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# Revision of the Late Devonian ptyctodonts (Vertebrata, Placodermi) from southern Poland

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## ABSTRACT

New studies on Frasnian ptyctodonts, including the revision of historic material in addition to the description of new material, have resulted in the detailed description of two species of *Ptyctodus* (*Ptyctodus obliquus*, *Ptyctodus kielcensis*), eight indeterminate specimens of *Ptyctodus* sp. from the Holy Cross Mountains and two specimens from Dębnik near Kraków, four indeterminate specimens of *Rhynchodus* sp., and two specimens of Ptyctodontidae gen. et sp. indet. from the Holy Cross Mountains. One of the described species (*P. kielcensis*) appears to be endemic for the Holy Cross Mountains region. Based on general knowledge of the Frasnian stratigraphy of the Holy Cross Mountains and on the conodont material obtained from the fragments of the sediments attached to specimens, it was possible to define the predetermined subdivision of the Frasnian as ranges of conodonts and the fauna to be placed within conodont zones. Previously only antiarchs, bottom-feeding placoderms, had been recovered from the Lower and Upper Kellwasser horizons from this area (Płucki); thus, the occurrence of ptyctodonts represents an additional placoderm taxon. This work describes the first placoderm remains from Dębnik near Kraków, which also represent the first described placoderms from an area other than the Holy Cross Mountains.

## Introduction

Ptyctodonts are a well-recognized group of specialized placoderms. They are traditionally considered as durophagous, clearly specialized feeders on hard-shelled prey in the ancient reef system. They were small to medium sized durophagous fishes, feeding on hard-shelled prey, and had highly reduced dermal armor. Among this group, sexual dimorphism (Watson 1938; Trinajstic et al. 2015), internal fertilization and viviparity have been identified (Long et al. 2008, 2009).

The ptyctodont fossil record mainly consists of tooth plates, composed of hard tubular dentine, which have excellent fossilization potential and occur in abundance in Middle to Late Devonian deposits. The histology of the tooth plates is well known and already described (Pander 1858; Gorizdro-Kulczycka 1934; Ørvig 1980; Janvier 1996).

The first data regarding ptyctodonts from the Holy Cross Mountains was published by Kulczycka (1933; in further papers Gorizdro-Kulczycka), who recorded the occurrence of two genera: *Ptyctodus* and *Rhynchodus* in the Upper Devonian (Frasnian) of the Wietrznia and Kadzielnia quarries in the city of Kielce. However, this short paper provided no details regarding morphology and taxonomy. Further studies on Frasnian ptyctodonts (Gorizdro-Kulczycka 1934) resulted in detailed descriptions of several specimens, including three species of *Ptyctodus* (*Ptyctodus obliquus*, *Ptyctodus kielcensis* and *Ptyctodus czarnockii*), one undetermined specimen of *Ptyctodus* sp. from the Tudorów quarry (easternmost part of the Holy Cross Mountains) and one *Rhynchodus marginalis*. Three of the described species (*P. kielcensis*, *P. czarnockii*, *R. marginalis*) were specific to the Holy Cross Mountains region and were distinguished as new taxa. It is worth noting that an additional described species, *Ptyctodus calceolus*, dated as Middle Devonian from the Wołyń area (recent Ukraine), will be not taken into consideration in this paper. Ivanov and Ginter (1997) further studied the ptyctodonts from the Holy Cross Mountains and questioned the identifications given by Gorizdro-Kulczycka (1934). Following this work, several paleontological studies have been published, the most important being Kulczycki (1957), which represents the only monographic work of Upper Devonian

fishes from the area and which all subsequent works (Ivanov and Ginter 1997; Szrek 2020) refer to. However, the monograph did not focus on ptyctodonts, the taxon was mentioned only briefly (Rakociński et al. 2016; Szrek 2020). A study by Gorizdro-Kulczycka (1934) remains the most detailed description of this group from the Holy Cross Mountains. Ivanov and Ginter (1997) suggested that *Ptyctodus czarnockii* was, in fact, a species of *Rhynchodus*, similar to *Rhynchodus tetrodon*, and that *Ptyctodus kielcensis* and *Ptyctodus obliquus* also represent the *Rhynchodus*.

In order to resolve the taxonomy of the material originally described by Gorizdro-Kulczycka (1934), a review of the material and redescription was undertaken by the authors of this paper. However, the examination of the collections showed that many of the specimens, including one identified as *Rhynchodus marginalis*, were not present, most likely as a result of damage to part of the collection during World War II. Determination of the taxonomic position of the missing specimens was not possible from the illustrations alone. Thus, from the many specimens described by Gorizdro-Kulczycka (1934), only four are available: PGI-NRI 1697.II.1 (*P. kielcensis*; Gorizdro-Kulczycka 1934, pl. II, fig. 5), PGI-NRI 5.II.69 (*Ptyctodus* sp.; pl. II, fig. 6), PGI-NRI 5.II.72 (*P. obliquus*; pl. II, fig. 4) and PGI-NRI 5.II.75 (*P. czarnockii*; pl. I, fig. 3), described in detail below.

The occurrence of ptyctodonts in sediments from the Holy Cross Mountains was interpreted to indicate continental, freshwater to brackish-lagoonal nearshore conditions (Liszkowski and Racki 1993). In addition, their co-occurrence with hard-shelled organisms, including numerous bivalves and predominantly *Buchiola*, was used to support a benthic mode of life (Rakociński et al. 2016) in addition to oxic bottom water conditions.

The aim of the present paper is to revise the material of ptyctodonts described by Gorizdro-Kulczycka (1934) based on additional material discovered over the last 25 years.

## Geological setting

Part of the collection (PGI-NRI 1697.II.1, PGI-NRI 5.II.69, PGI-NRI 5.II.72 and PGI-NRI 5.II.75) studied by Gorizdro-Kulczycka (1934) and the specimens described here for the first time (PGI-NRI 5.II.68, PGI-NRI 5.II.70, PGI-NRI 5.II.71, PGI-NRI 5.II.73, PGI-NRI 5.II.74, MWG UW ZI/43/0075, OS-224-14, OS-224-16, PGI-NRI 1697.II.11, PGI-NRI 1697.II.13 and PGI-NRI 1697.II.15) were collected in the Wietrznia quarry in the city of Kielce, located in the western part of the Holy Cross Mountains (about 190 km south of Warsaw), in a chain of hills known as the Kadzielnia Range. The range is built up of Upper Devonian rocks and belongs structurally to the western part of the Kielce–Łagów Synclinorium. The Late Devonian facies evolution of the present-day Kadzielnia Range area is still under discussion. Synsedimentary block tectonics resulted in a wide variety of marine environments in this small area, mainly during the Frasnian Stage (Szulczewski 1971, 1973, 1995). The age of the specimens described by Gorizdro-Kulczycka (1934) was determined based on brachiopods. Their age in standard conodont zonation may be ranged from the *Palmatolepis falsiovalis* zone to the Early *Palmatolepis triangularis* zone.

The specimen MWG UW ZI/43/0034 described here was found in Płucki, near Łagów. The outcrop is in the central part of the Holy Cross Mountains, about 36 km east of Kielce and 190 km south of Warsaw. The outcrop is situated on the southern slope of the Łagowica River Valley, in the eastern part of the Kielce–Łagów Synclinorium. The section exposed represents the Upper Devonian record, and more precisely the Frasnian–Famennian transition. The section is precisely dated, based on conodonts. Two conodont zones were distinguished: *Palmatolepis linguiformis* and *Palmatolepis triangularis*.

The Płucki site is widely known among researchers of the Upper Devonian of the Holy Cross Mountains. The exposed layer of dark limestone with numerous fossils was considered to be the equivalent of the famous Upper Kellwasser Limestone Horizon (Upper Kellwasserkalk), dating as Frasnian–Famennian transition and documenting the end of the second Late Devonian faunal crisis (after the Lower Kellwasser Event). Szrek and Salwa (2020) included a description and interpretation of the entire section exposed at the site as a record of underwater landslide, which comprised mixed sediments from different environments. This explains the significant differences in the composition of the section, presented by various authors who probably had a different profiling site exposed in a narrow vertical range (see Szrek and Salwa 2020, fig. 1). Details about stratigraphy, environment, and paleontological settings are available in Szrek (2020) and Szrek and Salwa (2020) and references therein.

Typical landslide structures occur mainly in the lower part of the section, above the Kellwaser-like horizon. The uppermost sequence records calm deep-water succession of the Łysogóry Basin with more than 150 meters of rhythmically bedded marly limestones and shales (Racki et al. 2002; Woroncowa-Marcinowska 2006).

## Materials and methods

All the material analyzed was found in the carbonate deposits of Poland from two localities: the Holy Cross Mountains and Dębnik (near Kraków). The specimens described here were found at different times. The specimens (Fig. 1A, B, E–G; Fig. 2C–E, H–K) were photographed and described by Gorizdro-Kulczycka (1934). Thin sections were made of some specimens: PGI-NRI 5.II.75 (Gorizdro-Kulczycka 1934, pl. I, fig. 3; Fig. 2H–K) and PGI-NRI 5.II.68 (Fig. 3I–K) were cut by Gorizdro-Kulczycka for histological studies and the results were illustrated (Gorizdro-Kulczycka 1934, pl. I, figs 4–6; pl. II, figs 1–3; pl. III). The rest of the specimens were prepared mechanically.

