal scutes of

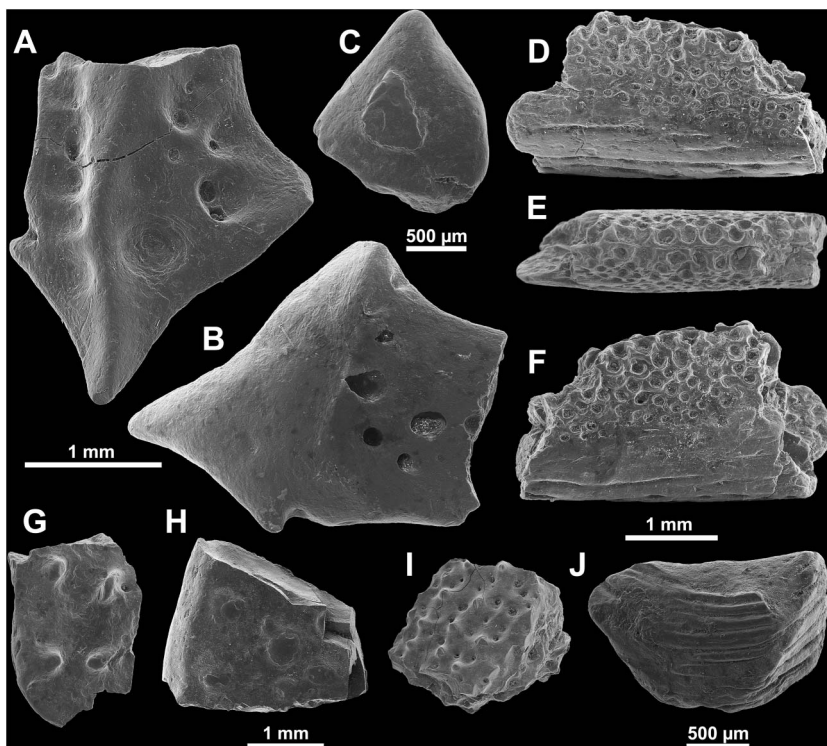


Fig. 23
Osteichthyes indet. remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). (A, B) VER 2016.2836. (C) VER 2016.2837. (D–F) VER 2016.2838. (G) VER 2016.2839. (H) VER 2016.2840. (I) VER 2016.2841. (J) VER 2016.2842.

some chondrosteian fishes (e.g., acipenserids), however, its ornamentation is made up by less fine details.

Specimen VER 2016.2837. (Fig. 23C) is flat, but still thick. The suggested inner surface is smooth, whereas the other side has a central, flattened tubercle. In general, this specimen is strongly similar to some acipenseriform elements, e.g., the dorsorostal skull bones and dorsal scales of *Psammorhynchus longipinnis* (Fig. 5 in Grande and Hilton 2006).

Specimen VER 2016.2838. (Fig. 23D–F) is weakly flattened, and covered both by longitudinal ridges and circular pits, ordered in a honeycomb-like fashion. Both sides of the specimen bear this kind of surface pattern. This specimen does not belong to any known local amphibian (Z. Szentesi, personal communication, 2016), or small-sized lizard (L. Makádi, personal communication, 2016), but its general morphology is similar to fish skull elements or fin spines (e.g., this specimen in the view of Fig. 23E is similar to the acipenserid pectoral fin spine reported by Hilton and Grande 2006, Fig. 6.3).

