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Fish remains from the Lower Cretaceous (Valanginian-Hauterivian) of Hárskút (Hungary, Bakony Mts)

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Abstract – Lower Cretaceous (Valanginian-Hauterivian) fish remains, collected in the Közöskút Ravine (nearby Hárskút, Hungary) in the 1960s are detailed here. Although the material is poorly preserved, it is of great importance, because this geographical region and stratigraphical provenance are relatively undersampled for marine vertebrates. The collected material includes four orders of fish: Hexanchiformes, Synechodontiformes, Semionotiformes and Pycnodontiformes. This is the first, actualized report of some of the Hárskút fish taxa from the Mesozoic of Hungary. The results add important data to the distribution of the identified taxa, especially to that of *Gyrodus*. With 20 figures and 1 table.

Key words – *Gyrodus*, Hauterivian, Hárskút, Hexanchidae, *Lepidotes*, *Sphenodus*, Valanginian

INTRODUCTION

Our knowledge on the Mesozoic marine fishes of the Pannonian Basin is yet incomplete. Only a few papers describe these faunas (or faunal elements) in detail (e.g., ŐSI *et al.* 2013, 2016; PÁSZTI 2004; SZABÓ *et al.* 2016*a*, *b*; SZABÓ & ŐSI 2017), while further works mention Mesozoic fish remains shortly (e.g., DULAI *et al.* 1992; FŐZY & SZENTE 2014). A large amount of Mesozoic fish remains were collected in the last century, however, most of them were found during excavations after invertebrate faunas.

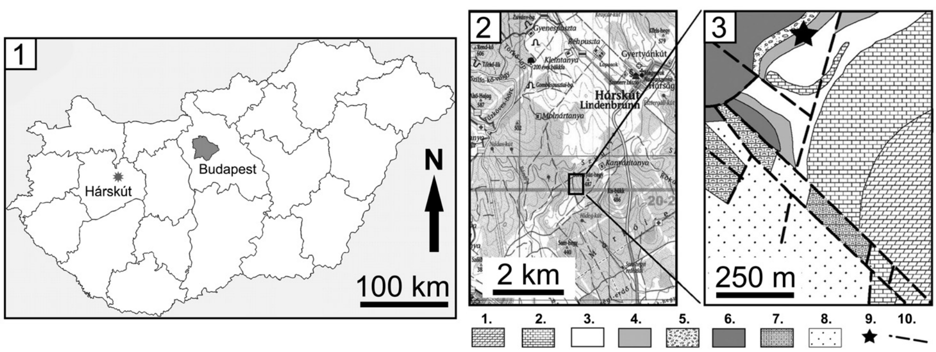
Field works, carried out in the 1960s in the outcrop of the Közöskút Ravine near Hárskút (Hungary, Bakony Mts) yielded a few tooth remains of various chondrichthyans and osteichthyans. The locality was first described by FÜLÖP (1964) as an important locality for Early Cretaceous fossils. Later on, the outcrop and the collected invertebrate fauna was re-investigated by FŐZY *et al.* (2010). Among the Hárskút fish fossils, collected in 1960–1962, FÜLÖP (1964) figured only a tooth of *Sphenodus* sp., and listed a tooth of *Sphaerodus neocomiensis* (see below). Főzy *et al.* (2010) also mentions „isolated teeth of pycnodont and cartilaginous fishes", but aside from these, the collected vertebrate material remained unpublished.

Up to date, some of the collected Hárskút fish taxa have not been reported from the Pannonian Basin; however, their regional occurrence in the Lower Cretaceous is not necessarily surprising. The collected fish fauna includes two shark and two bony fish forms, representing different trophic groups. To alleviate the aforementioned incompleteness of our knowledge on the Lower Cretaceous fish faunas of Hungary, here I describe the re-discovered material in detail.

LOCALITY AND GEOLOGICAL BACKGROUND

The studied outcrop, named Közöskút Ravine (geographical coordinates: 47° 9' 58.17" N, 17° 47' 11.48" E) is situated about 2.5 km E-SE from the village of Hárskút (southwestern part of the central Bakony Mts, Hungary) (Figs 1–3). During the last decades different sections of the Mesozoic succession of the Közöskút Ravine were sampled. Among them, the present study concentrates to the one, referred to as section HK-12, Közöskút Ravine at Hárskút. This section could be easily mistaken for an other nearby section, originally labelled as Hárskút 12/a (see Főzy *et al.* 2010 and Főzy 1990).