The specimens from the PGI-NRI 1697.II collection were found by Czarnocki, slightly prepared mechanically with a needle, and identified by Szrek (Woroncowa-Marcinowska and Szrek 2004).

The specimens described here were studied and photographed, using a Nikon D80 camera with an AF Micro Nikkor 60 mm 1:2:8D lens.

*Institutional abbreviations:* **PGI-NRI** – Polish Geological Institute-National Research Institute, Warsaw, Poland; **OS** – Holy Cross Mountains Branch of the Polish Geological Institute-National Research Institute, Kielce, Poland; **MWG** – Faculty of Geology, University of Warsaw, Warsaw, Poland.

## Systematic paleontology

Order PTYCTODONTIDA Woodward, 1891
Family PTYCTODONTIDAE Gross, 1932
Genus *PTYCTODUS* Pander, 1858
Species *Ptyctodus obliquus* Pander, 1858
(Figs 1–3; Fig. 4A–D)

The genus *Ptyctodus* is generally known solely from its distinctive broad and robust dental plates. The tritoral surface of the tooth plate is characterized by a flat or convex surface, oblique shapes and clearly visible ends of the vascular canals, arranged in parallel lines, perpendicular to the extension of the jaw. The function of the tooth plates is considered to be for crushing and grinding.

*PTYCTODUS OBLIQUUS* Pander, 1858
**Right upper tooth plate PGI-NRI 5.II.72**
Fig. 1A, B; Gorizdro-Kulczycka 1934, pl. II, fig. 4

*Locality and age.* Wietrznia quarry in Kielce, Upper Devonian, Frasnian, limestone with *Rhynchonella coronula* Drevern (Gorizdro-Kulczycka 1934), horizon II sensu Czarnocki (1947), *Palmatolepis falsiovalis*–Early *P. hassi* conodont zones (Ivanov and Ginter 1997; Szrek 2020).

*Description*. The specimen, an almost complete right upper tooth plate, is well preserved; however, the internal upper edge remains embedded in the sediment. The tooth plate measures 71 mm in length, 9 mm in width, and 43 mm in height at the highest preserved part. It is strongly compressed laterally, inwardly curved, and the external surface forms a gently sigmoidal curvature in the antero-posterior direction. The most posterior part of the tooth plate is broad and rounded, lacking a tritoral surface and separated from the tritoral surface by a transverse crescent-shaped groove. The tritoral surface appears behind the groove and continues forwards as a wide (8 mm) and elevated platform-like shiny surface with a clearly visible tubular dentine structure (see Fig. $1A_1$), getting thinner towards the front. The posterior part of the tooth elevation is marked by a transverse crescent-shaped ridge. The anterior part of the tritoral surface is completely different and represents a thin (2 mm) and slat-shaped form, which is curved downwards and externally. The tip of the tooth plate is slightly elevated and beak-shaped, with a small nodule.

*Remarks.* The anterior dorsal process is preserved but incomplete, and it is interpreted as extending upwards adjacent to the autopalatine, which is not preserved. This specimen was originally described by Gorizdro-Kulczycka (1934, pl. II, fig. 4) as *Ptyctodus obliquus*, but revised by Ivanov and Ginter (1997), and assigned to the genus *Rhynchodus* on the characters of a "curved oblique biting surface and well-developed anterior dorsal process". However, the well-developed anterior dorsal process is not a feature assigned only to *Rhynchodus*. The tooth plate is relatively big and robust, and the posterior portion of the tritoral surface is broad and platform-like with a rounded posterior margin. Therefore, we interpret the tritoral surface of the tooth plate as more typical of the genus *Ptyctodus,* and very similar to *P. obliquus* (Denison 1978, fig. 18G).

**Partial tooth plate PGI-NRI 5.II.73**
Fig. 1C, D

*Locality and age.* Same as above.

*Description.* The specimen represents a small portion of the lower tooth plate. Its lower edge remains attached to the sediment, but the tooth plate does not continue downwards. The measurements of the tooth plate are 14 mm in length, 7 mm in width, and 3 mm in height. The tritoral surface is broad and relatively flat, with a well-preserved tubular dentine structure, which is obliquely laminated in relation to the extension of the jaw (see Fig. $1C_1$). The tritoral surface slants obliquely to the lingual surface.

*Remarks.* The tooth plate presumably continues forwards. One side of the tritoral surface is clearly complete and can be identified as the posterior margin of the tooth plate. The broad, flat and gently oblique tritoral surface, as well as its rounded posterior margin, are characteristic of the genus *Ptyctodus* and very similar to *P. obliquus* (Denison 1978, fig. 18G).

*PTYCTODUS KIELCENSIS* Gorizdro-Kulczycka, 1934
**Lower tooth plate PGI-NRI 1697.II.1 (holotype)**
Fig. 1E–G; Gorizdro-Kulczycka 1934, pl. I, fig. 5

*Locality and age.* Wietrznia quarry in Kielce, Upper Devonian, Frasnian, limestone with *Rhynchonella cuboides* Sow. (Gorizdro-Kulczycka 1934), horizon III sensu Czarnocki (1947), *Palmatolepis falsiovalis*–Early *P. hassi* conodont zones (Ivanov and Ginter 1997; Szrek 2020).

*Description*. The specimen represents an almost complete left lower tooth plate. Its lower and internal surfaces are still covered by sediment. The preserved portion of the tooth plate is 55 mm long, 7 mm wide on the anterior part, and approximately 15 mm high. The posterior portion is curved internally and widens significantly to a maximum width of 14 mm at the posterior margin. On the upper edge of the tooth plate, there is a tritoral surface, which is clearly bisected, and the tubular dentine structure is somewhat visible but not well defined. On the posterior part of the tritoral surface, there is a transverse crescent-shaped groove, which separates the tritoral surface from the non-functional part of the tooth plate. Before the groove, the tritoral surface is gently elevated but generally flat, likely due to wear or erosion. The anterior part of the tritoral surface begins as a central tubercle (2 mm wide), which extends to a very thin (1 mm wide) and slat-shaped form, positioned along the external edge of the upper surface of the tooth plate. The tip of the tooth plate is broken off.

*Remarks*. The specimen described and illustrated by Gorizdro-Kulczycka (1934, pl. II, fig. 5; Fig. 1G) is better preserved: the tip is still present and more features are visible, e.g. the central tubercle is more pronounced, and the tritoral surface on the anterior part is curved internally and reaches the end of the tooth plate (Fig. 1G).

According to Ivanov and Ginter (1997), the material described by Gorizdro-Kulczycka (1934) as *Ptyctodus kielcensis* should be assigned to the genus *Rhynchodus* because the shape of the triturating surface could not be determined. However, these authors did not have access to the holotype of this species at that time. Here we confirm that the specimens described by Gorizdro-Kulczycka (1934) represent the genus *Ptyctodus* because the biting surface can be determined to have a broad tritoral surface, there is a wide lower edge of the lower jaw, a swelling on the middle part of the jaw, a convex tritoral surface, and a crescent indentation on the upper edge of the posterior part – all morphological features that distinguish this taxon from the other species of the genus *Ptyctodus*. Locating the type collection and the holotype of the species *P. kielcensis* has demonstrated the presence of these diagnostic features and confirms the validity of the specimen as *P. kielcensis* (Gorizdro-Kulczycka 1934).

However, in the above-mentioned collections, many remains of the genus *Ptyctodus* were found but most of them are damaged, and their assignment to the species *P. kielcensis* remains uncertain.

*PTYCTODUS* sp.

**Lower tooth plate MWG UW ZI/43/0075**

Fig. 2A, B

*Locality and age.* Wietrznia quarry in Kielce, Upper Devonian, Frasnian, *Palmatolepis falsiovalis*–Early *P. hassi* conodont zones (Ivanov and Ginter 1997; Szrek 2020).

*Description.* The specimen MWG UW ZI/43/0075 (Fig. 2A, B) is 37 mm long and represents a part of an incomplete right lower tooth plate. The lateral and bottom surfaces of the tooth plate are covered by sediment, but the posterior part and tritoral surface are clearly visible. The tooth plate is gently curved internally. On the most posterior part, the tubular dentine structure is almost invisible due to poor preservation. The tritoral surface occurs on an elevated surface, which slopes downwards to form a transverse crescent-shaped groove. Behind the groove, the tritoral surface slopes upwards, forming a gentle elevation with a prominent longitudinal ridge, which extends forwards in the middle part the tooth plate. The ridge gradually decreases in size towards the anterior portion of the tooth plate. On the lateral sides, there are clearly visible vascular canals, stretching obliquely forwards.

*Remarks.* This specimen shows features very similar to the specimen PGI-NRI 5.II.69 (Fig. 2C–E) and we assume that it belongs to the same species.

