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Original article

Late Cretaceous (Santonian) pycnodontid (Actinopterygii, Pycnodontidae) remains from the freshwater deposits of the Csehbánya Formation, (Iharkút, Bakony Mountains, Hungary)

Restes de pycnodontidés (Actinopterygii, Pycnodontidae) du Crétacé supérieur (Santonien) des sédiments d'eau douce de la Formation Csehbánya (Iharkút, Montagne Bakony, Hongrie)

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ABSTRACT

Isolated but well-preserved remains of pycnodontiform fishes from the Upper Cretaceous (Santonian) Csehbánya Formation at Iharkút, western Hungary are described here. The assemblage contains cranial (premaxilla/dentary, vomers, prearticulars, teeth) and postcranial (possible contour scales) remains allowing the identification of the Iharkút pycnodontiforms as cf. *Coelodus* sp. Supported by sedimentological and stable isotope studies, the Iharkút fossils represent one of the few certainly freshwater occurrences of the group in the Upper Cretaceous of Europe. An estimated value of minimum number of individuals indicates that the remains of at least 28 individuals were hitherto discovered, suggesting that these medium-sized hard-shelled prey consuming fishes were quite abundant in the Iharkút freshwater habitats.

Mots clés :
Préarticulaire
Vomer
Dent molariforme
Dent incisiforme
Pycnodontidae
Coelodus
Paléoécologie
Crétacé supérieur
Formation Csehbánya

RÉSUMÉ

Des restes isolés, mais bien préservés, de poissons pycnodontiformes du Crétacé supérieur (Santonien) de la Formation Csehbánya à Iharkút, à l'ouest de la Hongrie, sont décrits ici. L'assemblage contient des éléments crâniens (prémaxillaire/dentaire, vomers, préarticulaires, dents) et postcrâniens (possibles écailles de contours) permettant une identification du pycnodontiforme d'Iharkút comme cf. *Coelodus* sp. Supportés par des études sédimentaires et d'isotopes stables, les fossiles d'Iharkút représentent une des rares présences de ce groupe dans le Crétacé supérieur d'Europe dans des environnements d'eau douce. Une estimation du nombre minimum d'individus indique que les restes d'au moins 28 individus ont été découverts jusqu'ici, suggérant que ces poissons qui consommaient des proies à coquille étaient relativement abondants dans les environnements dulçaquicoles d'Iharkút.

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1. Introduction

Pycnodontiforms are a remarkable and distinctive group of actinopterygian fishes that has been known for over two centuries (e.g., see in Agassiz, 1833–1843; Knorr, 1768; Volta, 1809) and they have always called the attention of paleontologists. The rounded, laterally flattened body shape, the frontal flexure of the skull, the well-developed dorsal and anal fins, the mostly prognathous snout and the highly developed and specialized heterodont dentition are the most characteristic features of the group (Kriwet, 2005; Licht, 2011; Licht and Kogan, 2011; Poyato-Ariza, 2003, 2005). Pycnodontiforms were small to medium-sized fishes with an average length of about 25 cm, although some species (e.g., *Gyrodus circularis*) reached 2 meters in full length (Kriwet and Schmitz, 2005). They have been found in Triassic (Tintori, 1981) to Eocene (Longbottom, 1984; Poyato-Ariza, 2005) sediments, mostly in America and Europe, but they have been reported also from Africa and Asia (Poyato-Ariza, 2003, 2005). Their remains are known primarily from marine deposits, but they occur in brackish to freshwater sediments as well (e.g., Poyato-Ariza et al., 1998; Kocsis et al., 2009). Although these fishes are known by well-preserved, complete specimens mainly from fossil-Lagerstätten, fragmentary remains of the dentition are also common and important finds of many vertebrate localities (Kriwet, 2005; Poyato-Ariza, 2003).

Numerous species of several pycnodontiform genera are known from different Late Cretaceous localities in Europe (e.g., Bazzi et al., 2015; Berreteaga et al., 2011; Friedman, 2012; Kriwet, 2002; Licht and Kogan, 2011; Poyato-Ariza, 2010, 2013; Schultz and Paunović, 1997; Vullo et al., 2009). Hungarian pycnodontid fishes have been reported as molariform and branchial teeth from the Santonian of the Ajka Coal Formation (Ősi et al., 2016), and as well-preserved prearticulars from the Campanian of Sümeg (western Hungary) (Szente and Főzy, 2012).

The aims of this paper are to describe the pycnodontid remains from the Upper Cretaceous (Santonian) Csehbánya Formation of the Iharkút continental vertebrate fossil site (western Hungary, Bakony Mountains), summarize their morphological features, and compare them with other pycnodontid fossils.

2. Locality and geological setting

The locality is in an abandoned open-pit bauxite mine close to the villages Németbánya and Bakonyjákó, in the area of the former village Iharkút (47° 13′ 52″ N, 17° 39′ 01″ E) (Fig. 1A). The open-pit was created in the late 1990's for mining the bauxite lenses Németbánya II and III. A detailed geological background and a sedimentological approach on the bone-yielding Csehbánya Formation has been elaborated by Botfalvai et al. (2015), thus here only a brief summary is presented (Fig. 1).

The Iharkút vertebrate locality is located in the Transdanubian Central Range, a tectonic block situated on the northern part of the triangular-shaped Apulian microplate between Africa and Europe during the Mesozoic (Csontos and Vörös, 2004; Csiki-Sava et al., 2015). The bedrocks of the Iharkút locality belong to the Upper Triassic Main Dolomite Formation. In this formation tectonically controlled and karstified sinkholes with a depths of 50 to 90 m were filled up by the Upper Cretaceous (pre-Santonian) Nagytárkány Bauxite Formation. This bauxite was mined in the area from the 1970's. Whereas in some places the bauxite could be mined directly from below surface, at the Iharkút vertebrate locality, this red ore, together with the karstified paleosurface of Triassic rocks was covered by a 50 m thick sequence of alluvial flood plain deposits of the Csehbánya Formation. At the locality, this formation is composed of alternating coarse basal breccia, sandstone, siltstone and paleosol beds (Jocha-Edelényi, 1988; Ősi and Mindszenty, 2009; Botfalvai et al., 2015). Sedimentary structures (Botfalvai et al., 2016) as well as the mollusc (Ősi, 2012; Szente, I., pers. comm.; Szentesi, 2008) and ostracod fauna (Monostori, M., pers. comm., 2003) indicate a freshwater environment during the deposition of the Csehbánya Formation. Palynological results refer to a Santonian age of this formation (Bodor and Baranyi, 2012). Bone-yielding beds in the Csehbánya Formation in various stratigraphic horizons produced a rich and diverse fossil assemblage of isolated and associated bones, teeth and plant remains. Regarding pycnodontiform fish fossils, the most productive sequence (SZÁL-6 site) is a greyish coarse basal breccia covered with sandstone and brownish siltstone that produced 99% of the fossils described here. In addition, another horizon of bone-yielding beds (SZÁL-1) within the Csehbánya Formation is worth to be mentioned, since besides various vertebrate fossils, some pycnodontiform remains have been discovered there as well. At the locality, the Csehbánya Formation is only partially covered by the Middle Eocene Iharkút Conglomerate Formation.