The HK-12 section exposes 28 metres of Lower Cretaceous pelagic carbonates. The ravine provides Lower to Middle Jurassic Rosso Ammonitico-type suc-



Figs 1–2. Geographical position of the HK-12 section (Hárskút) (Fig 2. modified after Főzy *et al.* 2010). – **Fig. 3.** Simplified geological map of the vicinitiy of the studied section. – 1 = Triassic Dachstein Limestone. – 2 = Lower and Middle Jurassic carbonates. – 3 = Upper Jurassic cephalopod limestone. – 4 = Lower Cretaceous Biancone-type carbonate. – 5 = Lower Cretaceous cephalopod marl. – 6 = Aptian crinoidal limestone. – 7 = Post-Aptian carbonates. – 8 = Tertiary deposits. – 9 = Location of the section HK-12. – 10 = Detected or supposed faults (modified after Főzy *et al.* 2010)

cession with repeated gaps, as the result of non-deposition (Fülöp *et al.* 1969; Galácz 1975). The Upper Jurassic is represented by the Lókút Radiolarite Formation and the overlying Pálihálás Limestone Formation. The Pálihálás Limestone passes upwards into the Upper Tithonian-Berriasian Szentivánhegy Limestone Formation. This is followed by the Biancone-type cherty marls of the Valanginian Mogyorósdomb Limestone Formation. The youngest Mesozoic formations, exposed in the HK-12 section are the uppermost Hauterivian cephalopod-bearing marl and the Aptian beds of the Tata Limestone Formation (Főzy *et al.* 2010) (Fig. 4).

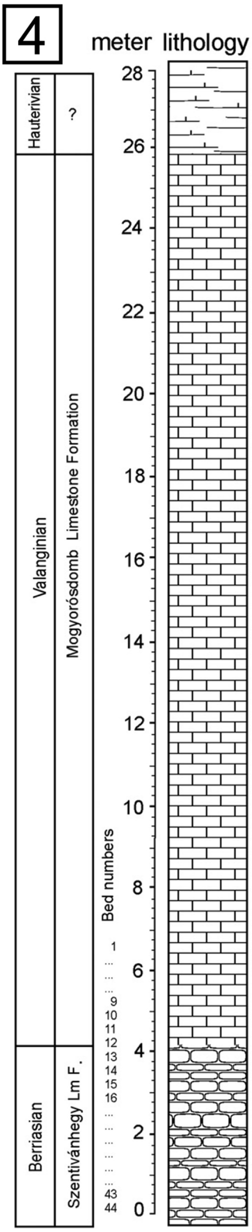
The Berriasian beds of the section (beds 45–13) yielded a moderately diverse cephalopod fauna, including the zonal index species for the Tirnovella occitanica and Fauriella boissieri Zones, representing the Middle and Upper Berriasian. Beds 12–10 yielded a rich Early Valanginian ammonite fauna (beds 12, 11: Thurmanniceras pertransiens Zone; bed 10: Busnardoites campylotoxus Zone), while beds 9–1 are assigned to the early Late Valanginian (Saynoceras verrucosum Zone) (for field photographs see Figs 5–6). According to its rich ammonite fauna, a marl pit at the top of section HK-12 most probably represents the latest Hauterivian (Főzy *et al.* 2010). The latter assemblage was assigned to the Barremian by Fülöp (1964), however, during their revision, Főzy *et al.* (2010) did not recognize any typical early Barremian ammonite form listed by Fülöp.

MATERIAL AND METHODS

All here described fish remains were collected in the 1960s, during field work collection supervised by József Fülöp. The specimens were originally housed in the collection of the Mining and Geological Survey of Hungary (MBFSZ; Geological and Geophysical Institute of Hungary by earlier name). The material had been forgotten for decades, then it was re-discovered by István Főzy.

Altogether 11 fish teeth were collected from the Valanginian-Hauterivian formations of the Közöskút Ravine. The Valanginian Mogyorósdomb Limestone Formation yielded most of the fish teeth (9 teeth), while only two teeth came from the Hauterivian cephalopod-bearing marl at the top of the section. No Berriasian beds of the Közöskút Ravine yielded any vertebrate remain (Table 1).