**Incomplete lower tooth plate PGI-NRI 5.II.69**

Fig. 2C–E; Gorizdro-Kulczycka 1934, pl. II, fig. 6

*Locality and age.* Wietrznia quarry in Kielce, Upper Devonian, Frasnian, limestone with *Rhynchonella coronula* Drevern (Gorizdro-Kulczycka 1934), horizon II sensu Czarnocki (1947), *Palmatolepis falsiovalis*–Early *P. hassi* conodont zones (Ivanov and Ginter 1997; Szrek 2020).

*Description.* The specimen represents a partial tooth plate 36 mm long, 13 mm wide, and 14 mm high. Its lower surface is still covered by sediment. The lateral sides of the tooth plate are eroded, probably taphonomic, but show longitudinal sections of vascular canals, extending obliquely forwards. The tritoral surface is not well preserved but the tubular dentine structure is still visible (Fig. $2E_1$). The tritoral surface is generally broad (7 mm) and convex. On its posterior portion, there is a transverse crescent-shaped groove, and immediately behind it is an elevated surface with a prominent longitudinal ridge extending forwards.

*Remarks.* All features of this specimen resemble those of MWG UW ZI/43/0075 (Fig. 2A, B) and we suggest that it belongs to the same species.

**Left lower tooth plate PGI-NRI 5.II.75 (holotype)**

Fig. 2H–K; Gorizdro-Kulczycka 1934, pl. I, fig. 3

*Locality and age.* Same as above.

*Description.* The specimen represents a poorly preserved portion of a left lower tooth plate. The most posterior part was cut off for histological studies by Gorizdro-Kulczycka (1934, pl. I, figs 4–6; pl. II, figs 1–3; pl. III, figs 1–4). The preserved fragment of the tooth plate is 58 mm long, approximately 20 mm wide, high-crested and laterally compressed. The lower edge of the specimen remains covered by sediment and the lateral surfaces are abraded, either taphonomically or through preparation. On the upper portion of the specimen, there is a tritoral surface that measures 44 mm long and 9 mm wide. Its posterior part is elevated, broad and shiny, and the tubular dentine structure (parallel lines perpendicular to the extension of the jaw; Fig. $2K_1$) is visible. The anterior part of the tritoral surface sits well below the main dorsal margin of the tooth; it is thin (2 mm), slat-shaped and curved lingually.

*Remarks.* This specimen was described by Gorizdro-Kulczycka (1934, pl. I, fig. 3) as a holotype of *Ptyctodus czarnockii* together with another specimen (pl. I, figs 1, 2), which was not found in the museum's collections. According to the author, the specimen was an upper tooth plate, and the other holotype was a lower tooth plate. Neither of the tooth plates belonged to the same individual but the shapes of the functional surfaces were supposed to fit each other. The specimen examined here (PGI-NRI 5.II.75) was identified by Ivanov and Ginter (1997) as a portion of a lower tooth plate, which, they stated, was difficult to attribute to a definite genus. According to Ivanov and Ginter (1997), the second (lost) holotype was identified as an upper tooth plate "with curved oblique anterior part and flat posterior part of the biting surface, characteristic of *Rhynchodus*, and is very similar to that of *R. tetrodon* (Jaekel, 1903)". However, in our opinion, the specimen PGI-NRI 5.II.75 belongs to the lower tooth plate and, based on the shape of the tritoral surface (broad and flat) and general robustness, this specimen should be assigned to genus *Ptyctodus* (Eastman 1898a, figs 1–40). Due to the other holo-

type being lost, the determination of the taxonomic position of the other holotype cannot be resolved from the illustrations alone.

**Fragment of the left lower tooth plate PGI-NRI 5.II.70**
Fig. 2F, G

*Locality and age.* Same as above.

*Description.* This specimen comprises the posterior part of an incomplete left lower tooth plate. The preserved part measures 30 mm long and its posterior is much wider than the anterior (7 mm and 5 mm, respectively). The external surface of the tooth plate is covered by sediment. The tooth plate has a low crest, and the external (labial) surface is more convex than the internal (lingual) surface. The most posterior part of the tooth plate is rounded and lacks a tritoral surface. The posterior part of the tritoral surface is rounded and gently convex, but the internal serrated edge (arranged with ridges; Fig. 2G) is probably the result of erosion. On the middle part of the specimen, there is an asymmetrical bulge approaching the external edge. Along the internal edge, there is a small cavity, defined by a sharp, high edge, which extends towards the anterior end of the specimen. The external edge tapers towards the internal edge and the thickness of the tooth plate decreases. The tubular dentine structure is clearly visible (Fig. $2F_1$). Both the external and internal surfaces are smooth.

*Remarks.* Based on the shape of the biting surface, which is broad and relatively flat, presumably because of the crushing and/or grinding function, we assign this tooth plate to the genus *Ptyctodus*. Due to the incompleteness of the tooth and the poor state of preservation, the tooth plate cannot be attributed to any species.

**Fragment of the right lower tooth plate PGI-NRI 5.II.71**
Fig. 3D–F

*Locality and age.* Same as above.

*Description.* The specimen is an incomplete and poorly preserved tooth plate that measures 25 mm long and 5 mm wide. The tritoral surface is elevated and oblique. The tubular dentine is arranged as parallel lines perpendicular to the extension of the jaw (Fig. $3E_1$, $E_2$). The structure of the tubular dentine is also visible from underneath the tooth plate, arranged in the same way (Fig. 3F). The external side of the tooth plate shows longitudinal sections of vascular canals extending obliquely forwards (Fig. 3D).

*Remarks.* The tritoral surface is generally broad, flat and oblique, which is characteristic of the genus *Ptyctodus*. However, there are no diagnostic features, which makes it difficult to attribute this tooth plate to a definite species.

**Fragment of the right upper tooth plate PGI-NRI 5.II.74**
Fig. 3G, H

*Locality and age.* Same as above.

*Description.* The specimen is a 16 mm long incomplete tooth plate. The specimen is still in the sediment, and only the lower (tritoral) and internal surfaces are exposed. This visible portion is the posterior part of a right upper tooth plate. The tritoral surface has a tubular dentine structure, which is poorly preserved. The most posterior part of the preserved portion of the tooth plate is a bit wider than the anterior part (7 mm and 6 mm, respectively) and exposed in cross-section. The tooth plate lacks a tritoral surface. The functional surface is separated from the non-functional surface by a transverse crescent-shaped groove, which extends forwards, forming an asymmetrical surface; however, this is probably caused by erosion. On the anterior part of the preserved portion of the tooth plate, there is a crack with a cross-section exposed, which shows a continuation of the tooth plate. The natural height and curvature of the upper edge of the tooth plate are visible. The upper edge becomes narrower towards the dorsal margin, which is typical of upper tooth plates and may represent the base of an anterior dorsal process.

*Remarks.* Based on the shape of the tritoral surface, this specimen should be assigned to genus *Ptyctodus*. However, because of the poor state of preservation and the lack of diagnostic features, a definitive taxonomic determination cannot be made.

**Fragment of the lower tooth plate PGI-NRI 5.II.68**
Fig. 3I–K

*Locality and age.* Wietrznia quarry in Kielce, Upper Devonian, Frasnian, horizon II sensu Czarnocki (1947), *Palmatolepis falsiovalis*–Early *P. hassi* conodont zones (Ivanov and Ginter 1997; Szrek 2020).

*Description.* The specimen represents an anterior part of a lower tooth plate. The specimen is highly eroded, and its lower and external surfaces are still in the sediment. The posterior part of the tooth plate was cut off for histological studies by Gorizdro-Kulczycka (1934). The preserved portion of the tooth plate measures 28 mm long and 15 mm high, and it is gently inwardly curved. The posterior part is wider than the anterior part (11 mm and 6 mm, respectively), and it is characterized by a swelling (5 mm high) on the upper edge, which is best seen in a cross-section (Fig. 3K).

*Remarks.* The tritoral surface of the specimen is highly eroded but suggests a broad and elevated surface on the posterior part, and a slightly lower and asymmetrical surface on the anterior part, which resembles the general morphological pattern of the tooth plates of ptyctodonts from the Holy Cross Mountains. On the anterior lower edge, there is a small recess, which has been probably caused by the breaking off of the edge of the tooth plate, rather than the larger articular process.

**Fragment of the lower tooth plate MWG UW ZI/43/0051**
Fig. 3A–C

*Locality and age.* Górno, Upper Devonian, Frasnian.

*Description.* The specimen is an incomplete small tooth plate, measuring 6.5 mm in length, 2 mm in width, and 2 mm in height. The lower surface of the tooth plate is still embedded in the sediment. It represents the posterior part of the lower

tooth plate and has a clearly visible, flat and relatively broad tritoral surface that becomes narrower towards the back (Fig. 3B). The tubular dentine structure is clearly visible (Fig. 3C). No other features were found.