3. Material and methods

The pycnodontid remains described here were discovered in the years 2000–2015 at two different sites of the Iharkút locality. The earliest site discovered was SZÁL-1, producing one vomer, three prearticulars, 102 molariform teeth and four incisiform teeth. The second and most productive site was SZÁL-6, where one dentary or premaxilla, five vomers, 79 prearticulars, 889 molariform teeth, 123 incisiform teeth, 85 branchial teeth and two contour scales have been found through hand-quarrying the bone-yielding beds of the Santonian Csehbánya Formation at Iharkút, and during the processing of the screen-washed material of the SZÁL-6 site.

All specimens are housed in the Hungarian Natural History Museum (Magyar Természettudományi Múzeum [MTM]), where they were cleaned and prepared mechanically in the technical labs of the Department of Paleontology and Geology. For mechanical preparation, needles and vibro-tool were used. The fossils are rich in pyrite, and with a few exceptions, they are dark brownish or black in color. In order to stop (or at least slow down) the oxidization of the pyrite, bones were treated with polyvinyl butyral (PVB). Broken bones were repaired with cyanoacrylate (superglue).

We used a Hitachi S-2600N and a Hitachi S-2360N scanning electron microscope for scanning electron microscopic photography. Pictures of the contour scales were taken with a QImaging MP5.0 digital microscope camera under a Nikon LV 100 polarized light microscope, and processed with Image Pro Insight 8.0 software.

The character-based taxonomic assignment of the Iharkút pycnodontiform remains is based on the characters (ch.; see in the "Taxonomic assignment" section) listed by Poyato-Ariza and Wenz (2002). The figured molariform, incisiform and branchial teeth and the contour scales have individual numbering.

4. Systematic paleontology

Superclass Osteichthyes Huxley, 1880
Class Actinopterygii Cope, 1887
Order Pycnodontiformes Berg, 1937
Suborder Pycnodontoidei Nursall, 1996
Superfamily Pycnodontoidea Agassiz, 1833
Family Pycnodontidae *sensu* Poyato-Ariza and Wenz, 2002
Genus ***Coelodus*** Heckel, 1854

cf. *Coelodus* sp.

Material: 1?dentary/premaxilla (VER 2015.215.), 6 vomers (SZÁL-1: V.2001.244; SZÁL-6: V 2010.154.1., V 2010.240.1., VER 2015.192., VER 2015.213., VER 2015.214.), 82 prearticulars (left ones from SZÁL-1: V 2000.26., VER 2015.174.; left

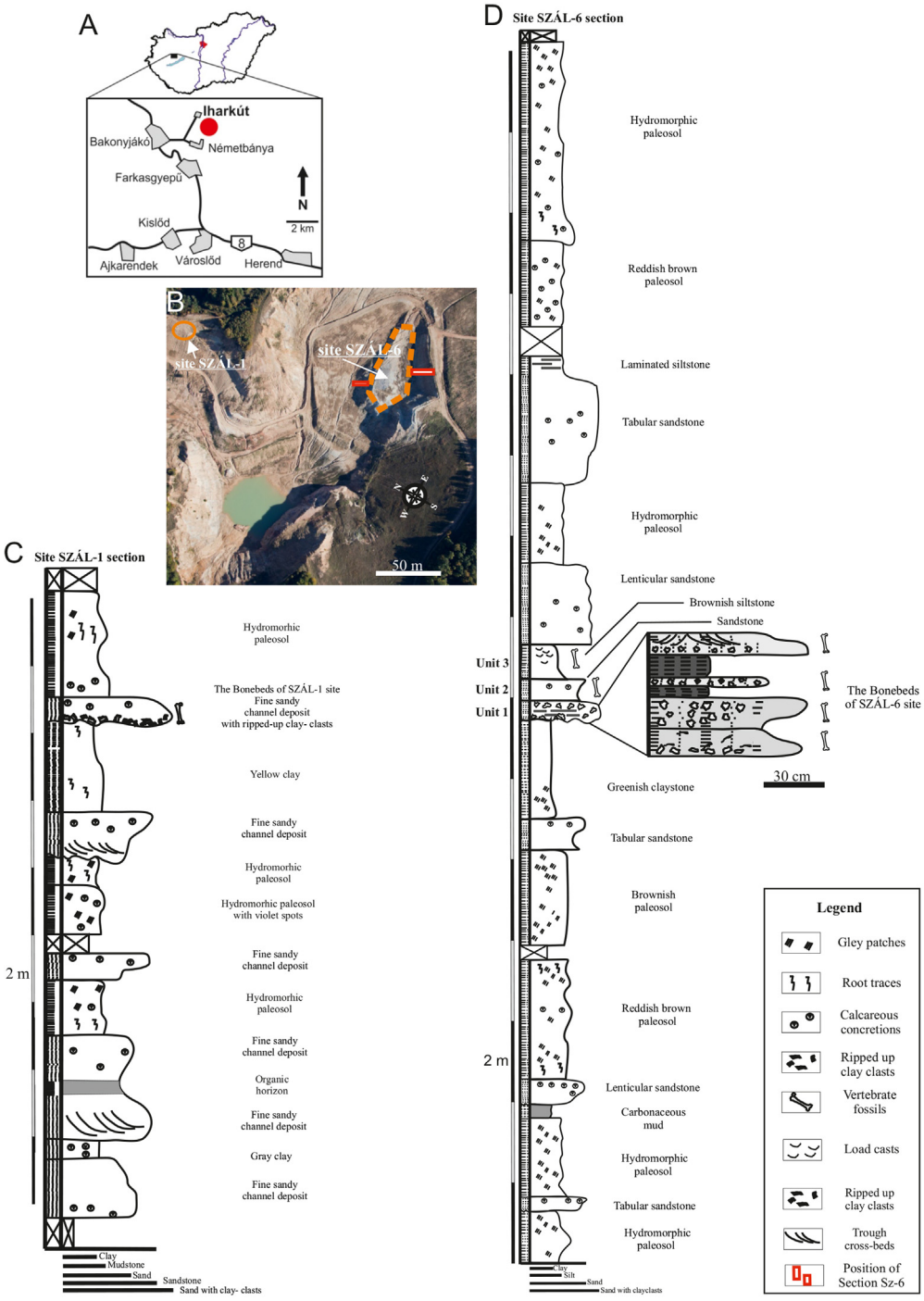

Fig. 1. A. Location map of the Iharkút vertebrate locality. B. Aerial photo of the Iharkút open-pit, showing the position of the SZÁL-1 and SZÁL-6 sites. C. Stratigraphic section of site SZÁL-1. D. Stratigraphic section of the SZÁL-6.
A. Localisation du site des vertébrés de Iharkút. B. Photo aérienne de la carrière à Iharkút, montrant la position des sites SZÁL-1 et SZÁL-6. C. Section stratigraphique du site SZÁL-1. D. Section stratigraphique du site SZÁL-6.
Modified after Botfalvai et al. (2015).

ones from SZÁL-6: V 2010.132.1., V 2010.133.1., V 2010.134.1., V 2010.136.1., V 2010.137.1., V 2010.138.1., V 2010.139.1., V 2010.140.1., V 2010.141.1., V 2010.142.1., V 2010.144.1., V 2010.147.1., V 2010.148.1., V 2010.150.1., V 2010.152.1., V 2010.238.1., V 2010.241.1., VER 2015.166., VER 2015.167., VER 2015.168., VER 2015.169., VER 2015.170., VER 2015.171., VER 2015.172., VER 2015.173., VER 2015.175., VER 2015.176., VER 2015.177., VER 2015.178., VER 2015.179., VER 2015.180., VER 2015.181., VER 2015.182., VER 2015.183., VER 2015.184., VER 2015.185., VER 2015.186., VER 2015.187., VER 2015.188., VER 2015.299., VER 2015.300., VER 2015.301., VER 2015.302.; right one from SZÁL-1: V.2001.83.; right ones from SZÁL-6: V 2010.131.1., V 2010.135.1., V 2010.143.1., V 2010.145.1., V 2010.146.1., V 2010.149.1., V 2010.151.1., V 2010.153.1., V 2010.239.1., V 2010.242.1., VER 2015.189., VER 2015.190., VER 2015.191., VER 2015.193., VER 2015.194., VER 2015.195., VER 2015.196., VER 2015.197., VER 2015.198., VER 2015.199., VER 2015.200., VER 2015.201., VER 2015.202., VER 2015.203., VER