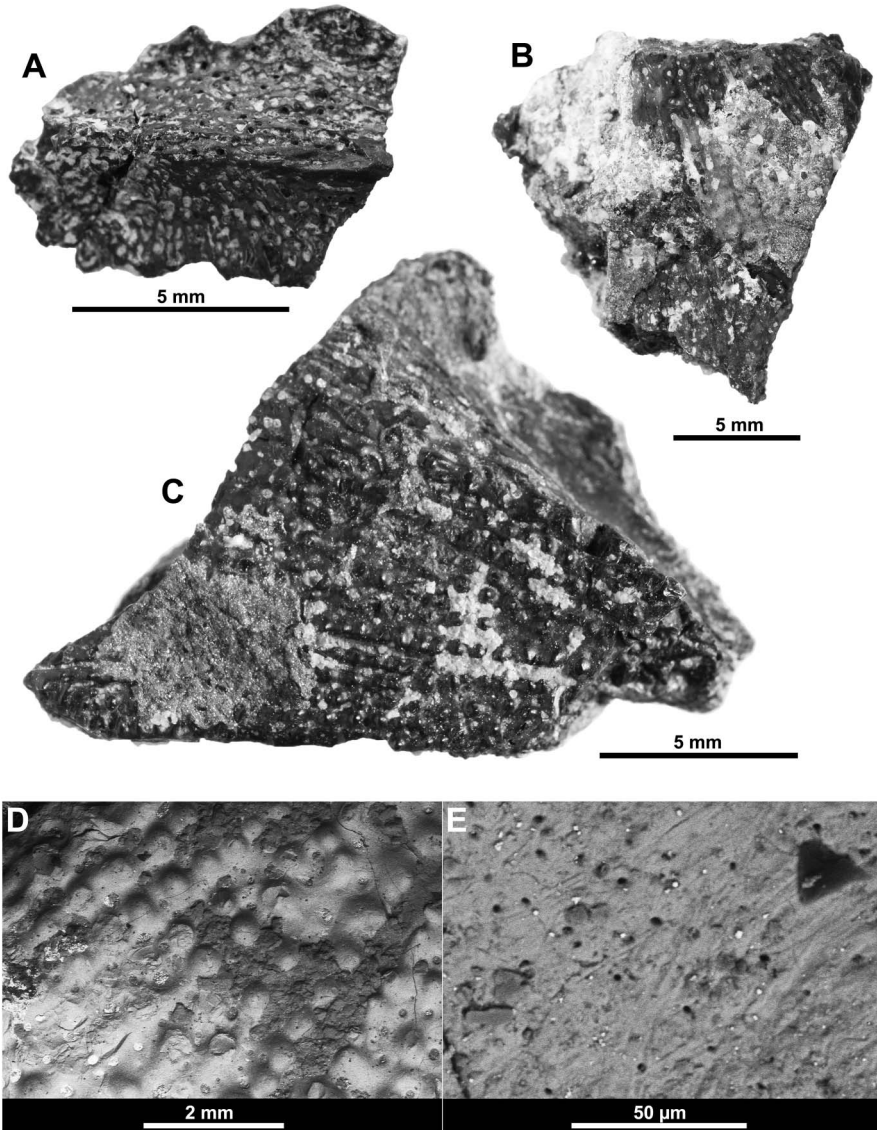


Fig. 24
Osteichthyes indet. remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary) with comparing material on A. (A) VER 2016.2843. in outer view; (B) VER 2015.281.B in outer view; (C) VER 2015.281.A in outer view; (D, E) scanning electron photography of the surface of specimen VER 2015.281.A (C of the current figure)

Specimen VER 2016.2838. is also similar to some osteichthyan jaw fragments shown by Sweetman et al. (2014, Fig. 11I, L) both in size and shape. However, the Iharkút specimen bears its pattern (tooth positions on the specimens of Sweetman et al. 2014) on both sides.

Specimen VER 2016.2839. (Fig. 23G), VER 2016.2840. (Fig. 23H) and VER 2016.2841. (Fig. 23I) are similar to each other. They are flattened and fragmentary remains. They are osseous, more or less smooth on their presumed inner side, whereas the other (suggested outer) side bears different pattern of bulges, circular pits, and pores. This tuberculate sculpturing does not bear ganoine, therefore, these remains do not indicate any lepisosteiform affinity. Squamulae of some osteoglossid taxa are generally flattened and bear similar ornamentation (e.g., Fig. 5 in Taverne et al. 2007; Fig. 9C, D in Haddoumi et al. 2016). However, these Iharkút specimens are smooth and flat on their inner side, without margins raised in the form of a ridge. Becker et al. (2010, Fig. 4G–J) reported possible pycnodontiform skull fragments from the Late Maastrichtian–Paleocene of Hot Spring County (Arkansas, USA) with similar sculpturing.

Specimen VER 2016.2842. (Fig. 23J) is pebble-like, rounded in every views and irregular in shape. It shows several overlapping, shiny units, weakly similar to the tooth plates of some tetraodontiform fish taxa (e.g., Fig. 19 in Otero et al. 2009; Text-Fig. 18 in Otero et al. 2010).