*Remarks.* Based on the shape of the functional (tritoral) surface, the specimen should be assigned to the genus *Ptyctodus*. Due to its small size and the lack of characteristic features on the tritoral surface, which may be caused by the stage of development or wear, we hypothesize that the tooth belongs to a juvenile individual.

**Partial tooth plate PGI-NRI 1809.II.26**
Fig. 4A, B

*Locality and age.* Dębnik quarry near Kraków, Upper Devonian, Frasnian.

*Description.* The specimen is a small fragment of a tooth plate, measuring 8 mm in length, 4 mm in width, and 4 mm in height, and the state of preservation is very poor. The posterior part of the tooth plate is sloped and rounded, lacking a tritoral surface. The upper surface of the specimen presents a flat tritoral surface with a visible tubular dentine structure in the form of horizontal parallel lines that are perpendicular to the extension of the jaw (Fig. 4A, B). On the lateral surfaces, there are lines that extend obliquely forwards, which are longitudinal sections of vascular canals.

*Remarks.* The specimen is highly eroded. However, it is possible to assign this fragment to the genus *Ptyctodus* based on some characteristic features, such as the broad and flat shape of the tritoral surface. Determination at species level cannot be made.

**Fragment of the lower tooth plate JKA.D1**
Fig. 4C, D

*Locality and age.* Dębnik quarry near Kraków, Upper Devonian, Frasnian.

*Description.* The specimen represents the posterior part of an incomplete lower tooth plate, measuring 14 mm in length, 5 mm in width, and 6 mm in height. The tooth plate is low-crested and curved internally. The posterior end is sloped and rounded and lacks a tritoral surface. There is a tritoral surface located on the upper surface of the specimen, which is relatively wide and flat, with a highly eroded tubular dentine structure. The specimen is broken at the anterior end, exposing the internal structure of the tooth plate in cross-section (Fig. 4D).

*Remarks.* Based on the shape of the tritoral surface, this specimen can be assigned to genus *Ptyctodus*. However, due to the incomplete nature of the tooth, lack of diagnostic features and poor state of preservation, taxonomic determination to species level cannot be resolved.

*RHYNCHODUS* Newberry, 1873
Fig. 5A–D; Newberry 1873, figs 1–4
Species *Rhynchodus secans* Newberry, 1873

The tritoral tooth plates of *Rhynchodus* are generally narrow and sharp-shaped. The anterior part of the lower tooth plate is characterized by an apex that is curved upwards, behind which a narrow tritoral surface (probably with the crushing-cutting function) extends backwards to terminate at an elevation that continues until the end of the tooth plate. In lateral view, the surface is slightly convex. The shape of the upper tritoral tooth plate is very characteristic, being higher on the anterior portion and several times lower on the posterior part, giving them a beak-like appearance. The function of the jaw (cutting rather than grinding) was different than in genus *Ptyctodus*.

*RHYNCHODUS* sp.
**Complete set of tooth plates OS-224-14**
Fig. 5A

*Locality and age.* Wietrznia quarry in Kielce, Upper Devonian, Frasnian, horizon II sensu Czarnocki (1947), *Palmatolepis falsiovalis*–Early *P. hassi* conodont zones (Ivanov and Ginter 1997; Szrek 2020).

*Description.* The specimen represents a full completement of tooth plates, comprising two lower tooth plates and one upper tooth plate preserved as bone tissues, and one upper tooth plate preserved mostly as an imprint. The lower tooth plates are 20 mm and the upper plates 18 mm in length. The lower tooth plates are generally long and low-crested, with a cracked surface (Fig. 5A$_1$), and characterized by a small "beak" protruding upwards at the anterior end.

Behind the "beak", there is a biting surface that extends almost to the posterior end of the jaw, which is much higher than the anterior part (6 mm and 4 mm, respectively). The posterior end of the lower tooth plate is asymmetrical, with the upper edge protruding backwards.

One of the upper tooth plates is preserved as an imprint, but the overall morphology is still visible. The upper tooth plates are characterized by a very thin (2 mm) posterior part and a prominent "beak" on the anterior edge. There is also an anterior dorsal process that in life would have fitted into the autopalatine, but this has not been preserved. The total height of the anterior part of the upper tooth plate is 11 mm.

In addition, there is another bony element, though poorly preserved (Fig. 5A$_2$). This element measures approximately 16 mm in length and 17 mm in width, and has a triangular shape.

*Remarks.* Specimen OS-224-14 is the only preserved ptyctodont found in the Holy Cross Mountains, which allows clear observation of the features of both the upper and lower tooth plates of a single individual. The tooth plates are generally thin and fragile, probably due to fossilization. The overall morphology corresponds to the genus *Rhynchodus* (Eastman 1898a, figs 41–47; 1898b; 1904, fig. 1; 1907; Denison 1978, fig. 18A–C), but the features found in the specimen do not fit any of the previously described species. In addition to the visible jaw apparatus, there is another element that is partially preserved and mostly visible as an imprint (Fig. 5A$_2$). It appears to be a median dorsal plate and, based on its size, likely belongs to the same individual, although this cannot be confirmed, as the specimen is fragmentally preserved.

**Lower tooth plate OS-224-16**
Fig. 5B

*Locality and age.* Same as above.

*Description.* The specimen represents a complete, isolated lower tooth plate that measures 22 mm in length, 4 mm in height on its anterior part, and 10 mm in height on its posterior part. The tooth plate is generally long and low-crested. The anterior end of the tooth plate is characterized by a small "beak" protruding upwards, while the posterior end is asymmetrical, with the upper edge protruding backwards. The biting surface is sharp and a bit wider on the posterior part of the tooth plate.

*Remarks.* The tooth plate is very thin and fragile, probably as a result of taphonomic processes. The general morphology of this specimen is similar to that of specimen OS-224-14 (Fig. 5A$_1$), but slightly larger in size. It is evident that both individuals, OS-224-16 and OS-224-14, belong to the same species.

**Upper tooth plate PGI-NRI 1697.II.11**
Fig. 5C

*Locality and age.* Same as above.

*Description.* The specimen is a complete upper tooth plate that measures 8 mm long. The anterior part of the tooth plate is higher than the posterior part (5 mm and 3 mm, respectively). The general shape of the tooth plate is trenchant, with a prominent anterior dorsal process. The biting surface is very thin, sharp and beak-shaped.

*Remarks.* Based on the shape of the biting surface, the specimen can be assigned to the genus *Rhynchodus* (Eastman 1898a, figs 41–47; 1898b; 1904, fig. 1; 1907; Denison 1978, fig. 18A–C).

**Upper tooth plate PGI-NRI 1697.II.15**
Fig. 5D

*Locality and age.* Same as above.

*Description.* The specimen is a partial upper tooth plate, measuring 15 mm in length. The anterior part of the tooth plate is 8 mm high, while the posterior is 6 mm high and still covered by sediment. The general shape of the tooth plate is trenchant, with a very thin and sharp biting surface that ends in a prominent beak-shaped process; however, the tip is broken off.

*Remarks.* The shape of the biting surface is typical of the genus *Rhynchodus* (Eastman 1898a, figs 41–47; 1898b; 1904, fig. 1; 1907; Denison 1978, fig. 18A–C).

**PTYCTODONTIDAE** gen. et sp. indet.
**Lower tooth plate PGI-NRI 1697.II.13**
Fig. 5E

*Locality and age.* Same as above.

*Description.* The specimen represents an almost complete lower tooth plate, measuring 13 mm in length, and its lower surface and one of the lateral surfaces are covered by sediment. The anterior part of the tooth plate is rounded and measures 4 mm in height. On the lower edge of the posterior part, there is an articular process that measures 7 mm in height. The biting surface on the posterior part is relatively broad and flat, and it gets thinner towards the anterior part, which is sharp and gently protruding upwards. The functional surface also has a gentle ridge along one of the edges in an antero-posterior direction. However, the posterior part of the tooth plate is slightly shifted due to fossilization, which has resulted in the discontinuity of the rectilinear ridge. The articular ossification of the Meckelian cartilage can be traced behind the posterior margin of the tooth plate.

*Remarks.* The tooth plate has features of both genera *Ptyctodus* and *Rhynchodus* but differs from the other specimens in the studied collection. The state of preservation is different from that of other *Rhynchodus* tooth plates in the collection – the plate is preserved three-dimensionally, whereas all others are extremely flattened. Thus, it may be possible to study the morphology of the biting surface and precisely interpret its function as part of further work. The size of the examined specimen is the same as that of all other *Rhynchodus* tooth plates in the collection; however, this specimen differs in general shape. The functional surface is broad and flat, suggesting a grinding function of the tooth plate. In comparison to other *Ptyctodus* specimens in the collection, the size of the examined specimen is small; thus, it is likely that this specimen belongs to a juvenile individual of that genus. The cutting-like anterior edge of the examined specimen is very short and forms a gentle "beak". This is in line with the juvenile forms with sharp-edged tooth plates of the species of *Ptyctodus* (e.g. *P. compressus*; *P. panderi*) that Eastman (1898a) identified as having a relatively shorter cutting edge and less marked constrictions than adult individuals, since the cutting edge narrows throughout ontogeny due to wear. However, the undeveloped functional surface may also apply to the juvenile forms of the genus *Rhynchodus*; if so, it definitely belongs to a different species than those known from the studied collection, due to its size and robustness. The tubular dentine structure is not visible (contrary to the specimen MWG UW ZI/43/0051; Fig. 3C), which may be due to lack of development in the juvenile stage or due to taphonomy. The taxonomic affiliation of this specimen remains uncertain.