2015.204., VER 2015.205., VER 2015.206., VER 2015.207., VER 2015.208., VER 2015.209., VER 2015.210., VER 2015.211., VER 2015.212., VER 2015.297., VER 2015.298.), 1118 isolated tooth remains (molariforms from SZÁL-1: V 2000.30.1-2., V.2001.233., VER 2015.216.1-2., VER 2015.217.1-63., VER 2015.218., VER 2015.225., VER 2015.226.1-6., VER 2015.227.1-12., VER 2015.229.; molariforms from SZÁL-6: V.2001.58, V.2001.241, VER 2015.116., VER 2015.117., VER 2015.118., VER 2015.119., VER 2015.216.3-4., VER 2015.217.64-132., VER 2015.221., VER 2015.222., VER 2015.223., VER 2015.224., VER 2015.227.13-30., VER 2015.228., VER 2015.303., VER 2015.304.; incisiforms from SZÁL-1: V 2000.30.3-5., VER 2015.229.; incisiforms from SZÁL-6: VER 2015.230., VER 2015.231., VER 2015.232., VER 2015.233.), 85 branchial tooth remains (VER 2015.234., VER 2015.235., VER 2015.236.), 3 possible scale remains (VER 2015.220., VER 2016.1947.).

5. Description and comparisons

5.1. Cranial elements

5.1.1. Dentary/premaxilla

A single pycnodontid bone element with one *in situ* preserved incisiform tooth (VER 2015.215., Fig. 2) is either a fragmentary premaxilla or dentary. The similarity of the premaxillae and dentaries in many pycnodont taxa, the possible morphological plasticity, and the isolated and fragmentary preservation make the identification of the specimen VER 2015.215. impossible, until better preserved specimens are discovered.

A similar remain was published by Sweetman et al. (2014, fig. 10A) as “premaxillary or dentary tooth”.

5.1.2. Vomers

Six fragmentary pycnodontid vomers are known from Iharkút. The base of the vomers is missing on all specimens. Among them, the most completely preserved specimen (V 2010.154.1., Fig. 3A) bears the less worn and highest number of preserved teeth (although there are isolated, well-preserved vomerine teeth). On this specimen, the teeth are arranged in five rows: one principal row, and two-two lateral rows on both sides. The anterior end of this vomer is missing, but there are five teeth left in the principal vomerine tooth row. The dentition of specimen V 2010.154.1. shows a slightly worn, crenulated ornamentation around the grooves of the teeth. Tooth crowns are devoid of any central papilla or ridge (the ornamentation of the teeth can be observed much better on some of the isolated teeth).

The principal vomerine teeth are slightly elongated transversely and have an oval, bilaterally symmetrical contour in occlusal view. They form an anteroposteriorly extended series with regularly increasing size. These symmetrical principal vomerine teeth bear transversal, slightly bent grooves located close to their anterior margin. There is a short gap between the principal vomerine teeth, but there are no additional teeth inserted between them (as is the case in the genus *Proscinetes* Gistl, 1848).

There are five preserved teeth in the right and six preserved teeth in the left first lateral tooth row with tooth size increasing posteriorly. The first lateral vomerines are asymmetrical, circular to D-shaped in occlusal view, and an anteroposterior groove can be observed on the lateral side of these teeth. The second lateral vomerines (four in the right and five in the left second lateral row) are also asymmetrical and pear-shaped in occlusal view and bear an oval to pear-shaped groove. The size of the second lateral vomerine teeth increases posteriorly, and they are the smallest in the whole vomerine dentition. The two lateral rows of vomerine teeth are juxtaposed against one another on both sides of the vomer, but there is a gap between the principal vomerine tooth row and the first lateral vomerine tooth rows. This feature can be seen on the vomer of *Macropycnodon streckeri* (Hibbard, 1939) (see Shimada et al., 2010; this genus has been considered as junior synonym of *Acrotemnus* Agassiz, 1836 by Vullo and Courville, 2014), *Coelodus toncoensis* (see the original description by Benedetto and Sánchez, 1972, pl. I.4,5), and?*Ocloedus toncoensis* published by Gonella et al. (2012, fig. 3D).

5.1.3. Prearticulars

This paired bone has a triangular shape in occlusal view. The precise contour of the prearticular bone cannot be observed on any Iharkút prearticulars due to preservational factors. The coronoid process, best preserved on specimen V 2010.147.1. (Fig. 4E), shows a massive, high and wide coronoid process, with a straight dorsal

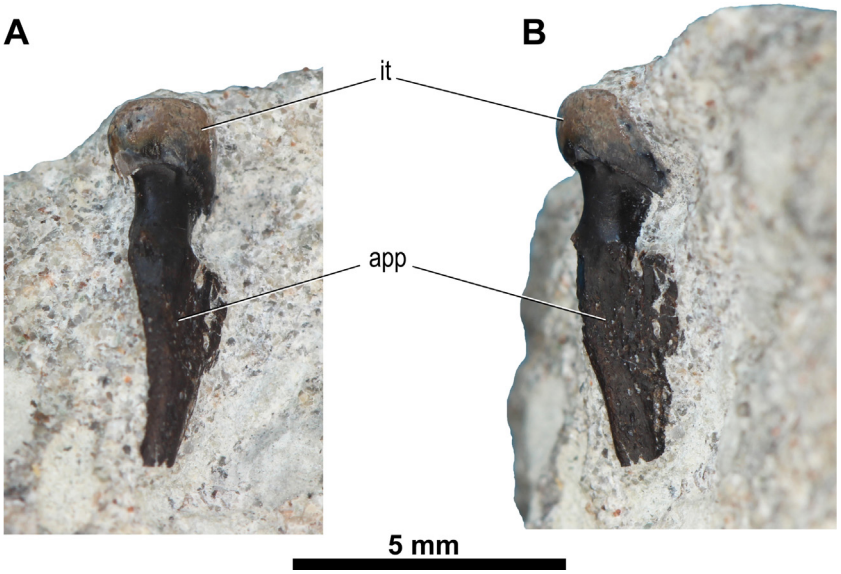

Fig. 2. cf. *Coelodus* sp. dentary or premaxilla (VER 2015.215.) from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A. In labial view. B. In lateral view. Abbreviations: app: ascending processal portion; it: incisiform tooth.
Dentaire ou prémaxillaire (VER 2015.215.) de cf. Coelodus *du Crétacé supérieur (Santonian) de la Formation Csehbánya (Iharkút, Hongrie). A. En vue labiale. B. En vue latérale. Abréviations : app : portion processive ascendante ; it : dent incisiforme.*