Specimen VER 2016.2843. (Fig. 24A) more closely looks like an acipenserid scute in having a high, central ridge with finely detailed ornamentation of circular holes and pits on its both sides, arranged in rows radiating from the central ridge. The dermal scutes of *Acipenser albertensis* (Pl. 21, Fig. 9 in Lambe 1902; Fig. 3 in Hilton and Grande 2006) or the ventral scutes of the extant *Acipenser brevirostrum* (Fig. 104 in Hilton et al. 2011) have very similar morphology. It is worth mentioning that specimen VER 2016.2843. is irregular on its other (presumed inner) surface, unlike acipenseriform scutes, which mostly have a flat or smooth inner surface. Specimens VER 2015.281.A (Fig. 24C–E) and VER 2015.281.B (Fig. 24B) are thicker and more robust than specimen VER 2016.2843., and their sculpturing consists of circular tubercles arranged in longitudinal rows. Skull elements of several silurid taxa also show similar ornamentations and morphologies (Fig. 12 in Otero et al. 2010; Fig. 6A, B in Otero et al. 2015).

Discussion

Diet of Iharkút fishes

The Iharkút ichthyofauna is composed of fish taxa with two main types of diet, ichthyophagous and durophagous forms.

Modern *Tractosteus* sp. are characterized by a very wide range of prey preference, however, the majority of their diet is made up by smaller fishes (Grande 2010).

Moreover, exceptionally preserved fossils of gars (among them full-body fossils of *Atractosteus* specimens) display prey preferences of various fossil gar taxa (e.g., Fig. 345 in Grande 2010).

Pycnodontiform fishes (represented by cf. *Coelodus* sp. at the Iharkút site; Szabó et al. 2016b) are all typically durophagous fishes with markedly heterodont dentition (Poyato-Ariza 2003; Kriwet 2005). The rich malacofauna (Szabó and Szente, in prep.) could have been a stabile food source for these fishes (Szabó et al. 2016b). Extant *Amia calva* is a voracious, fish-eating predator (Berry 1955; Grande and Bemis 1998). There are impressive, articulated fossils of amiid fishes demonstrating ichthyophagous predaceous dietary habits of some species (e.g., Fig. 119 in Grande and Bemis 1998). Ellimmichthyiform fishes are typical surface-feeder predators, fed on small surface-dwelling fishes (e.g., Grande 1984). Full-body specimens of *Diplomystus* have been found in the Eocene of the Green River Formation (USA) with *Knightia* specimens in their stomach and mouth (e.g., Fig. II.45 in Grande 1984).

Since diet of extant members of the order Salmoniformes is not standard (there are carnivorous, bottom, and plankton feeders among them; Pike et al. 1990; Nelson 2006) and their remains at the Iharkút locality are restricted to two vertebrae, their feeding preference remains highly uncertain.

Among the indeterminate actinopterygian teeth, there are teeth with morphology suited for carnivorous (morphotypes 1, 2, 3, and 8) and durophagous feeding habits (morphotypes 4, 5, and 9). Indeterminate actinopterygian tooth morphotype 6 is similar to some teeth of predatory characiforms and to incisiforms of some pycnodontiform taxa, whereas morphotype 7 seems to be suited for feeding on hard-prey, since it has an ornamented, relatively large, horizontal occlusal surface. Up to now, typically and clearly microphagous or filter-feeding fishes have not been identified undeniably within the Iharkút fish fauna.

There is no direct evidence for predational relations between any local fish taxa, because they are isolated elements, but some fossils show that these fishes were predators and preys too. Coprolites of piscivorous or partially piscivorous vertebrates are known from the Iharkút locality, since partially digested ganoid scales and pycnodont teeth have been found in some Iharkút coprolites (Segesdi et al. 2016; M. Segesdi, personal communication, 2016). This shows that these fishes were part of the food chain of the Iharkút ecosystem, and together with lepisosteids and pycnodontids the newly identified Iharkút fishes could have provide a much wider scale of prey for the local fish-eating forms, than we previously thought.

