# Chondrichthyan fauna of the Frasnian–Famennian boundary beds in Poland

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New chondrichthyan microremains from several Frasnian–Famennian sections in the Holy Cross Mountains and Dębnik area (Southern Poland) are investigated and compared to previous data. The reaction of different groups of chondrichthyans to environmental changes during the Kellwasser Event is analysed. Following the extinction of phoebodont sharks of *Phoebodus bifurcatus* group before the end of the Frasnian, only two chondrichthyan species, viz. *Protacrodus vetustus* Jaekel, 1921 and *Stethacanthus resistens* sp. nov. (possibly closely related to "*Cladodus*" *wildungensis* Jaekel, 1921), occur in the upper part of Frasnian *Palmatolepis linguiformis* conodont Zone and persist into the Famennian. Global cooling is considered a possible cause of the extinction of Frasnian subtropical phoebodonts on Laurussian margins.

Key words: Chondrichthyes, Kellwasser Event, Devonian, Poland.

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## Introduction

Chondrichthyan faunas of the late *Palmatolepis linguiformis* and the *Palmatolepis triangularis* conodont zones on southern Laurussian margins substantially differ from those of the rest of the Frasnian and Famennian. The main difference is the absence of *Phoebodus*, a typical Mid- to Late Devonian pelagic, shelf dwelling shark (Ginter and Ivanov 1992). Therefore, the latest Frasnian–earliest Famennian gap in the Devonian phoebodont-based ichthyolith zonation (Ginter and Ivanov 1995; see also Ginter in Weddige 1997: column B700ds97) is called a "non-phoebodont interval". Other late Frasnian chondrichthyans, such as protacrodonts, characterised by crushing teeth, and cladodont-toothed stethacanthids, survived the Kellwasser biotic crisis quite well, and without notable changes persisted well into the Famennian. Protacrodonts and stethacanthids from the Frasnian–Famennian boundary beds were hitherto described from the South Urals and the Holy Cross Mountains (Ginter and Ivanov 2000), Moravia (Ginter 1991), and Kuznetsk Basin (Ivanov et al. 1992). This paper adds new data on sharks from the Kellwasser time and shortly after, based on the recently collected material from the Holy Cross Mountains and the Cracow Upland (southern Poland).

Specimens are housed in the following institutions: Institute of Geology, Warsaw University (abbreviated IGPUW) and the Institute of Palaeobiology, Polish Academy of Sciences (abbreviated ZPAL) in Warsaw.

## Characteristics of the localities

Three sections spanning the Frasnian–Famennian boundary were sampled bed by bed (for location of most samples, see Racka 2000): the middle wall of the Kowala–Wola Quarry in the south-western Holy Cross Mts, south of Kielce; an artficial trench on the eastern bank of Łagowica River, between the village of Płucki and the town of Łagów, eastern Holy Cross Mts; and a ditch (Z-17) in a wood close to Dębnik, north-west of Cracow (Fig. 1). The sections studied consist of various carbonate rocks, representing deep intrashelf basins (Kowala, Płucki) or the slope of a carbonate platform (Dębnik). Stratigraphic condensation or substantial hiatuses, such as the absence of the Early *Pa. triangularis* conodont Zone, characteristic of many other South Poland localities (Szulczewski 1989; Racki and Baliński 1998), were not observed here.

**Kowala**.—In the Kowala–Wola Quarry fish microremains (ichthyoliths) were recorded from marly limestones and shales, with chert intercalations, of the H-3 and H-4 units of Racki and Baliński (1998), representing the later part of the *Pa. linguiformis* conodont Zone through the Late *Pa. triangularis* Zone. Chondrichthyan teeth and/or scales were obtained from the following samples: Ko-SF and Kx-12 (*Pa. linguiformis* Zone), Ko-24 (basal Early *Pa. triangularis* Zone), Ko-35 and Ko-36 (Late *Pa. triangularis* Zone).