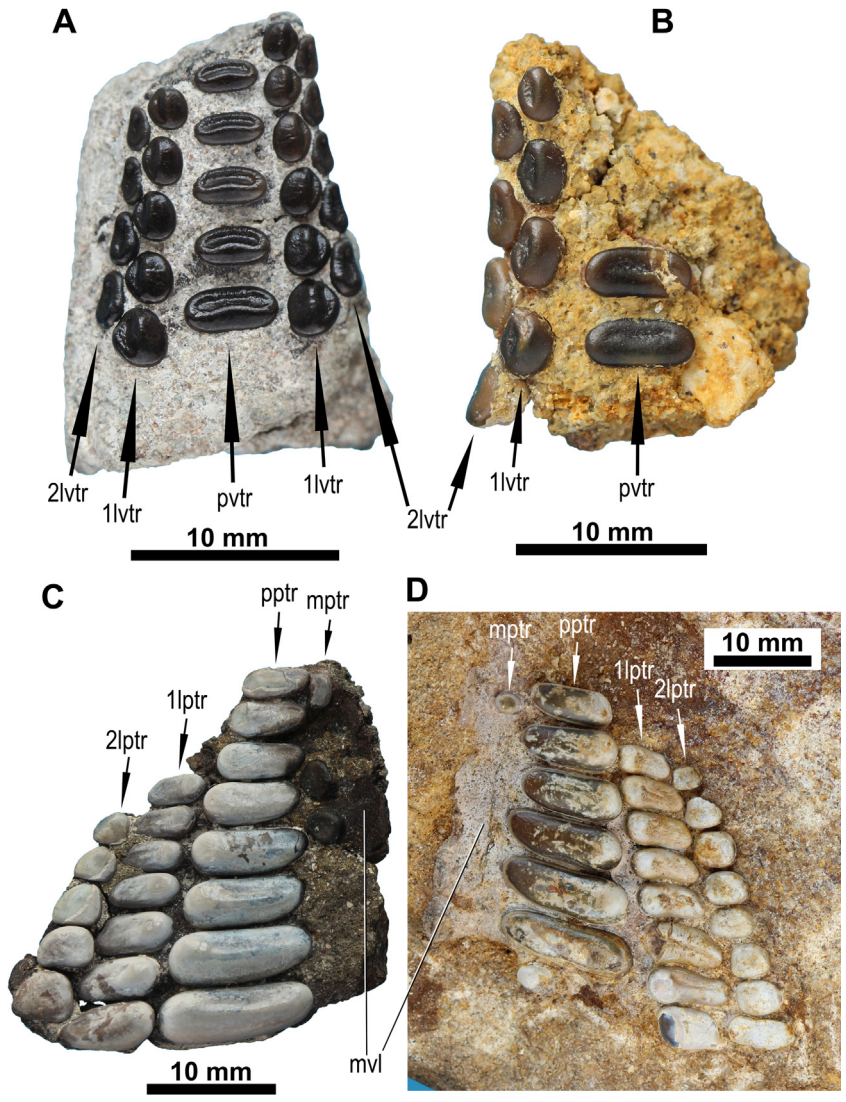

Fig. 3. cf. *Coelodus* sp. vomers and prearticulars from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A–B. Vomers (A: V 2010.154.1.; B: V 2001.244) in occlusal view. C. Left prearticular (V 2010.139.1.) in occlusal view. D. Right prearticular (V 2010.131.1.) in occlusal view. Abbreviations: 1lptr: first lateral prearticular tooth row; 2lptr: second lateral prearticular tooth row; 1lvtr: first lateral vomerine tooth row; 2lvtr: second lateral vomerine tooth row; mptr: medial prearticular tooth row; mvl: medioventral lamina; pptr: principal prearticular tooth row; pvtr: principal vomerine tooth row.
Vomers et préarticulaires de cf. Coelodus *sp. du Crétacé supérieur (Santonian) de la Formation Csehbánya (Iharkút, Hongrie). A–B. Vomers (A : V 2010.154.1. ; B : V 2001.244) en vue occlusale. C. Préarticulaire gauche (V 2010.139.1.) en vue occlusale. D. Préarticulaire droit (V 2010.131.1.) en vue occlusale. Abréviations : 1lptr : première rangée de dents préarticulaires ; 2lptr : deuxième rangée de dents préarticulaires ; 1lvtr : première rangée de dents vomériennes ; 2lvtr : première rangée de dents vomériennes ; mptr : première rangée de dents médiales ; mlv : lamelle médio-ventrale ; pptr : rangée de dents préarticulaires principale ; pvtr : rangée de dents vomériennes principale.*

surface. On the better preserved prearticulars a thin medioventral lamina is preserved between the principal tooth row and the medioventral oral margin of the preaticular. This lamina extends anterodorsally holding the medial prearticular tooth row.

The prearticular dentition is not symmetrical but consists of longitudinal rows of teeth of different length with the tooth size increasing posteriorly. Four tooth rows can be distinguished: a medial, a principal (or main), and two lateral tooth rows.

The anteriorly positioned, circular to subcircular contoured teeth of the medial row are the smallest in the prearticular dentition. In occlusal view, a weakly preserved, centrally or slightly laterally oriented groove can be observed. The highest number of the preserved medial teeth is three on specimen V 2010.139.1. (Fig. 3C). There is an empty tooth position among the three preserved medials of this prearticular, but the bony base of this tooth position does not show any sign of bearing a tooth. While the medioventral lamina can be observed on the smallest Iharkút pycnodontid prearticulars, only the biggest, well-developed prearticulars have medial tooth row on it, therefore the presence of medial teeth might refer to an ontogenetic stage.

The asymmetrical, elongated principal prearticular teeth bear a transverse groove, located anteromedially on the occlusal surface (Fig. 5C). The principal teeth have a straight or slightly concave anterior border in occlusal view. The posterior teeth of this row are the largest in the prearticular dentition with the posteriormost principal tooth of the largest prearticular specimen (V 2010.131.1., Fig. 3D) being 14.5 mm broad labiolingually and 4.5 mm long mesiodistally. Some principal prearticulars have worn, but still visible crenulations around their groove (e.g. on specimen VER 2015.204., see Fig. 4D). The highest tooth number in the principal row is 11 (eight preserved teeth and two clearly visible but empty tooth positions on the specimen V 2010.135.1., see Fig. 4B and C).

The teeth of the first lateral row are ovoid-shaped in occlusal view, but less elongated transversely than the principal teeth. The first lateral teeth have a medial, bulb-like surface bordered laterally by a transversal groove (Fig. 5D–H). On specimens V 2010.131.1.