Habitat preferences

Fishes of the Iharkút vertebrate fauna represent a diverse spectrum of habitat preferences. Whereas some forms are known to have inhabited dominantly freshwater environments, some groups are almost exclusively marine. In spite of these circumstances, their record certainly shows their synchronous existence in the same environment.

Lepisosteiform fishes live primarily in freshwaters, extant lepisosteid species, e.g., *A. spatula* (alligator gar), *Atractosteus tristoechus* (cuban gar), *Atractosteus tropicus* (tropical gar), and *Lepisosteus osseus* (longnose gar) occasionally occur in brackish and even marine waters (Scott and Crossman 1973; Bussing 1987; Barrientos-Villalobos and Espinosa de los Monteros 2008; Grande 2010). Nevertheless, there are numerous reports for lepisosteid occurrence in marine sediments (Wiley and Stewart 1977; Grande 2010).

Pycnodontiform fishes are typically marine forms (Poyato-Ariza et al. 1998), but a few reports from Africa (Cuny et al. 2010), America (Winkler et al. 1990; Cifelli et al. 1999; Eaton et al. 1999), Asia (Cavin et al. 2009), and Europe (Estes and Sanchíz 1982; Poyato-Ariza et al. 1998; Kocsis et al. 2009; Szabó et al. 2016b) document their freshwater occurrence.

The extant *Amia calva* inhabits only freshwaters of eastern North America, but the fossil record of amiids suggests that non-amiin amiids were marine, whereas members of Amiinae are exclusively non-marine (Grande and Bemis 1998). Ellimmichthyiform fishes were reported worldwide from both marine and freshwater sediments (Grande 1982, 1985; Hay et al. 2007; Alvarado-Ortega et al. 2008; Murray and Wilson 2013). Many extant salmoniform species are euryhaline and have anadromous life cycle (Romero 2003; Zydlewski and Wilkie 2013).

To sum up, one of the peculiar features of the Late Cretaceous continental Iharkút vertebrate fauna is the occurrence of various, dominantly marine groups among the terrestrial and freshwater vertebrates (not only fishes but mosasaurs as well; Makádi et al. 2012). However, sedimentological and geochemical studies on vertebrates (Kocsis et al. 2009; Botfalvai et al. 2015), along with the occurrence of freshwater molluscs (I. Szente, personal communication; Szentesi 2008; Ósi 2012), and ostracods (M. Monostori, personal communication, 2003) unambiguously indicate a freshwater environment during the deposition of the Csehbánya Formation. These data raise two hypotheses for this inconsistency: (1) The marine to brackish groups inhabited these freshwater regions only occasionally, and tolerated significant changes in water salinity as it is suggested by many groups occurring in other localities as well. (2) Alternatively, periodical influxes of marine water within the groundwater changed the salinity of the aquatic environments for certain periods in Iharkút resulting in the tolerance of some basically marine forms. Whatever is the truth, further sedimentological and geochemical investigations are needed to get closer to the solution.

Paleobiogeographical inferences

The Late Cretaceous fish fauna from Iharkút appears to be a mixture of groups with biogeographically different origins, a phenomenon that is practically true for all continental faunal elements of the European Late Cretaceous archipelago (Csiki-Sava et al. 2015). Lepisosteid fishes are among the most widespread continental fish elements reported from almost all the main Late Cretaceous localities of Europe

(Fig. 1 in Szabó et al. 2016a; see also Table 3 of this study). Some authors (Brito 2006; Brito et al. 2006, 2007) indicate a Gondwanan origin for the group. In Europe, some remains formerly referred to *A. africanus* (Arambourg and Joleaud 1943) were described from the Campanian of France (Cavin et al. 1996). Newer results suggest that the French remains show affinities to the genus *Lepisosteus*, therefore their Gondwanan origin seems to need a revision (Text-Fig. 4 in Gayet et al. 2002; Szabó et al. 2016a).

Besides lepisosteids, characiforms are considered as Gondwanan-derived fishes (Otero et al. 2008; Arroyave et al. 2013). Their Late Cretaceous remains from continental deposits are known from the France and Romania as well (Grigorescu et al. 1985; Otero et al. 2008), and their fossils are also known from marine deposits of Nardò (Taverne 2003). The indeterminate actinopterygian tooth morphotypes 5 and 6 suggest their presence in the Iharkút material as well.