**Median dorsal plate MWG UW ZI/43/0034**
Fig. 4E–H

*Locality and age.* Płucki, Holy Cross Mountains, Upper Devonian, Upper Frasnian, the so-called Upper Kellwasserkalk horizon, *Palmatolepis linguiformis* conodont zone.

*Description.* The specimen represents a median dorsal plate, measuring 15 mm in length and 10 mm in width at its midsection. In dorsal view (Fig. 4E), the plate has a pentagonal and slightly elongated shape. The plate is small; however, the keel is large and deep, and extends beyond the posterior margin of the dermal surface of the plate (Fig. 4G). The total height of the plate is 5 mm. Although the posterior edge of

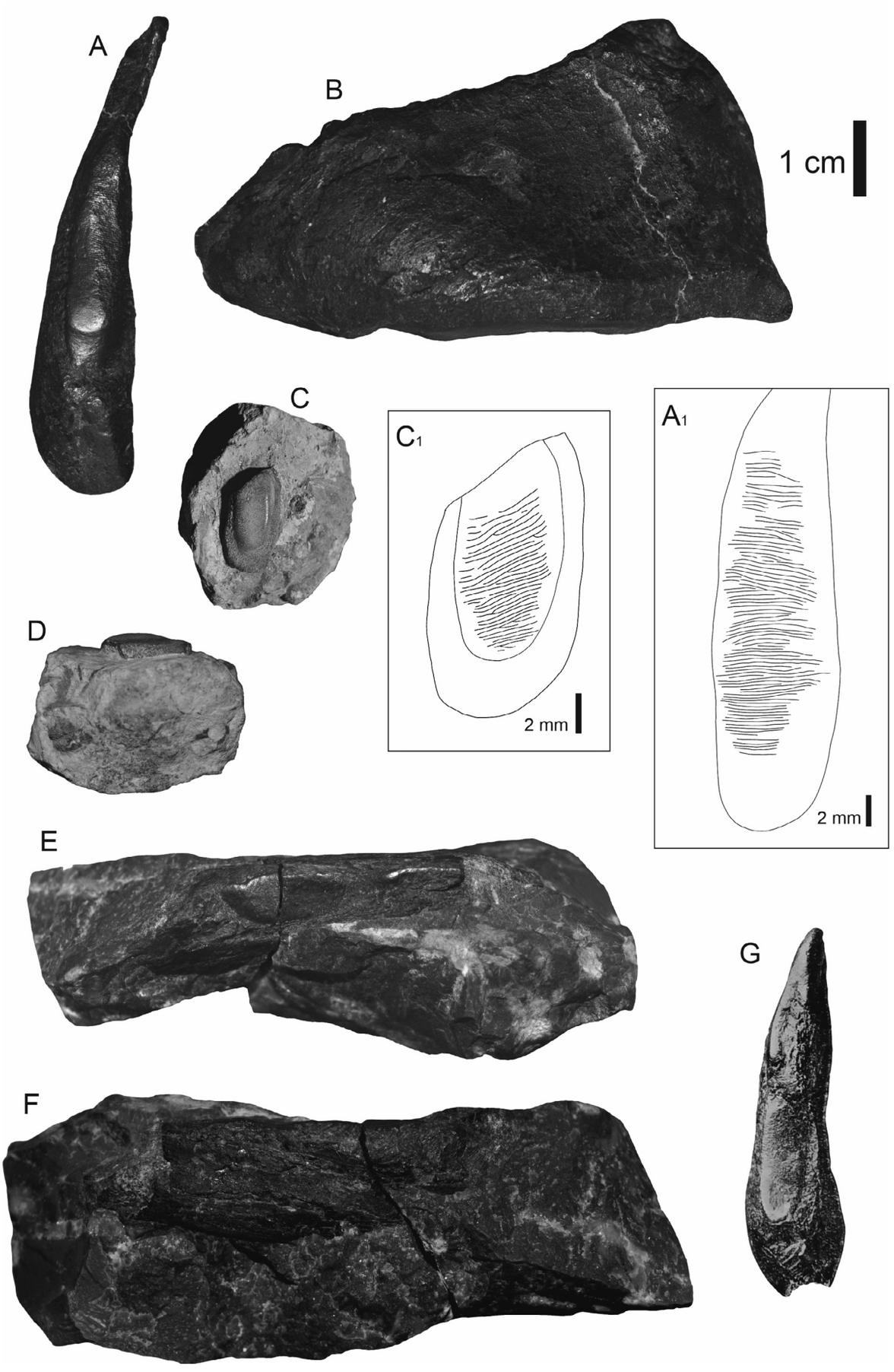


**Fig. 1.** **A, B** – *Ptyctodus obliquus*, right upper tooth plate, PGI-NRI 5.II.72: A – dorsal view, $A_1$ – sketch of the pattern of the semidentine canal openings, B – lateral view. **C, D** – *Ptyctodus obliquus*, partial tooth plate, PGI-NRI 5.II.73: C – dorsal view, $C_1$ – sketch of the pattern of the semidentine canal openings, D – lateral view. **E–G** – *Ptyctodus kielcensis*, lower tooth plate, holotype, PGI-NRI 1697.II.1: E – dorsal view, F – lateral view, G – figure from Gorizdro-Kulczycka (1934, pl. I, fig. 5).