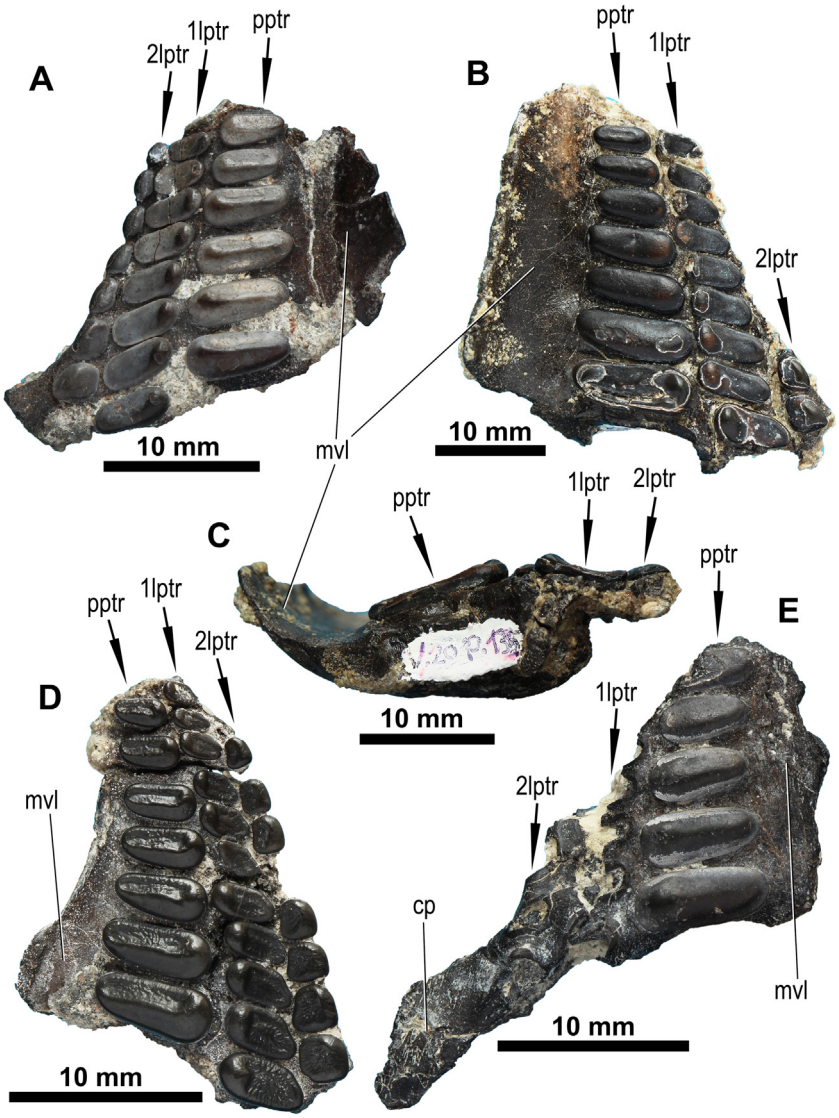

Fig. 4. cf. *Coelodus* sp. prearticulars from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A. Left prearticular (V 2010.140.1.) in occlusal view. B. Right prearticular (V 2010.135.1.) in occlusal. C. In posterior view. D. Right prearticular (VER 2015.204.) in occlusal view. E. Left prearticular (V 2010.147.1.) in occlusal view. Abbreviations: 1lptr: first lateral prearticular tooth row; 2lptr: second lateral prearticular tooth row; mvl: medioventral lamina; pptr: principal prearticular tooth row.
Préarticulaires de cf. Coelodus *sp. du Crétacé supérieur (Santonian) de la Formation Csehbánya (Iharkút, Hongrie). A. Préarticulaire gauche (V 2010.140.1.) en vue occlusale. B. Préarticulaire droit (V 2010.135.1.) en vue occlusale. C. En vue postérieure. D. Préarticulaire droit (VER 2015.204.) en vue occlusale. E. Préarticulaire gauche (V 2010.147.1.) en vue occlusale. Abréviations : 1lptr : première rangée de dents préarticulaires ; 2lptr : deuxième rangée de dents préarticulaires ; mlv : lamelle médio-ventrale ; pptr : rangée de dents préarticulaires principale.*

and VER 2015.204. some of these grooves have crenulated ornamentation around their margin. The highest number of *in situ* preserved first lateral teeth is 11 on specimen VER 2015.204.

The circular to subcircular second lateral teeth also have an ornamented groove (e.g. on specimen VER 2015.204.) but it is on the medial margin of the occlusal surface. The highest number of second laterals is eight, preserved on the specimen V 2010.131.1.

Based on the maximum number of teeth and tooth positions preserved in the different rows of different prearticular specimens, the prearticular dentition of the Iharkút pycnodontid is composed of at least three medials, 11 principals, 11 first and eight second laterals. The Iharkút prearticulars are similar to that of *Coelodus syriacus* Hussakof, 1916 in having a fourth, medial prearticular tooth row on a medioventral lamina. A similar medioventral lamina can be observed in *Coelodus toncoensis* Benedetto and Sánchez, 1972, however this species has only three prearticular tooth rows (Gayet et al., 2001, fig. 5H). The Paleogene species *Pycnodus pellei* Priem, 1903 has three regular prearticular tooth rows and one medial tooth on a medioventral lamina (Longbottom, 1984, fig. 21E) but differs from the Iharkút specimens in having a first lateral tooth row narrower than the second lateral row.

The prearticulars of the Jurassic *Proscinetes hugii* Fricke, 1876 and *Proscinetes minutus* Von Münster, 1846, and the Tertiary species *Pycnodus toliapicus* (Agassiz, 1843) bear also a similar medioventral lamina with a medial tooth row, but the Iharkút prearticulars differ from these in having different tooth row proportions and different tooth contours (see Licht, 2011; Longbottom, 1984).

5.1.4. Isolated teeth

Typically for pycnodonts, two different functional types of teeth have been found: molariforms (991 teeth) and incisiforms (127 teeth).

5.1.4.1. Molariform teeth. A total of 991 isolated molariforms (both vomerine and prearticular teeth) were found, most of them in the screen-washed material of SZÁL-6. They are dorsoventrally