The pycnodontiform *Coelodus* is also known from various Late Cretaceous sites in Europe (Schultz and Paunović 1997), but their truly continental occurrence is restricted to only a few localities (Szabó et al. 2016b).

Amiiform fossils were reported from various Mesozoic localities of the Iberian Peninsula (e.g., Estes and Sanchíz 1982; Grande and Bemis 1998; Torices et al. 2010; Martín-Abad and Poyato-Ariza 2013; Ortega et al. 2015). The subfamily Vidalmiinae, exclusively represented by adult individuals about 1.4–2 m in total length, were identified e.g., from the Berriasian–lower Valanginian of El Montsec (Spain; Grande and Bemis 1998; Martín-Abad and Poyato-Ariza 2013). However, the Iharkút record represents their first undisputable occurrence from the Late Cretaceous of Europe.

Remains of the elopiform family Phyllodontidae are known from the Lower Cretaceous of England (Fig. 3 in Sweetman 2013), from the Late Cretaceous of Spain (Cavin 1999; Poyato-Ariza et al. 1999; Berreteaga et al. 2011; Company et al. 2013; Pereda-Suberbiola et al. 2015) and from the Late Cretaceous of the French Petites-Pyrénées (Laurent et al. 1999, 2002). The Santonian Iharkút record further extends both the temporal and spatial distribution of the group within the Late Cretaceous, and suggests their continuous presence in the European Cretaceous.

Various ellimmichthyiform taxa were reported from the Upper Cretaceous marine sediments of Europe (e.g., Murray et al. 2016), but the Iharkút record seems to extend the European occurrence of Ellimmichthyiformes until the Santonian.

There is a questionably classified report about some remains of the salmoniform suborder Argentinoidei, belonging to the European genus *Nybelinoides brevis* (Traquair 1911) from the Wealdian (Early Cretaceous) of Bernissart (Belgium). If the identification of the vertebrae described here is correct, then they are the first European Late Cretaceous indication of this group.

In spite of the diverse fish fauna presented here from the Iharkút locality, various fish groups have not yet been encountered. According to Csiki-Sava et al. (2015), acipenseriforms, mawsoniids, palaeolabrids, albulids, osteoglossids, and sparids are known from other Late Cretaceous continental sites of Europe, but missing from the Iharkút ichthyofauna (Table 3), a phenomenon that might be related to different paleoecological factors of the sites.

Table 3
 Summary of the Late Cretaceous continental osteichthyan fish faunas of Europe (following Csiki-Sava et al. 2015; Marmi et al. 2016)

Taxon	Habitat	Western Hungary	Iberian Peninsula	Southern France	Romania	References
Lepisosteiformes	■	X	X	X	X	Blanco et al. (2017), Buffetaut et al. (1996, 1997, 1999), Csiki et al. (2008), Grigorescu et al. (1999), Laurent et al. (1999, 2002), Marmi et al. (2016), Ortega et al. (2015), Pereda-Suberbiola et al. (2015), Pérez-García et al. (2016), Szabó et al. (2016a), and Vasile and Csiki (2010)
Pycnodontiformes	▲	X	X			Blanco et al. (2017), Marmi et al. (2016), Ortega et al. (2015), Torices et al. (2011), and Szabó et al. (2016b)
Amiidae	●	X	X			Torices et al. (2011), Ortega et al. (2015), and this study
Elopiformes ^a	▲	X	X	X		Blanco et al. (2017), Beretegaga et al. (2011), Cavin et al. (2009), Pereda-Suberbiola et al. (2015), Laurent et al. (1999, 2002), Poyato-Ariza et al. (1999), and this study
Elimmichthyiformes	●	X				This study
Salmoniformes	●	?X				This study
Semionotiformes	●		X			Blanco et al. (2017)
Aspidorhynchiformes	▲		X			Blanco et al. (2017)
Cypriniformes	■		?X			Blanco et al. (2017)

Table 3 (Continued)