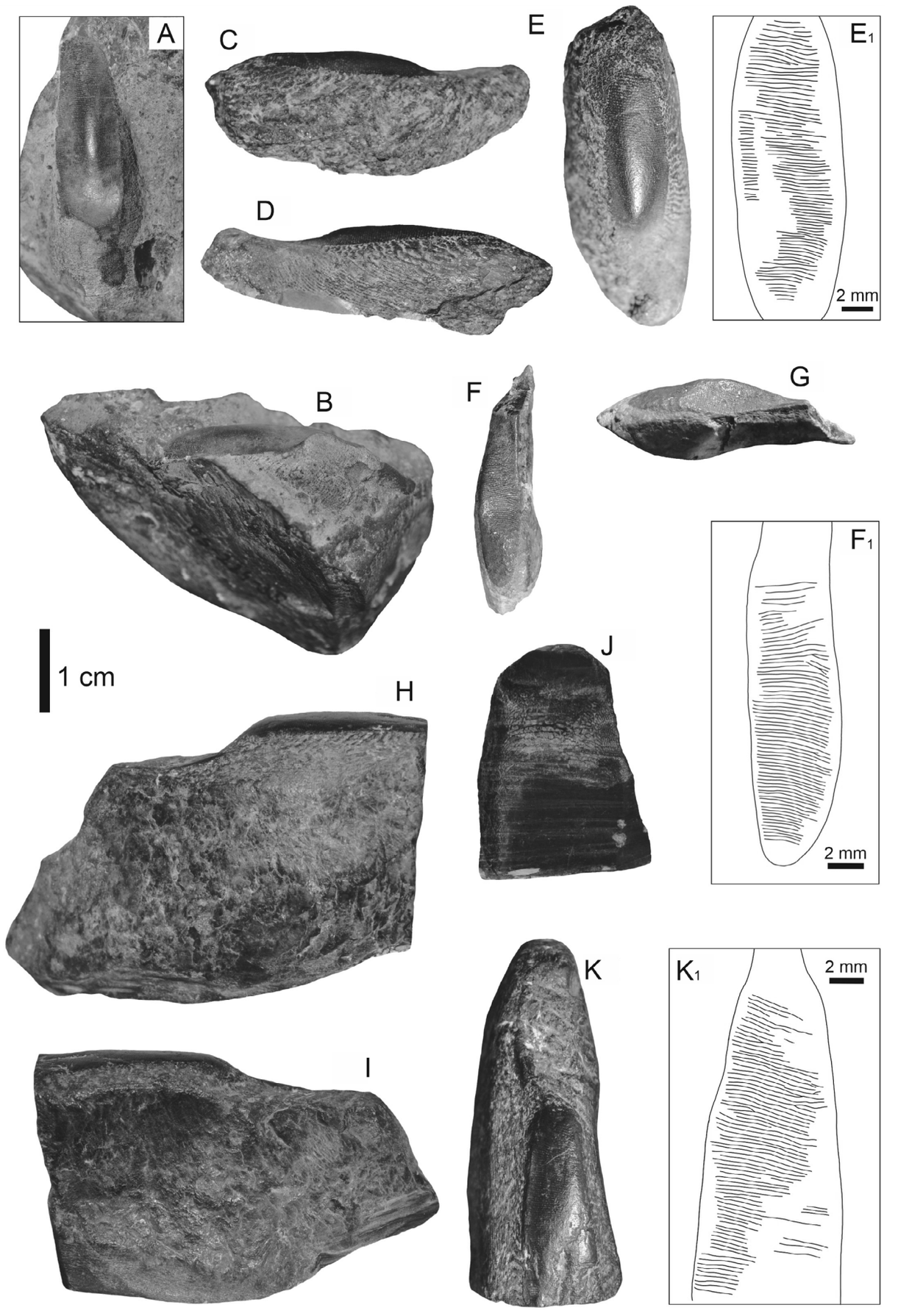


**Fig. 2.** **A, B** – *Ptyctodus* sp., lower tooth plate, MWG UW ZI/43/0075: A – dorsal view, B – lateral view. **C–E** – *Ptyctodus* sp., incomplete lower tooth plate, PGI-NRI 5.II.69: C – right lateral view, D – left lateral view, E – dorsal view, $E_1$ – sketch of the pattern of the semidentine canal openings. **F, G** – *Ptyctodus* sp., fragment of the left lower tooth plate, PGI-NRI 5.II.70: F – dorsal view, $F_1$ – sketch of the pattern of the semidentine canal openings, G – lateral view. **H–K** – *Ptyctodus* sp., left lower tooth plate, PGI-NRI 5.II.75: H – left lateral (labial) view, I – right lateral (lingual) view, J – cross-section, K – dorsal view, $K_1$ – sketch of the pattern of the semidentine canal openings.

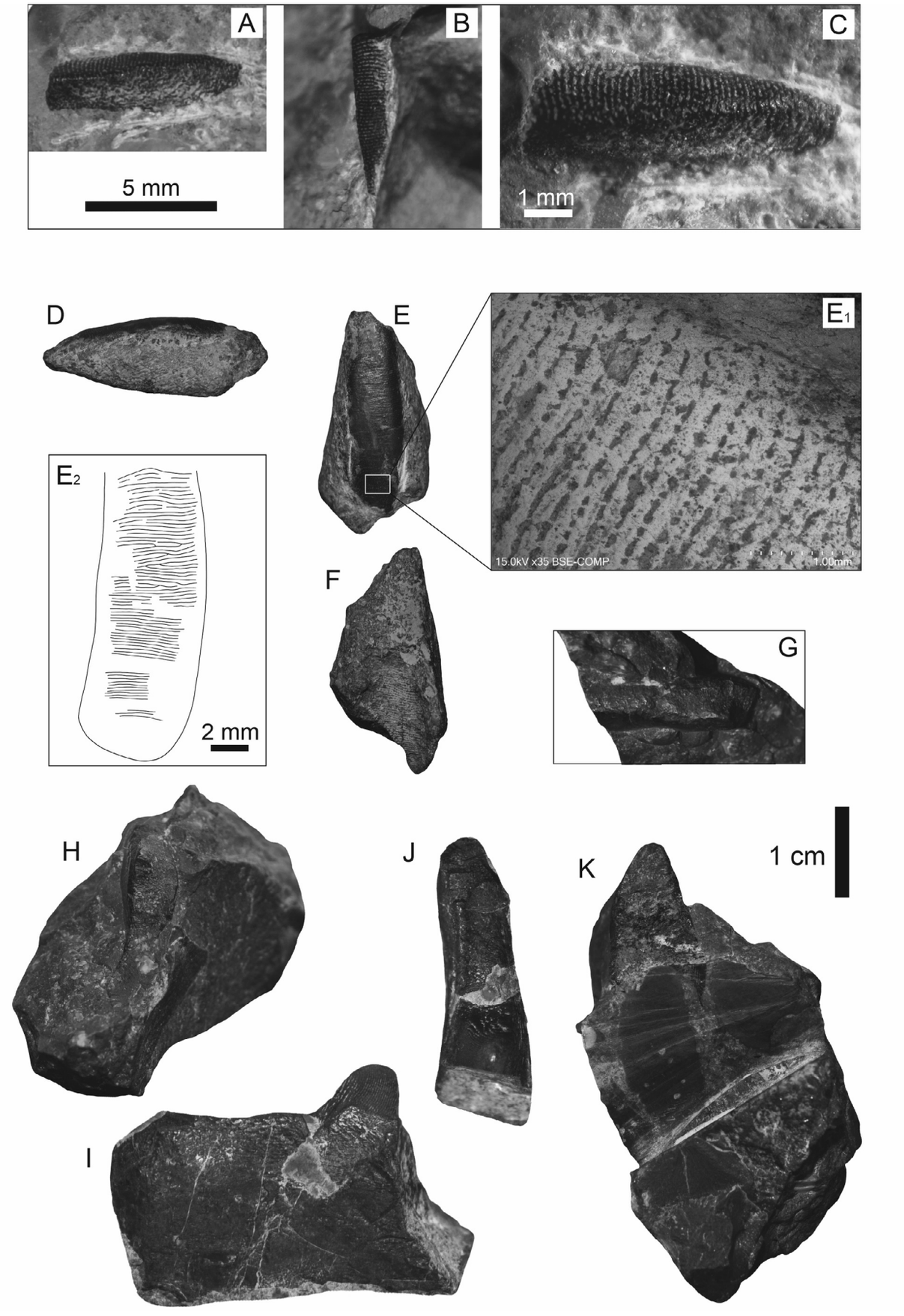


**Fig. 3. A–C** – *Ptyctodus* sp., fragment of the lower tooth plate, MWG UW ZI/43/0051: A – lateral view, B – dorsal view, C – tritoral surface. **D–F** – *Ptyctodus* sp., fragment of the right lower tooth plate, PGI-NRI 5.II.71: D – lateral view, E – dorsal view, $E_1$ – SEM magnified area marked on E, showing the structure of the tritoral surface, $E_2$ – sketch of the pattern of the semidentine canal openings, F – view from the base of the specimen with visible tubular dentine structure. **G, H** – *Ptyctodus* sp., fragment of the right upper tooth plate, PGI-NRI 5.II.74: G – dorsal view, H – cross-section. **I–K** – *Ptyctodus* sp., fragment of the lower tooth plate, PGI-NRI 5.II.68: I – lateral view, J – dorsal view, K – cross-section.