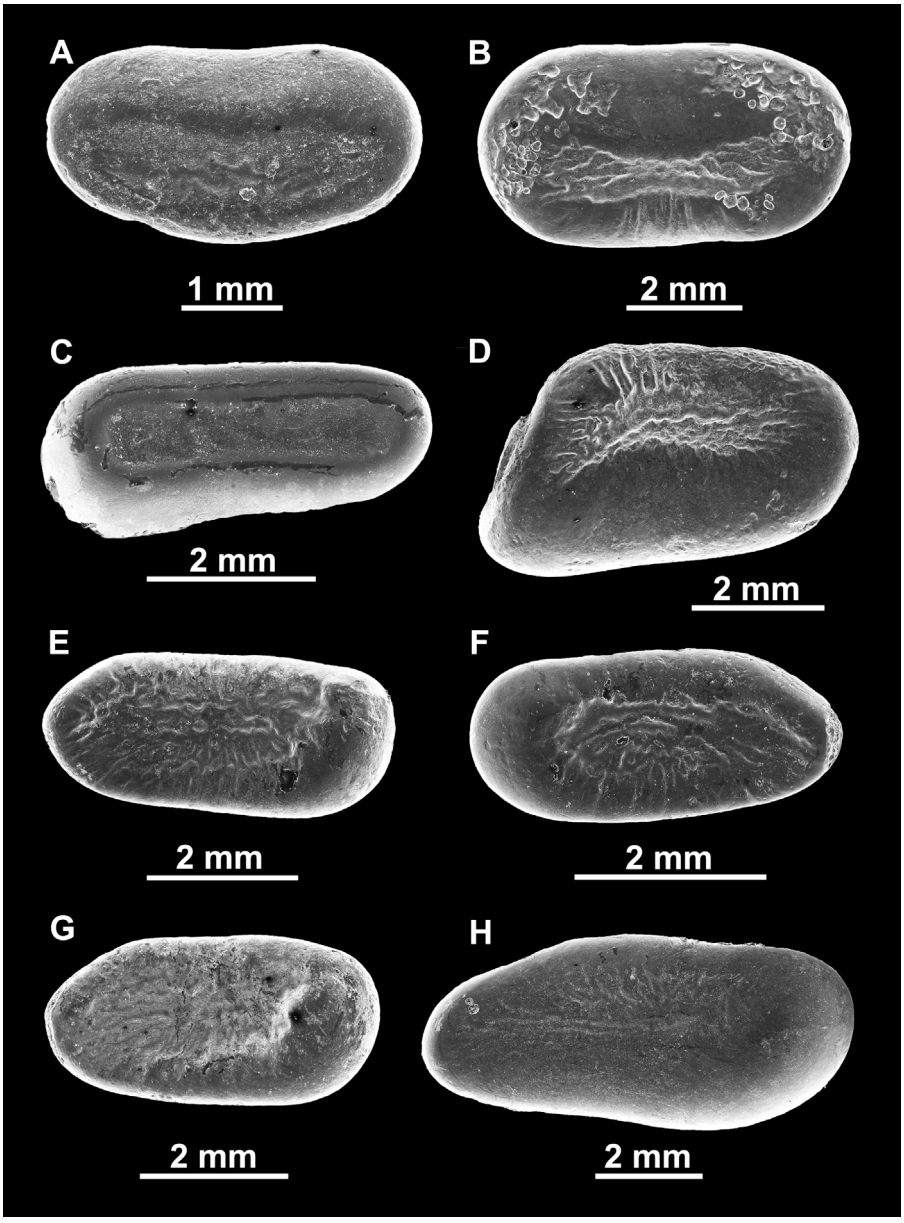

Fig. 5. cf. *Coelodus* sp. molariform teeth from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A. Principal vomerine tooth (VER 2015.217.65.). B. Principal vomerine tooth (VER 2015.226.1.). C. Left principal prearticular tooth (VER 2015.217.66.). D. ?left first lateral prearticular tooth (VER 2015.217.67). E. Left first lateral prearticular tooth (VER 2015.226.6.). F. Right first lateral prearticular tooth (VER 2015.226.4.). G. Left first lateral prearticular tooth (VER 2015.226.5.). H. Left first lateral prearticular tooth (VER 2015.226.2.). All specimens are in occlusal view.
Dents molariformes de cf. Coelodus *sp. du Crétacé supérieur (Santonian) de la Formation Csehbánya (Iharkút, Hongrie). A. Dent vomérienne principale (VER 2015.217.65.). B. Dent vomérienne principale (VER 2015.226.1.). C. Dent préarticulaire principale gauche (VER 2015.217.66.). D. ?première dent préarticulaire latérale gauche (VER 2015.217.67.). E. Première dent préarticulaire latérale gauche (VER 2015.226.6.). F. Première dent préarticulaire latérale droite (VER 2015.226.4.). G. Première dent préarticulaire latérale gauche (VER 2015.226.5.). H. Première dent préarticulaire latérale gauche (VER 2015.226.2.). Tous les spécimens sont en vue occlusale.*

flattened, mostly circular, D-shaped or oval in contour, and show different stages of wear and size (Fig. 5). On some well-preserved isolated molariforms the ornamentation of the occlusal surface can be well-observed. Similar isolated pycnodontid molariform teeth have been reported from the Santonian Ajka Coal Formation, near to Ajka (western Hungary) (Ősi et al., 2016, fig. 5C–E).

5.1.4.2. Incisiform teeth. The 127 pycnodontid incisiforms from Iharkút represent different positions and shows various stages of wear. Only with a few exceptions, they all have been found in the screen-washed material of the SZÁL-6 site. The surfaces of the Iharkút incisiform crowns are unornamented, unlike those of the molariforms. Since both the dentary and premaxilla bear one series of similar prehensile, grasping teeth in many pycnodonts (e.g., see Poyato-Ariza and Wenz, 2002, fig. 20; Kriwet, 2001, fig. 2; Kriwet, 2003, fig. 3), it is not clear whether they belong to the upper of lower dentition. Two different morphotypes can be distinguished in the Iharkút material:

- the first type of incisiforms is labiolingually flattened, and oblong to trapezoidal in shape (Fig. 6A–D). In labial view, they are typically wider as high, and dorsoventrally lower than the second morphotype. A gentle, labiolingual concavity can be observed on the crown of the better preserved specimens, therefore they are convex on the labial side. On these teeth the crown bears a clearly visible, labiolingually bent cutting edge on its occlusal

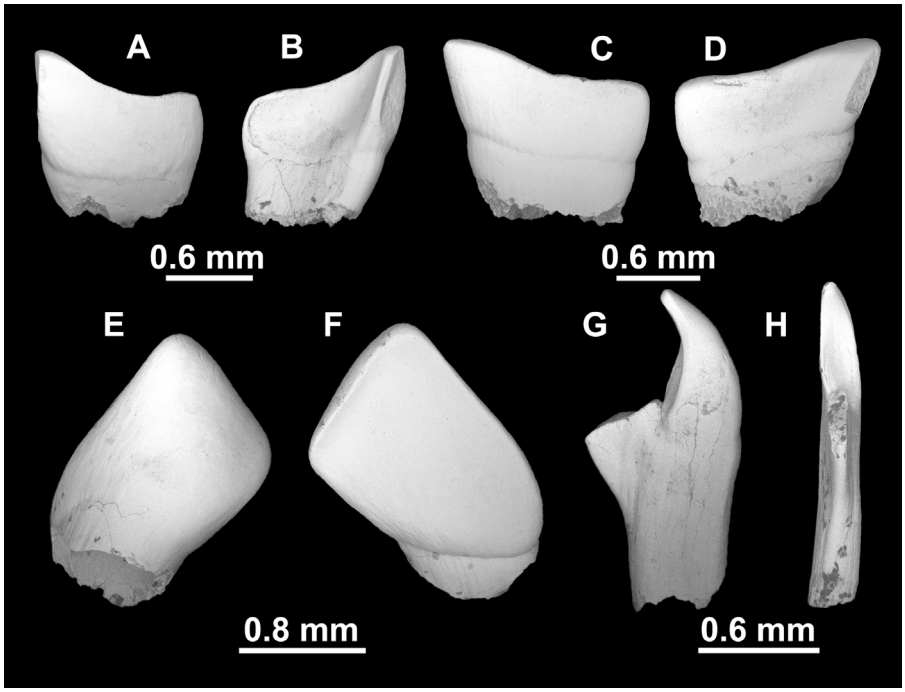

Fig. 6. cf. *Coelodus* sp. incisiform and branchial teeth from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A. Incisiform tooth (VER 2015.233.A) in labial. B. In lingual view. C. Incisiform tooth (VER 2015.233.B) in labial. D. In lingual view. E. Incisiform tooth (VER 2015.233.C) in labial. F. In lingual view. G. Branchial tooth (VER 2015.236.A) in lateral view. H. In occlusal view.
Dents incisiformes et branchiale de cf. Coelodus *sp. du Crétacé supérieur (Santonian) de la Formation Csehbánya (Iharkút, Hongrie). A. Dent incisiform (VER 2015.233.A) en vue labiale. B. En vue linguale. C. Dent incisiforme (VER 2015.233.B) en vue labiale. D. En vue linguale. E. Dent incisiforme (VER 2015.233.C) en vue labiale. F. En vue linguale. G. Dent branchial (VER 2015.236.A) en vue latérale. H. En vue occlusale.*

margin, that is horizontal or nearly horizontal, and wider than the base of the teeth. This type of incisiforms is similar to the pycnodontid incisiforms published by Berreteaga et al. (2011, fig. 3C–E), Buscalioni et al. (2008, fig. 7), Gayet et al. (2001, fig. 5G, I), Kriwet (2003, fig. 3D), Pouech et al. (2015, fig. 8G), Poyato-Ariza and Martín-Abad (2013, fig. 2D) and Sweetman et al. (2014, fig. 10B);

- the second type of incisiforms has a crown less flattened labiolingually than those of the first type. In labial view, these teeth are nearly as high as wide, quite oblong to trapezoidal in shape, and they reach their maximal width in the midline of the crown (Fig. 6E, F). They bear a mostly worn cutting edge on their acute-angled or nearly perpendicular occlusal margin. These teeth are similar to the pycnodontid incisiforms published by Kriwet (2003, fig. 3A, C) and Sweetman et al. (2014, fig. 10A).