Taxon	Habitat	Western Hungary	Iberian Peninsula	Southern France	Romania	References
Acipenseriformes	●				X	Grigorescu et al. (1985)
Characiformes	■		X	X	X	V. Codrea and C. Jipa (personal communication, 2011) [after Csiki-Sava et al. (2015)]; Grigorescu et al. (1985), and Otero et al. (2008)
Mawsoniidae	■			X		Cavin et al. (2005)
Palaeolabridae	●		X			Pereda-Suberbiola et al. (2015)
Albulidae	●		X			Ortega et al. (2015) and Torices et al. (2011)
Osteoglossiformes	●		X			Company et al. (2013)
Perciformes	▲		X	?X		Blanco et al. (2017), Laurent et al. (1999, 2002), and Marmi et al. (2016)

The habitat preferences are based on Froese and Pauly (2016; www.fishbase.org), Nelson (2006), and the data available on the webpage of Fossilworks (www.fossilworks.org) and Paleobiology Database (www.paleobiodb.org). Habitat preferences: ■ : dominantly freshwater forms; ● : taxa with mixed habitat preference; ▲ : dominantly marine forms

^aElopiform fishes are represented by Phyllodontids in Spain and France, while the Iharkút remains can be identified only on order rank

Large similarities of the Iharkút fish fauna to North American fish assemblages can be recognized. Brinkman et al. (2013) described Cenomanian–Late Campanian fish remains of the Grand Staircase region in Utah (USA). This assemblage includes remains of lepisosteids [with the genus *Lepisosteus*; however, according to Sigé et al. (1997), some lanceolate gar teeth suggest the presence of *Atractosteus*], *Coelodus*, vidalamiin and non-vidalamiin amiids, ellimmichthyiforms, Salmoniformes, indeterminate acanthomorph centra, all of which have been unearthed at the Santonian Iharkút site as well. It is worth mentioning that teleost centra type H of Brinkman et al. (2013) are similar to the Iharkút indeterminate teleost centra A3. Brinkman and Neuman published their first report on the fish centra of the Campanian Dinosaur Park Formation in 2002. Later on, Neuman and Brinkman (2005) listed the occurrence of lepisosteids [with *Lepisosteus* (*Atractosteus*) *occidentalis*], amiids (gen. indet.), a small elopiform (gen. indet.), ellimmichthyiforms, Esocoid/Salmoniformes (centra closely similar to the Iharkút specimens), an indeterminate acanthomorph (centra closely identical to the Iharkút indeterminate acanthomorph centra), and Teleost type H (centra closely similar to the Iharkút indeterminate teleost centra morphotype 3) in the Dinosaur Park fish assemblage. These taxa are all elements of the Iharkút fish assemblage as well. Fish fauna of the Maastrichtian Hell Creek Formation (Montana, USA) also consists of taxa overlapping with the Iharkút ichthyofauna (Brinkman et al. 2014). This fauna includes Lepisosteidae (genus and species indet.), Vidalamiinae, non-vidalamiin amiids, Salmoniformes (only on order rank), an indeterminate acanthomorph fish (centra comparable with the Iharkút indeterminate acanthomorph centra), and a Teleost centrum type HvB (comparable with the Iharkút indeterminate Teleost centrum morphotype 3).

The Iharkút Ellimmichthyiformes indet. 1 centra are most comparable with those of *Diplomystus*, which genus is known from China, Japan, Korea, Lebanon, and North America (Grande 1982; Chang and Maisey 2003; Yabumoto et al. 2006). Newbrey et al. (2010) described *H. armaserratus* from the Maastrichtian Horseshoe Canyon Formation (Alberta, Canada), with centra morphologically very similar to the Iharkút specimen VER 2016.2793.

The diverse Iharkút fish fauna significantly expands our knowledge of the Late Cretaceous European fish faunas. The mixture of predominantly marine and freshwater forms, together with taxa characterized by variable habitat preference complicates the biogeographical affinity of the Iharkút fish fauna but, on the basis of the available record, a North American affinity might be suggested.