All fish teeth are greyish to brownish in colour. All shark teeth are rootless, the preserved crowns are often damaged. The two bony fish teeth have nicely preserved crowns. Most teeth are still embedded in a piece of limestone-matrix, from which they are too risky to prepare without break/damage. The specimens were cleaned in tap water, no other chemical or mechanical method for preparation or conservation has been used.



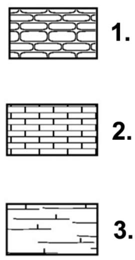


Fig. 4. Composite log of the HK-12 section. – 1 = Rosso Ammonitico-type limestone. – 2 = Biancone-type carbonate. – 3 = grey marl (modified after Főzy *et al.* 2010). – **Fig. 5.** Surface of bed 10 (photo courtesy of István Főzy). – **Fig. 6.** Marly limestone and clay above bed 10 (photo courtesy of István Főzy)

Table 1: Distribution of the fish taxa in the Berriasian-Hauterivian beds of the HK-12 section

	Berriasian	Valanginian			Hauterivian
		bed 8	bed 9	bed 10	
Hexanchidae indet.		X			
Sphenodus sp.				X	X
Lepidotes sp.					X
Gyrodus sp.			X		
Number of teeth	0	1	1	7	2
		9			

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Subcohort Neoselachii Compagno, 1977
Superorder Selachimorpha Nelson, 1984
Order Hexanchiformes Buen, 1926
Family Hexanchidae Gray, 1851

Hexanchidae indet.
(Figs 7–8)

Referred material – 1 lower tooth (MBFSZ 2017.237.1.); stratigraphic origin: Valanginian (HK-12/8).

Description – Only the crown is preserved, the full root is missing. The crown is embedded in a small piece of limestone, where it is displayed in lingual aspect. The preserved crown seems to be incomplete both mesially and distally; therefore the exact number of the mesial and distal cusplets can not be given. The crown is mesiodistally long, while apicobasally low, which refers to a possible lower tooth. Two, distally curved mesial cusplets are preserved. They distally increase in size, the mesial cutting edge of the first mesial cusplet is straight, while that of the second one is convex. The distal cutting edge of both mesial cusplets is weakly convex. The main cusp and the two distal cusplets are distally inclined, they show a characteristic, sigmoid contour (see on Fig. 8). This sigmoidism is given by the asymmetric convexity of their mesial cutting edge, and the weak convexity of their distal cutting edge. The preserved mesial and distal cusplets are nearly equal in size; however, the mesials are still smaller.

Remarks – Family Hexanchidae is the most abundant hexanchoid family, ranges from the Mesozoic to the Recent (Cappetta 2012). The Hárskút hexanchid specimen is reminiscent of the teeth of *Notidanodon*, a hexanchid genus, which was also present in the Lower Cretaceous (Cappetta 2012; Mutterlose 1984; Thies 1987; Ward & Thies 1987), however, since the tooth is too poorly preserved, here I describe it only as Hexanchidae indet.

Order Synechodontiformes Duffin et Ward, 1993
Family Orthacodontidae Glikman, 1957
Genus *Sphenodus* Agassiz, 1843

Sphenodus sp.
(Figs 9–15)

Referred material – 8 teeth (MBFSZ 2017.238.1. – MBFSZ 2017.245.1.); stratigraphic origin: Valanginian (HK-12/10) and Hauterivian (Barremian in Fülöp 1964).

Description – All here referred teeth are rootless. They are slender, pointed at the tip with smooth labial and lingual face. Both the labial and lingual faces are convex, which convexity is more expressed on the lingual side. The cutting edges are sharp on both sides of the crown. Following their upright crown, convex on both faces, the best preserved specimens may represent anterior teeth (distal teeth have more flattened, distally inclined crown).

Remarks – Here I follow Klug (2010), who included *Sphenodus* in Synechodontiformes. The genus represents a group of pelagic predatory neoselachians. Numerous species of *Sphenodus* have been described (Duffin & Ward 1993), several of which have later been regarded as synonymous and/or *nomina dubia* (see Kriwet *et al.* 2006).