Both morphotypes bear clearly visible occlusal marks. The two morphotypes might represent the dentary and premaxillary teeth or possibly two different stages of wear on a single morphotype. More complete, *in situ* specimens are needed to verify any of these hypotheses.

5.1.5. Branchial teeth

All 85 branchial teeth from Iharkút are isolated remains (although branchial teeth of pycnodonts are arranged in groups; Kriwet, 2005) and with a few exceptions they have been found in the screen-washed matrix of the SZÁL-6 site. They are fragmentary, and most of them are just claw-like, slightly translucent with flattened apexes, but some more complete specimens are pedicellate (Fig. 6G and H). Based on the morphological grouping of Kriwet (2005), the Iharkút pycnodontid brachials belong to the first morphotype with a ventral prominence being slender and an oral surface only poorly developed (see also in Kriwet, 2005, fig. 59).

Similar pycnodontid branchial teeth have been published by Brinkman et al. (2013, fig. 10.5.D–E), Garrison et al. (2007, fig. 22B), Ősi et al. (2016, fig. 5A) and Vullo and Courville (2014, fig. 5A).

5.2. Postcranial elements

5.2.1. Contour scales

The contour scales (or median scales, or midline scales) of pycnodontid fishes are different from all other scales of the pycnodont body including dorsal ridge scales and ventral keel scales (Poyato-Ariza and Wenz, 2002). Three possible pycnodontid contour scale remains are known from Iharkút, both have been found in the screen-washed material of the SZÁL-6 site (Fig. 7). Specimen VER 2015.220.A (Fig. 7A–C) has two slightly curved spines, a smaller anterior one and a bigger posterior one with an empty spine position between them. The preserved spines are increasing in size posteriorly, which is characteristic for the contour scales of most pycnodont taxa (see Poyato-Ariza and Wenz, 2002). Specimen VER 2015.220.B (Fig. 7D–F) has only one preserved, distally curved spine. Specimen VER 2016.1947. (Fig. 7G–I) has four spines, increasing in size posteriorly. The second spine of this specimen is more curved anteriorly than posteriorly.

The position of these isolated scales cannot be identified because of the similarity of the dorsal and ventral contour scales and due to intra- and interspecific variability. Isolated contour scales referred to *Coelodus* sp. have been published by Sweetman et al. (2014, fig. 13N–P) and are similar to the Iharkút specimens in having posteriorly curved spines. A *Coelodus* sp. midline scale, morphologically similar to the Iharkút specimens has been published by Brinkman et al. (2013, fig. 10.5.F). Specimen VER 2016.1947. resembles to the published pycnodontiform scales of Poyato-Ariza and Wenz (2002, fig. 39A).

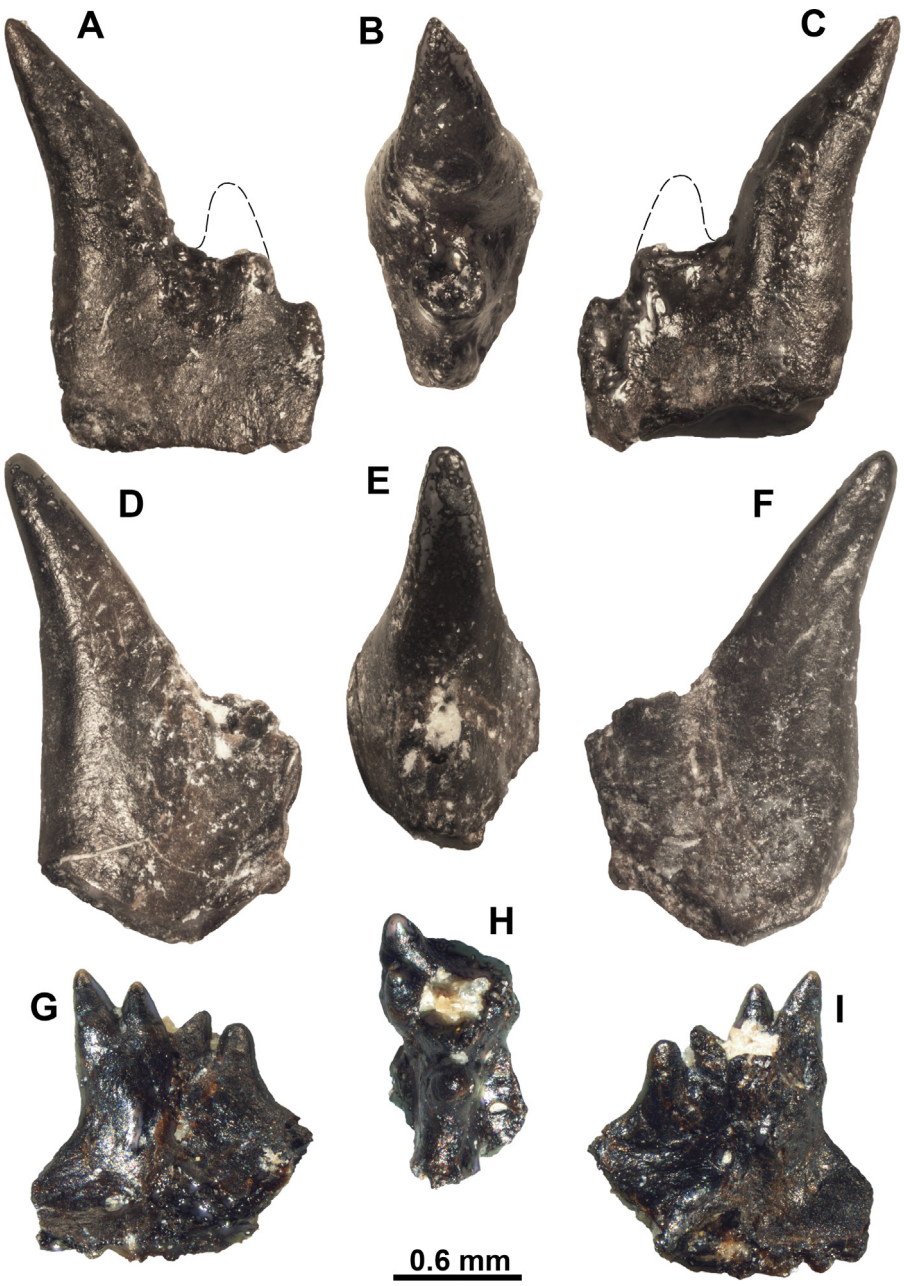

Fig. 7. cf. *Coelodus* sp. possible contour scales from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Hungary). A, C. Possible contour scale (VER 2015.220.A) in lateral view. B. In dorsal or ventral view. D, F. Possible contour scale (VER 2015.220.B) in lateral view. E. In dorsal or ventral view. G, I. Possible contour scale (VER 2016.1947.) in lateral view. H. In dorsal or ventral view.
Possibles écailles de contour de cf. Coelodus *sp. du Crétacé supérieur (Santonian) de la Formation Csehbánya (Iharkút, Hongrie). A, C. Possible écaille de contour (VER 2015.220.A) en vue latérale. B. En vue dorsale ou ventrale. D, F. Possible écaille de contour (VER 2015.220.B) en vue latérale. E. En vue dorsale ou ventrale. G, I. Possible écaille de contour (VER 2016.1947.) en vue latérale. H. En vue dorsale ou ventrale.*