These patterns in the faunal similarities or differences could have simple causes. Csiki-Sava et al. (2015) concluded that since the Late Cretaceous European, Gondwana-derived fish taxa did not display strong saltwater tolerance (based on recent analogies), migration of fish taxa from Gondwanan regions to Europe could have happened via land bridges and fluvial connections. This indicates that the trans-Tethyan continental faunal connections could have been more widespread than previously thought. According to this hypothesis, it is worth mentioning that mapping and description of European Late Cretaceous fish faunas (both from marine and

freshwater sediments) are much less complete and detailed, than that of North America (and some from Asia). Descriptions and re-descriptions of some Late Cretaceous fish materials were performed by numerous authors in the last few years (e.g., Berreteaga et al. 2011; Callapez et al. 2014; Corral et al. 2016; Marmi et al. 2016), but a great amount of material still needs to be reviewed (or studied). This future work, perhaps completed by extensive screen-washing procedures in other localities as was carried out in the last 16 years in Iharkút, certainly will enormously increase the fish material and provide much more insights into the diversity and biogeographical aspects of the Late Cretaceous European continental fish fauna.

Conclusions

The Iharkút ichthyofauna is much more diverse than previously assumed, including *Atractosteus* sp., cf. *Coelodus* sp., an indeterminate vidalamiini, a non-vidalamiini amiid, an indeterminate elopiform, two indeterminate ellimmichthyiform taxa, a possible indeterminate salmoniform, at least one indeterminate acanthomorph, and at least one indeterminate teleost taxon (which is different from all other local fishes in the morphology of the centra; Fig. 25). Some groups (ellimmichthyiforms, vidalamiini, and possibly salmoniforms) are first reported from Iharkút among the European

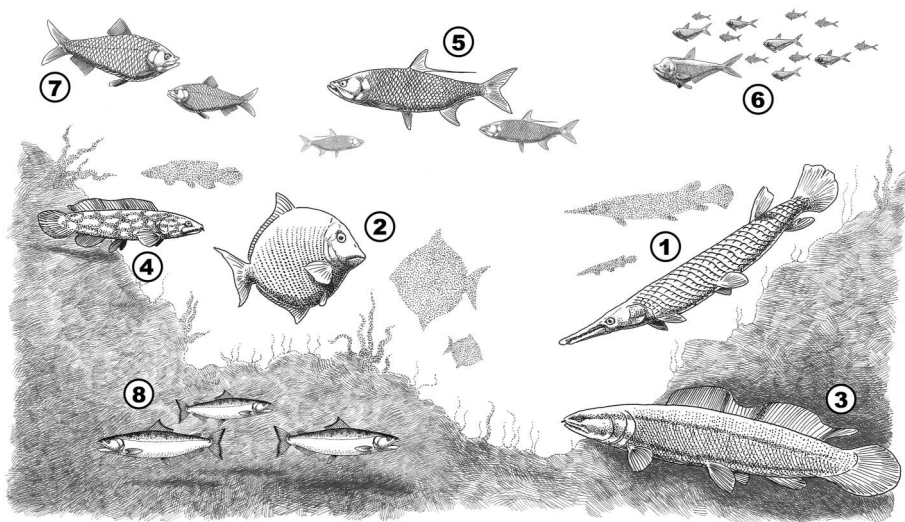


Fig. 25
Schematic reconstruction of the Santonian fish fauna of the Iharkút vertebrate site. The picture shows all local fish taxa identifiable at least on order rank. (1) *Atractosteus* sp., (2) cf. *Coelodus* sp., (3) Vidalamiinae indet., (4) Amiidae indet., (5) Elopiformes indet., (6) Ellimmichthyiformes indet. 1, (7) Ellimmichthyiformes indet. 2, and (8) cf. Salmoniformes indet.

Late Cretaceous faunas. Moreover, the described specimens that are taxonomically indeterminate (teeth, tooth-bearing skull elements, cycloid scales, and unidentified elements) indicate that this study does not show the final number of the Iharkút fish taxa.

The vast majority of the represented taxa are ichthyophagous predators, but durophagous feeders also are present, while clearly microphagous and filter feeder fish taxa are absent in the collected material. Brackish or saltwater ecosystems might have been relatively close to the Iharkút environment, since many taxa with salt water tolerance, including forms that are typically thought of as fully marine, are present in the fauna.

Some of the Iharkút fish taxa are already known from other Late Cretaceous localities of Europe, but the revealed fish fauna shows large similarities to North American fish assemblages. This similarity seems to be unique, most probably because of the lack of information on the Late Cretaceous European ichthyofaunas.

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