Only complete teeth allow a specific description (Cappetta 2012). Because of their poor preservation, the torsion and height of the Hárskút cusps (important features for specific identification; see Böttcher & Duffin 2000, Table 1) are not investigeable. Therefore, following the low number and poor preservation of the Hárskút orthacodontid teeth here I describe them only as *Sphenodus* sp. Teeth of *S. nitidus*, a species reported from the Upper Jurassic and the Lower Cretaceous bear a distal cutting edge developed at the tip of the cusp only (Böttcher & Duffin 2000, Table 1; see also Kanno *et al.* 2017, Table 1), which character is absent in the Hárskút specimens.

Fülöp (1964, pl. 17, fig. 10) illustrated specimen MBFSZ 2017.245.1. as *Odontaspis* sp. The general crown morphology of *Sphenodus* and numerous odontaspids is very similar, which may have led Fülöp to the misidentification.

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Cope, 1887
Division Holostei Müller, 1844
Order Semionotiformes Arambourg et Bertin, 1958
Family Semionotidae Woodward, 1890
Genus *Lepidotes* Agassiz, 1832

Lepidotes sp.
(Figs 16–17)

Referred material – 1 tooth (MBFSZ 2017.246.1.), stratigraphical origin: Hauterivian (Barremian in Fülöp 1964).

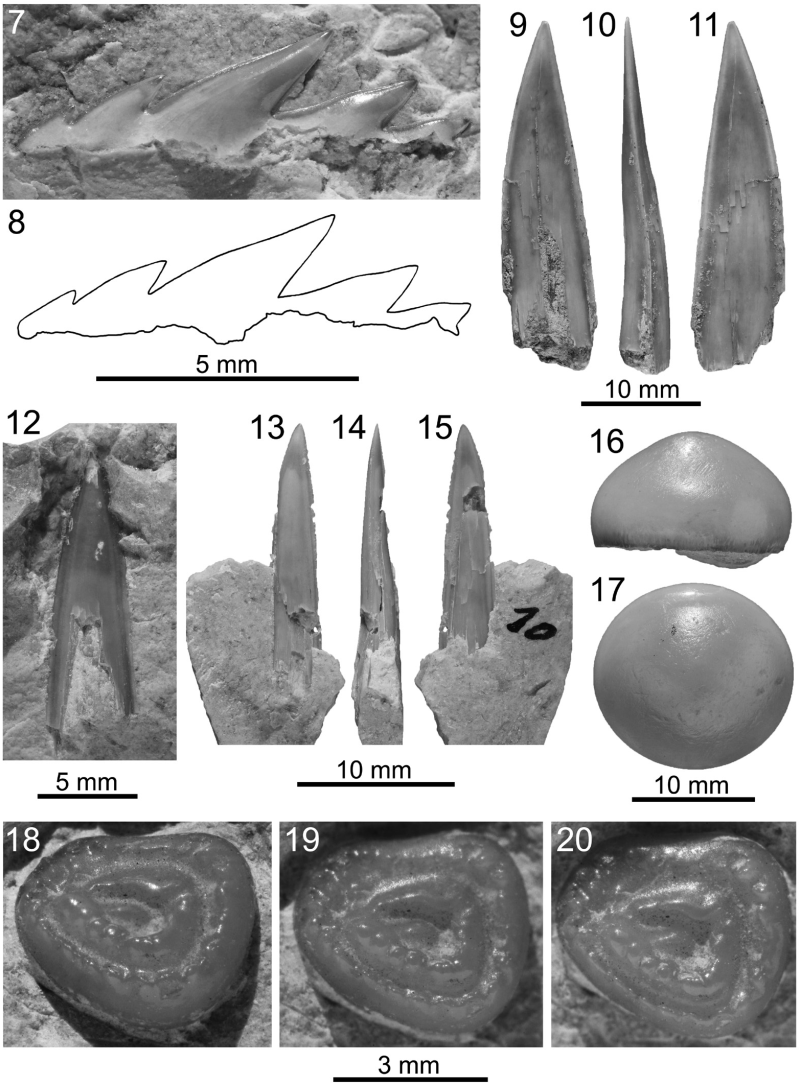
Description – The tooth is large and circular in occlusal view. The profile view is hemispherical, a worn, large central protuberance (or central papilla) is present, which is more visible in this view. The enamel is thick and shiny, it bears various signs of wear. The tooth base bears fine apicobasal ridges all around. This tooth remain was listed as *Sphaerodus neocomiensis* by Fülöp (1964, p. 55).