5.3. Taxonomic assignment

Although the pycnodontid fossils from Iharkút are all isolated elements, following parsimony, we believe that they belong to a single taxon until more complete material justifies the opposite. The Iharkút pycnodontid can be identified as the member of the order Pycnodontiformes based on the following characters: crushing vomerine teeth (ch. 36), crushing prearticular teeth (ch. 43) and prearticular teeth forming rows (ch. 44). Unfortunately, neither the five synapomorphies of the suborder Pycnodontoidei, nor the two synapomorphies of the superfamily Pycnodontoidea, nor the six-nine synapomorphies of the family Pycnodontidae (sensu Poyato-Ariza and Wenz, 2002) can be studied on the Iharkút material. It is clear, however, that these remains do not belong to the family Coccodontidae Berg, 1940, because the vomerine teeth are not triangular in contour (ch. 36).

Comparison of the detailed morphology of the vomers, prearticulars, isolated teeth, branchial teeth and contour scales with those of other pycnodontiforms shows that the Iharkút material is most similar to certain species of *Coelodus* Heckel, 1854. Nevertheless, it differs from *Coelodus saturnus* Heckel, 1854 in having four prearticular tooth rows. The genus *Coelodus* Heckel, 1854 was described with three regular prearticular tooth rows. Even so, in *Coelodus syriacus* Hussakof, 1916 a medial tooth is present representing a

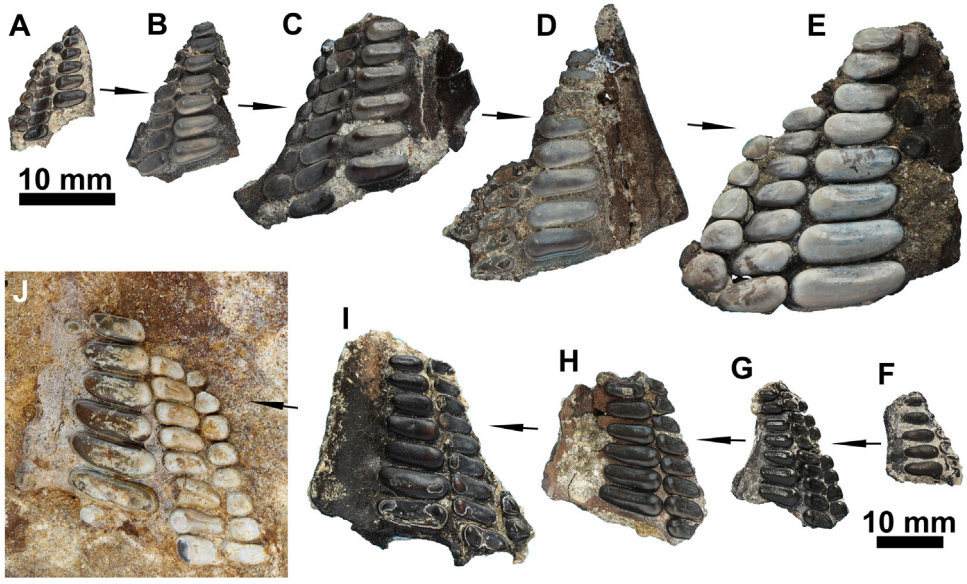

Fig. 8. Ontogenetic stages of the Iharkút cf. *Coelodus* sp., represented by left (A–E) and right (F–J) prearticulars (A: VER 2015.178.; B: V 2010.134.1.; C: V 2010.140.1.; D: VER 2015.184.; E: V 2010.139.1.; F: V 2010.149.1.; G: VER 2015.204.; H: VER 2015.209; I and J: V 2010.131.1.). All specimens are in occlusal view.
Stades ontogénétiques du cf. Coelodus *sp. de Iharkút représentés par les préarticulaires gauches (A–E) et droits (F–J) (A : VER 2015.178. ; B : V 2010.134.1. ; C : V 2010.140.1. ; D : VER 2015.184. ; E : V 2010.139.1. ; F : V 2010.149.1. ; G : VER 2015.204. ; H : VER 2015.209. ; I et J : V 2010.131.1.). Tous les spécimens sont en vue occlusale.*

fourth, medial prearticular tooth row. This suggests that the presence or absence of teeth on the prearticular might be related to the ontogenetic stage or intraspecific variation.

To sum up, we describe the Iharkút pycnodontid remains as cf. *Coelodus* sp., until more complete material helps to clarify their more precise taxonomic identification.

6. Paleoecological inferences

Although most of the pycnodontids have been found in marine deposits, they also occurred in nonmarine sediments in Africa (Cuny et al., 2010), America (Cifelli et al., 1999; Eaton et al., 1999; Winkler et al., 1990), Thailand (Cavin et al., 2009) and Europe (Estes and Sanchíz, 1982; Kocsis et al., 2009; Poyato-Ariza et al., 1998) as well. From a paleoecological point of view, the pycnodontiform remains from Iharkút are of great importance since they have been discovered in freshwater sediments. Besides pycnodonts, remains referred to the unique freshwater mosasauroid *Pannoniasaurus inexpectatus* (Makádi et al., 2012) are also present at the Iharkút vertebrate site. The calculated value of the minimum number of individuals for pycnodont fishes is 28 denoting these fishes the third most frequent group (after pterosaurs and albanerpetontid amphibians) in the Iharkút vertebrate fauna (Botfalvai et al., 2015). This suggests that these medium-sized fishes may have been quite abundant faunal elements of the Iharkút freshwater habitats. The large number of fossils representing different ontogenetic stages (Fig. 8), their taphonomical aspects (Botfalvai et al., 2015), and the stable isotope composition measured on their teeth (Kocsis et al., 2009) suggest that these fishes were not opportunistic or seasonal migrants but they truly inhabited the Iharkút freshwater environments during the Santonian.

There are several possible reasons for the great abundance of these fishes in Iharkút. One explanation might be related to their diet. Pycnodontid fishes were mainly durophagous animals with a specialized heterodont dentition being able to feed on different food sources, such as corals, echinoids, bivalves, gastropods, decapods and even other, smaller actinopterygians (Kriwet, 2001; Poyato-Ariza, 2005). Fossils of bivalves and gastropods are quite abundant in some horizons of the Csehbánya Formation represented by several taxa, including *Schwardtinia*? sp., *Hadraxon* cf. *csingervallense* (Tausch, 1886), *Czabalaya*? sp., *Gastrobulimus munieri* (von Hantken, 1878), *Auriculinella* sp., *Parateinostoma* sp., *Strophostomella* cf. *cretacea* (Tausch, 1886), *Pyrgulifera* spp., numerous unidentified gastropod operculae (2–3 mm in diameter), and *Unio* sp. (Ősi, 2012; Szente, I., pers. comm.; Szentesi, 2008). Pyritized shell negatives show the presence of the genus *Szaboella* Bandel and Riedel, 1994 as well. Here, we suggest that these mollusks were a potential food resource for these fishes, though until now there is no direct evidence for these predator-prey relationships.

Disclosure of interest

The authors declare that they have no competing interest.

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