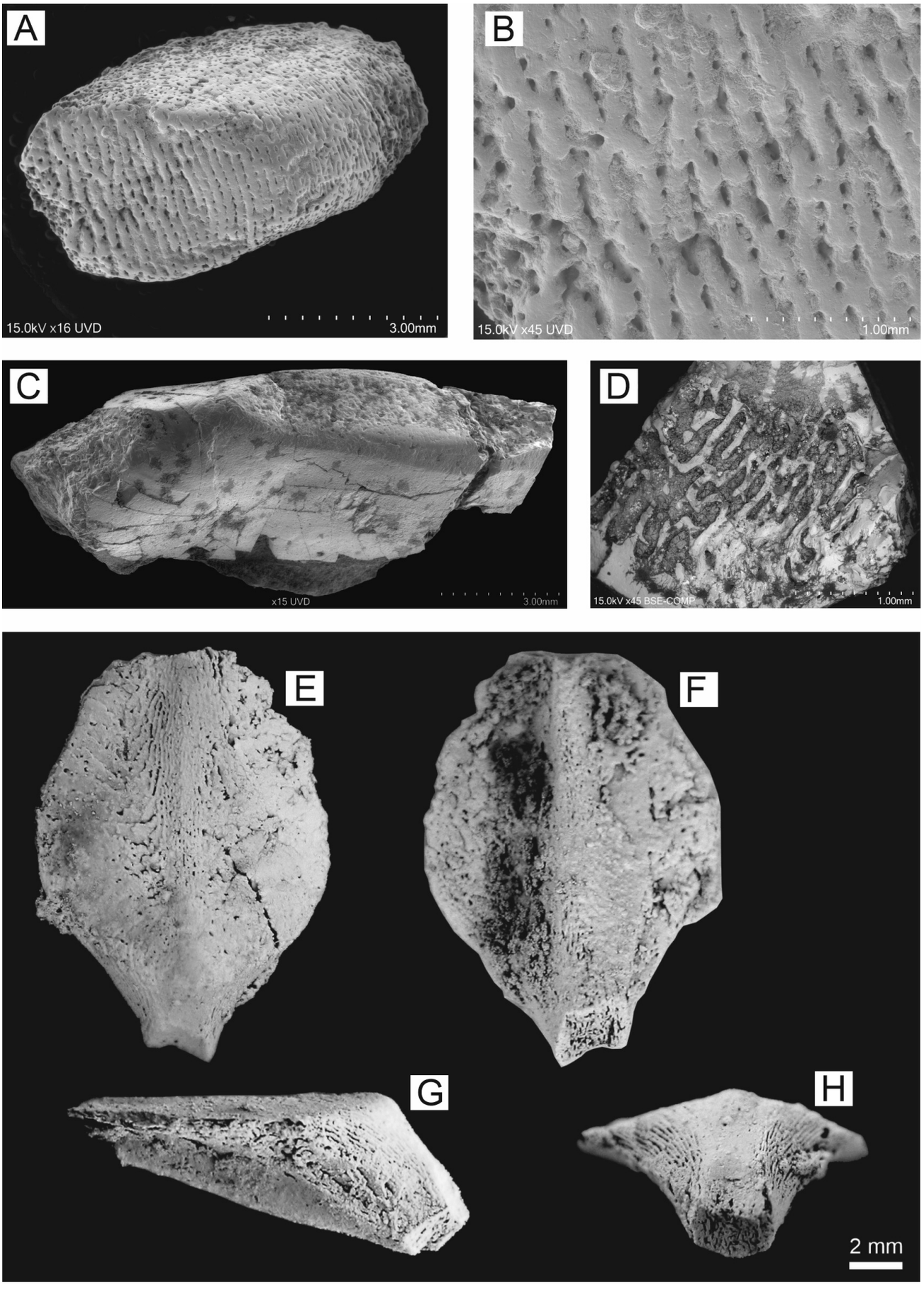


**Fig. 4.** **A, B** – *Ptyctodus* sp., partial tooth plate, PGI-NRI 1809.II.26, SEM photography: A – dorsal view, B – magnification, showing the tritoral surface. **C, D** – *Ptyctodus* sp., fragment of the lower tooth plate, JKA.D1, SEM photography: C – lateral view, D – cross-section. **E–H** – Ptyctodontidae gen. et sp. indet., median dorsal plate, MWG UW ZI/43/0034, SEM photography: E – dorsal view, F – visceral view, G – lateral view, H – view from the back.

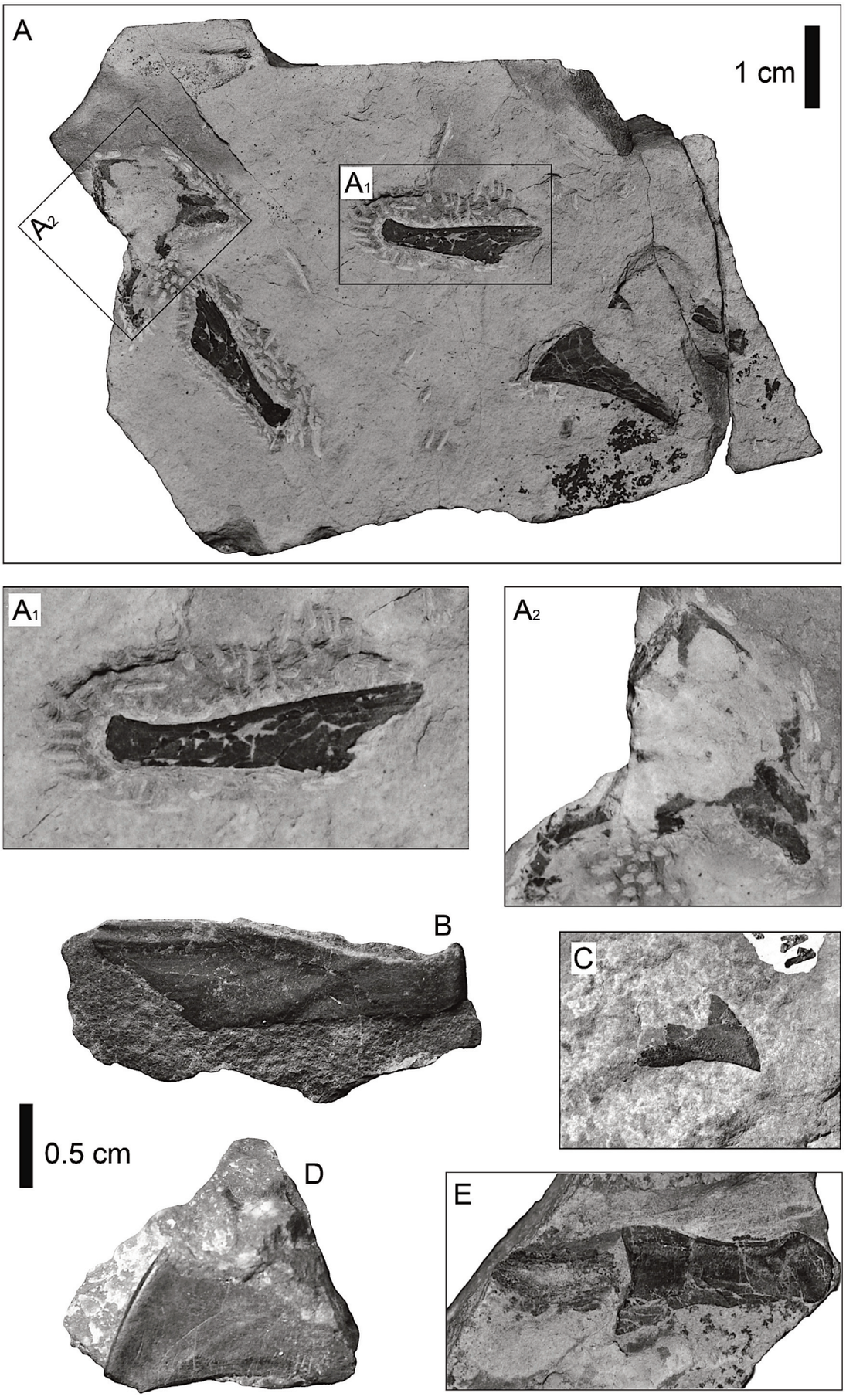


**Fig. 5.** **A** – *Rhynchodus* sp., complete set of tooth plates, OS-224-14: A – dorsal view, $A_1$ – magnified area marked on A, showing one of the lower tooth plates, $A_2$ – magnified area marked on A, showing a putative median dorsal plate. **B** – *Rhynchodus* sp., lower tooth plate, OS-224-16. **C** – *Rhynchodus* sp., upper tooth plate, PGI-NRI 1697.II.11. **D** – *Rhynchodus* sp., upper tooth plate, PGI-NRI 1697.II.15. **E** – Ptyctodontidae gen. et sp. indet., lower tooth plate, PGI-NRI 1697.II.13.

the keel is not preserved, there is evidence of a spoon-shaped cavity on its most posterior part (Fig. 4H).

*Remarks.* The median dorsal plates differ in different ptyctodont genera. The described plate is strongly abraded and partly broken, resulting in the loss of diagnostic features; thus, precise taxonomic determination is impossible. No traces of overlapping surfaces or ornamentation are preserved due to the erosion of the specimen after acid etching of the conodont sample from which this plate was revealed. Its massive structure, especially the shape of the keel, generally corresponds to the same features described by Ørvig (1960, fig. 4B) for *Ctenurella gladbachensis*. The pentagonal and slightly elongated shape approaches it to *Kimbryanodus williamburyensis* illustrated by Trinajstic and Long (2009, fig. 8).

## Discussion and conclusion

The revision of the historic collection, collected before World War II, and the study of new material resulted in the confirmation of the following taxa: *Ptyctodus obliquus*, *Ptyctodus kielcensis*, *Ptyctodus* sp., *Rhynchodus* sp. and Ptyctodontidae gen. et sp. indet. The revision of taxa *Rhynchodus marginalis* and *Rhynchodus czarnockii* cannot be made due to the material being lost. All the material analyzed was found in the carbonate deposits of Poland from four localities: Wietrznia quarry, Górno and Płucki, representing the Holy Cross Mountains region, and Dębnik, near Kraków.

The age estimation proposed by Gorizdro-Kulczycka (1934) was based on the subdivision of the Frasnian (Lower, Middle, Upper; horizon I, horizon II, horizon III sensu Czarnocki 1947). However, based on general knowledge of the regional Frasnian stratigraphy of the Holy Cross Mountains and on the conodont material obtained from the fragments of the sediments attached to Gorizdro-Kulczycka's and our specimens, we were able to revise the subdivision to ranges of conodonts: *Palmatolepis falsiovalis*–Early *P. hassi* (Ivanov and Ginter 1997; Szrek 2020). Therefore, the genera *Ptyctodus* and *Rhynchodus* from the Wietrznia quarry represent *Palmatolepis falsiovalis*–Early *P. hassi* conodont zones (Ivanov and Ginter 1997; Szrek 2020), while the ptyctodonts from Płucki represent *P. linguiformis* conodont zone (Szrek 2020, fig. 4).

This work describes the first placoderm remains from Dębnik near Kraków, which also represent the first described placoderms from an area other than the Holy Cross Mountains. Although there are additional ptyctodont specimens reported in the literature, including a median ventral plate, a medial dorsal spine and three tooth plates (Ivanov and Ginter 1997), these are currently unavailable to us because this material is located in St Petersburg University.

The main difference between the genera *Ptyctodus* and *Rhynchodus*, clearly visible in the material from the Holy Cross Mountains, lies in the size and robustness of the jaws. We propose that the reason for this anatomical difference was prey preferences. Species of the genus *Ptyctodus* possessed much more robust dental plates with flat tritoral surfaces, while *Rhynchodus* had oblique tritoral surfaces, which were more suited for softer prey. The evidence to support this includes the fact that specimens of *Ptyctodus* are found only in granular limestones associated with crinoids and large brachiopods, while *Rhynchodus* occurs in quasi-pelitic limestones with a sparse fauna of small brachiopods. It would be useful to analyze such distribution in other regions with different facies types.