Remarks – Almost any large, robust crushing tooth from the Mesozoic may be identified erroneously as *Lepidotes* sp. (Forey *et al.* 2011). Isolated teeth of *Lepidotes* lack distinguishing characters, which often makes it difficult to differentiate them from related taxa (Nordén *et al.* 2015). The Hárskút specimen has very general characteristics, however, it still shows close morphological affinities with the teeth of the fish described widely as *Lepidotes maximus* (see e.g., Etheridge & Willett 1889, pl. 15; Jain 1984, pl. 2, fig. C; Schneider *et al.* 2013, fig. 8F). Numerous nominal species of *Lepidotes* have been described, a part of them probably represents *nomina dubia*, and indeed the genus requires an exhaustive revision.

A similar tooth, found in the Barremian of Zirc, was figured by Fülöp (1964, pl. 29, figs 9, 10) as *Sphaerodus neocomiensis*. *Sphaerodus* is a widely used, early synonym name for *Lepidotes*. The Zirc tooth may represents an other tooth remain of *Lepidotes*, based on its simple morphology of hemispherical shape and the presence of a central protuberance on the occlusal surface.

Division Halecostomi Regan, 1923
Order Pycnodontiformes Berg, 1937
Family Gyrodontidae Berg, 1940
Genus *Gyrodus* Agassiz, 1833

Gyrodus sp.
(Figs 18–20)



Figs 7–8. Hexanchidae indet. lower tooth (MBFSZ 2017.237.1.) from bed HK-12/8 (Valanginian). – **7.** Lingual view. – **8.** Line drawing of the same specimen, for showing the sigmoidity of the acrocone and accessory conules. – **Figs 9–11.** *Sphenodus* sp. (MBFSZ 2017.245.1.) from the uppermost (Hauterivian) part of the HK-12 section. – **9.** Lingual view. – **10.** Profile view. – **11.** Labial view. – **Fig. 12.** *Sphenodus* sp. tooth (MBFSZ 2017.238.1.) from bed HK-12/10 (Valanginian), ?lingual view. – **Figs 13–15.** *Sphenodus* sp. tooth (MBFSZ 2017.241.1.) from bed HK-12/10 (Valanginian). – **13.** Lingual view. – **14.** Profile view. – **15.** Labial view. – **Figs 16–17.** *Lepidotes* sp. tooth (MBFSZ 2017.246.1.) from the uppermost (Hauterivian) part of the HK-12 section. – **16.** Profile view. – **17.** Occlusal view. – **Figs 18–20.** *Gyrodus* sp. tooth (MBFSZ 2017.247.1.) from bed HK-12/9 (Valanginian), in three different views showing the occlusal surface

Referred material – 1 tooth (MBFSZ 2017.247.1.); stratigraphical origin: Valanginian (HK-12/9).

Description – The tooth remain is embedded in a piece of stone-matrix, exposed in occlusal aspect. The tooth is flattened, and has a pear to trapezoid shape in occlusal view. A well-marked central tubercle (or central papilla) is present, which is surrounded by an apical ring, running all around the central papilla, covered by crenulations. Near the occlusal margin, a second apical ring is present, also bearing roundish crenulations. In profile view, the inner apical ring is apicobasally higher, than the outer, larger one. Following these features, the tooth is unambiguously referred to the genus *Gyrodus*. Based on the preserved characters it can not be determined whether the tooth belonged to the vomerine or the prearticular dentition.

Remarks – *Gyrodus* ranges from the Middle Jurassic to the Early Cretaceous. The genus includes 32 species, among them two, *G. hexagonus* and *G. circularis* were based on more than isolated remains, including articulated skeletons (Kriwet & Schmitz 2005). The Early Cretaceous reports of the genus are rare and questionable. *G. atherfieldensis* from the Aptian of England is characterized by smooth teeth (possible result of wear or abrasion). When unworn, teeth of *G. minor* (Aptian of England), *G. contiguidens* (Hauterivian of France) and *G. sculptus* (Neocomian of France) exhibit an ornamentation similar to that of other *Gyrodus* species (Kriwet & Schmitz 2005 and references therein). The attribution of a dental remain described as *G. ellipticus* remains arguable, since it displays similarities with *Coelodus* and *Ocloedus* (after Kriwet & Schmitz 2005). Isolated, sculptured pycnodont teeth from the Valanginian of France were assigned to genus *Gyrodus* by Pictet *et al.* (1858–60).

Since only one Hárskút fish tooth is assigned to *Gyrodus*, due to the high variancy of the pycnodontiform dentition, I do not attempt to describe it closer than genus rank. A high similarity to the teeth of *G. hexagonus* is recognized (see Kriwet 2005, fig. 30C, D), however, *G. hexagonus* is resricted to the Jurassic (Kriwet 2005; Poyato-Ariza & Wenz 2002).

DISCUSSION

The habitat preferences of the HK-12 fish taxa are in accordance with that of the collected invertebrate fauna, which includes both pelagic (ammonites, belemnites, rare nautiloids) and benthic (brachiopods, crinoids, echinoderms, etc.) faunal elements. Since the palaeogeographical position of Hárskút is given in a pelagic basin (Főzy *et al.* 2010), the partial or full pelagic lifestyle among the Hárskút fish forms is no surprise.

The fossil record of Hexanchiformes (cow sharks) is dominated by isolated tooth remains, although articulated skeletal remains are also known (Kriwet & Klug 2011 and references therein). Mesozoic hexanchiform remains are rather rare, only a few hexanchiform teeth, found in the Mesozoic of Hungary are known in Hungarian natural history collections (Szabó in prep.). Extant hexanchiforms are dominantly demersal to pelagic sharks, modern members of family Hexanchidae generally prefer rather deep waters at more than one hundred metres (Cappetta 2012).

The dominant selachian form of the Mogyorósdomb Formation is *Sphenodus* (represented by 7 teeth). The tearing-type dentition of *Sphenodus* implies a diet of cephalopods and fishes, which together with the general body shape (similar to that of carcharhiniform sharks) refers *Sphenodus* as an active pelagic predator (Cappetta 2012; Rees 2012; Thies & Reif 1985), but according to Underwood *et al.* (1999), it is unlikely that these sharks were rapid pursuit hunters. The quantitative dominance of *Sphenodus* is may related to the rich invertebrate fauna of the Mogyorósdomb Limestone, however, the presence of a large amount of smaller prey fishes is supposed. Hennig (1914) suggested that *Sphenodus* was a scavenger, because its teeth often co-occur with disarticulated vertebrate remains.

Species of the non-teleostean neopterygian *Lepidotes* are widely considered as durophagous predators with nektonic habits (e.g., Poyato-Ariza 2005; database of fossilworks.org). The presence of *Lepidotes* in the Hauterivian of the HK-12 section is might connected to the rich cephalopod fauna. By their strong, crushing dentition, semionotid fishes could be considered as possible predators of ammonites (see e.g., Martill 1990).

The distribution of *Gyrodus* implies that members of the genus were not only living in near-coastal habitats (where they found most of their food), but they also had a pelagic lifestyle, which enabled *Gyrodus* to cross deeper sea basins (Kriwet & Schmitz 2005). Pycnodontiform fishes are known from various localities of Hungary, such as Iharkút (Santonian; Szabó *et al.* 2016*b*), Ajka (Santonian; Ősi *et al.* 2016) and Sümeg (Campanian; mentioned in Főzy & Szente 2014). Pászti (2004) reported pycnodontiform fishes from the Lower Jurassic (Toarcian) Úrkút Manganese Ore Formation; however, the published specimens clearly represent other taxa (personal observation).

Unlike *Gyrodus*, *Sphenodus* and *Lepidotes* are common in most Mesozoic marine deposits around the world. Following the available data, genus *Gyrodus* seems to be restricted to Europe in the Early Cretaceous. The occurrence of this pycnodontiform in the Lower Cretaceous of Hárskút adds important data to our knowledge on its distribution patterns.

CONCLUSIONS

The pelagic Lower Cretaceous formations of the HK-12 section of the Közöskút Ravine yielded various fish remains. The presence of the demersal-pelagic hexanchids, the pelagic *Sphenodus* and the coastal-pelagic *Gyrodus* is more or less evident, while the occurrence of the nektonic semionotiform *Lepidotes* may be attributed to trophic reasons. *Sphenodus* and *Lepidotes* are widely reported from numerous localities around Europe. The present study provides the first report of *Gyrodus* from the Pannonian Basin. Further occurrence of more, rare Mesozoic fish taxa is expected in natural history collections of Hungary.

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