The occurrence of ptyctodonts in the Lower and Upper Kellwasser in Płucki provides an addition to the benthic placoderm (and vertebrate) taxa, which had previously been represented solely by antiarchs (Szrek 2004). The co-occurrence of numerous bivalves, brachiopods and trilobites (Szrek and Salwa 2020) supports the presence of durophagous fishes in this fauna. In other sites, ostracods have been recovered from the stomach area ptyctodonts and mud from antiarchs, further supporting these taxa as durophagous (Stensiö 1948; Denison 1978; Trinajstic and Roelofs 2022; Lebedev et al. 2022).

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### Author contributions

K. Grygorczyk and P. Szrek collected undescribed specimens, and together with O. Wilk designed the project and analyzed the data. Grygorczyk drafted the manuscript. All authors edited the manuscript.

## References

Czarnocki, J. 1947. Przewodnik XX zjazdu Polskiego Towarzystwa Geologicznego w Górach Świętokrzyskich w 1947 r (Guide of the 20th Congress of the Polish Geological Society in the Holy Cross Mountains in 1947). Państwowy Instytut Geologiczny, 1–18.

Denison, R. 1978. *Placodermi. Handbook of Paleoichthyology, Vol. 2.* (Schultze, H.-P., ed.). Gustav Fischer Verlag, Stuttgart, New York.

Eastman, C. R. 1898a. Dentition of Devonian Ptyctodontidae. *The American Naturalist*, **32**(379), 473–488.

Eastman, C. R. 1898b. Dentition of Devonian Ptyctodontidae (Continued). *The American Naturalist*, **32**(380), 545–560.

Eastman, C. R. 1904. On the dentition of Rhynchodus and other fossil fishes. *The American Naturalist*, **38**(448), 295–299.

Eastman, C. R. 1907. *Devonic Fishes of the New York Formations*. New York State Education Department, Albany.

Gorizdro-Kulczycka, Z. 1934. Ptyctodontidae górnodewońskie z Gór Świętokrzyskich (Upper Devonian Ptyctodontidae from the Holy Cross Mountains). *Prace Polskiego Instytutu Geologicznego*, **3**, 1–38.

Gross, W. 1932. Die Arthrodira Wildungens. *Geologische und Palaeontologische Abhandlungen*, **19**, 5–61.

Ivanov, A. and Ginter, M. 1997. Comments on the Late Devonian placoderms from the Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica*, **42**, 413–426.

Jaekel, O. 1903. Über Ramphodus nov. gen. einen neuen devonischen Holocephalen von Wildungen. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, **8**, 383–393.

Janvier, P. 1996. Early Vertebrates. In *Oxford Monographs on Geology and Geophysics*, **33**. Clarendon Press, Oxford.

Kulczycka, Z. 1933. Ptyktodonty górno-dewońskie z gór Świętokrzyskich (Upper Devonian ptyctodonts from the Holy Cross Mountains). *Posiedzenia Naukowe Państwowego Instytutu Geologicznego*, **36**.

Kulczycki, J. 1957. Upper Devonian fishes from the Holy Cross Mountains (Poland). *Acta Palaeontologica Polonica*, **02**(4), 285–380.

Lebedev, O. A., Johanson, Z., Kuznetsov, A. N., Tsessarsky, A., Trinajstic, K. and Isakhodzayev, F. B. 2022. Feeding in the Devonian antiarch placoderm fishes: a study based upon morphofunctional analysis of jaws. *Journal of Paleontology*, **96**(6), 1413–1430. https://doi.org/10.1017/jpa.2022.54

Liszkowski, J. and Racki, G. 1993. Ichthyoliths and deepening events in the Devonian carbonate platform of the Holy Cross Mountains. *Acta Palaeontologica Polonica*, **37**, 407–426.

Long, J. A., Trinajstic, K., Young, G. C. and Senden, T. 2008. Live birth in the Devonian. *Nature*, **453**, 650–652. https://doi.org/10.1038/nature06966

Long, J. A., Trinajstic, K. and Johanson, Z. 2009. Devonian arthrodire embryos and the origin of internal fertilization in vertebrates. *Nature*, **457**, 1124–1127. https://doi.org/10.1038/nature07732

Newberry, J. S. 1873. *Descriptions of Fossil Fishes.* Paleontology, **1**(P2). Geological Survey of Ohio, 245–355.

Ørvig, T. 1960. New finds of acanthodians, arthrodires, crossopterygians, ganoids and dipnoans in the Upper Middle Devonian calcareous flags (Oberer Plattenkalk) of the Bergisch Gladbach-Paffrath Trough. *Paläontologische Zeitschrift*, **34**, 295–335. https://doi.org/10.1007/BF02986872

Ørvig, T. 1980. Histologic studies of ostracoderms, placoderms and fossil elasmobranchs 4. Ptyctodontid tooth plates and their bearing on holocephalan ancestry: the condition of *Ctenurella* and *Ptyctodus*. *Zoologica Scripta*, **9**(1–4), 219–239.

Pander, C. H. 1858. *Über die Ctenodipterinen des devonischen Systems*. Saint Petersburg.

Racki, G., Racka, M., Matyja, H. and Devleeschouwer, X. 2002. The Frasnian/Famennian boundary interval in the South Polish–Moravian shelf basins: integrated event-stratigraphical approach. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **181**, 251–297.

Rakociński, M., Pisarzowska, A., Janiszewska, K. and Szrek, P. 2016. Depositional conditions during the Lower Kellwasser Event (Late Frasnian) in the deep-shelf Łysogóry Basin of the Holy Cross Mountains (Poland). *Lethaia*, **49**, 571–590. https://doi.org/10.1111/let.12167

Stensiö, E. 1948. On the Placodermi of the Upper Devonian of East Greenland. 2. Antiarchi: subfamily Bothriolepinae. With an attempt at a revision of the previously described species of that family. *Meddelelser om Grønland*, **139** (*Palaeozoologica Groenlandica*, 2), 635–661.

Szrek, P. 2004. The first articulated antiarch (Vertebrata, Placodermi) from the Upper Devonian of the Holy Cross Mountains (Central Poland). *Acta Geologica Polonica*, **54**, 401–406.

Szrek, P. 2020. Comments on distribution and taphonomy of Devonian placoderms in the Holy Cross Mountains, Poland. *Bulletin of Geosciences*, **95**, 231–39.

Szrek, P. and Salwa, S. 2020. High-energy events in the Frasnian–Famennian boundary interval of the Płucki section in the Holy Cross Mountains, Poland. *Facies*, **66**, 9. https://doi.org/10.1007/s10347-020-0593-0

Szulczewski, M. 1971. Upper Devonian conodonts, stratigraphy and facial development in the Holy Cross Mts. *Acta Geologica Polonica*, **21**(1), 1–129.

Szulczewski, M. 1973. Famennian–Tournaisian neptunian dykes and their conodont fauna from Dalnia in the Holy Cross Mountains. *Acta Geologica Polonica*, **23**, 15–59.

Szulczewski, M. 1995. Depositional evolution of the Holy Cross Mts. (Poland) in the Devonian and Carboniferous – a review. *Geological Quarterly*, **39**, 471–488.

Trinajstic, K. and Long, J. A. 2009. A new genus and species of ptyctodont (Placodermi) from the Late Devonian Gneudna Formation, Western Australia, and an analysis of ptyctodont phylogeny. *Geological Magazine*, **146**, 743–760. https://doi.org/10.1017/S001675680900644X

Trinajstic, K. and Roelofs, B. 2022. Placodermi diet. In *Encyclopedia of Animal Cognition and Behavior* (Vonk, J. and Shackelford, T. K., eds). Springer, Cham. https://doi.org/10.1007/978-3-319-55065-7_1175

Trinajstic, K., Boisvert, C., Long, J. A., Maksimenko, A. and Johanson, Z. 2015. Pelvic and reproductive structures in placoderms (stem gnathostomes). *Biological reviews of the Cambridge Philosophical Society*, **90**(2), 467–501. https://doi.org/10.1111/brv.12118

Watson, D. M. S. 1938. On *Rhamphodopsis*, a ptyctodont from the Middle Old Red Sandstone of Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **59**, 397–410.

Woodward, A. S. 1891. *Catalogue of the Fossil Fishes in the British Museum (Natural History)*, *Part II*. London.

Woroncowa-Marcinowska, T. 2006. Upper Devonian goniatites and co-occuring conodonts from the Holy Cross Mountains: studies of the Polish Geological Institute collections. *Annales Societatis Poloniae*, **76**, 113–160.

Woroncowa-Marcinowska, T. and Szrek, P. 2004. Zbiory Jana Czarnockiego w Muzeum Geologicznym PIG – nieustające źródło badań (Jan Czarnocki's collection at the Geological Museum PIG – a constant source of research). *Przegląd Geologiczny*, **52**, 638–639.