**Płucki**.—Three samples collected from the trench in Płucki yielded ichthyoliths. Sample P-1 (J. Dzik collection) comes
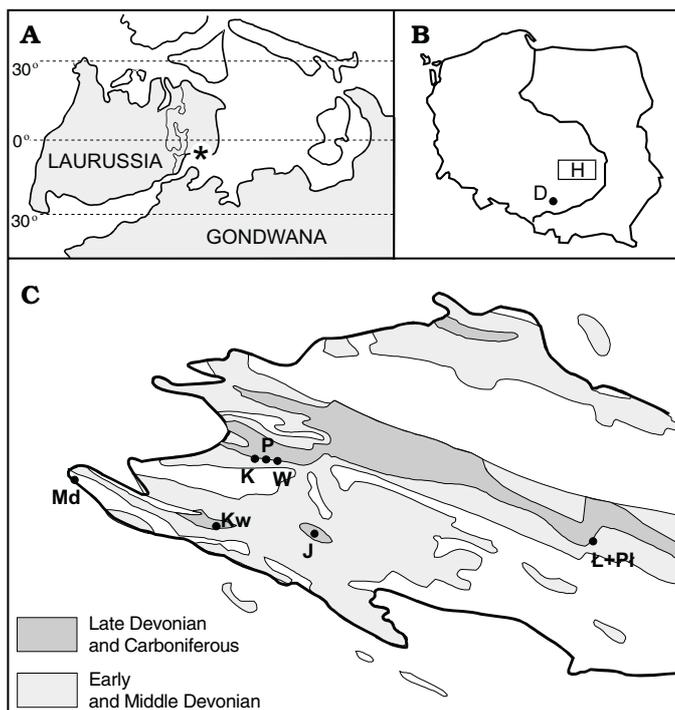
Fig. 1. **A**. Position of the study area (marked with asterisk) against a palaeogeographic reconstruction of the Late Devonian (after Scotese and McKerrow 1990, modified). **B**. Location of the Holy Cross Mountains (H) and Dębnik area (D) against a contour of Poland. **C**. Position of sections which yielded latest Frasnian–early Famennian chondrichthyan remains against a geological sketch map of western and central Holy Cross Mountains. J, Jabłonna; K, Kadzielnia; Kw, Kowala; Ł+Pł, Łagów and Płucki; Md, Miedzianka; P, Psie Górki; W, Wietrznia.

from an unknown position within a 30 cm thick, black cephalopod limestone layer of the latest *Pa. linguiformis* through the earliest Early *Pa. triangularis* age (bed 13 in Racka 2000). This layer, probably of local distribution, is the only example of typical Kellwasser Limestone facies in Poland. It is strongly fossiliferous, rich in goniatites, nautiloids, bivalves, entomozoacean ostracods (Olempska 2002) and conodonts, as well as arthrodire placoderms (Piotr Szrek personal communication 2000). Two other samples (M. Racka collection), whose age is determined as the Early *Pa. triangularis* Zone (Racka 2000), come from the top part of the lens described above (sample KW3 = sample 9 in Racka 2000) and overlying marly-nodular bed (sample KW4 = sample 10).

**Dębnik**.—Ichthyoliths were found from all samples from Dz-7 through Dz-19 (probable *Pa. linguiformis* through the Early *Pa. triangularis* zones) of the ditch Z-17. In this part of the section marly limestones intercalate with micritic, detrital and graded detrital limestones (Racka 2000). Chondrichthyan microremains occur in a 40 cm thick detrital limestone layer (samples Dz-13 and 14) and in the marly limestone just above (sample Dz-15), all of the Early *Pa. triangularis* age. Co-occurring brachiopods from ditch Z-17 are described by Baliński (2002, this volume).

**Other localities**.—Stratigraphy of the other Polish localities which yielded latest Frasnian or early Famennian chondrichthyan teeth and which I refer to herein, was thoroughly described by Szulczewski (1971: Kadzielnia, Psie Górki, Wietrznia) and Żakowa et al. (1983: Jabłonna); the material from the Miedzianka Hill comes from isolated samples collected from condensed limestones and dated by conodonts by Michał Szulczewski (personal communication 1989, samples M-5, M-EZ) and Grzegorz Racki (personal communication 1990, sample Md-I/1). The full list of ichthyoliths from these localities, all situated in the Holy Cross Mts, was presented by Ginter (1994).

# Material

## Chondrichthyans

**Teeth**.—Altogether, less than 40 teeth have been found thus far from the latest Frasnian *Pa. linguiformis* Zone and the early Famennian of the southern Poland (22 from Płucki, Kowala and Dębnik; Table 1). Apart from a few isolated specimens of *Phoebodus turnerae* Ginter and Ivanov, 1992 and "*Symmorium*" sp. from the *Palmatolepis rhomboidea* Zone, teeth of only two shark species occur in the material: a cladodont, assigned here as *Stethacanthus resistens* sp. nov. and a protacrodont, *Protacrodus vetustus* Jaekel, 1921.

**Scales and denticles**.—The collection of more than 40 chondrichthyan denticles (Table 1) is composed mainly of compound "ctenacanth" scales (Fig. 4A, B), minute mono- to tricuspid mucous membrane denticles and unusual branchial denticles, with a single or multiple, branching rows of odontodes on a thin, flat base (Fig. 5A, B). A variety of denticles from Płucki was illustrated by Ginter (1995: fig. 2C–G).

## Associated ichthyoliths

Microremains of osteichthyan origin: simple, conical actinopterygian teeth; rhomboid palaeoniscoid scales (Fig. 7C; Ginter 1995: fig. 3A–F); pieces of jaws and other bones (Fig. 7E); and striated sarcopterygian teeth (among them parasymphysial fangs of the onychodont *Strunius rolandi*; Fig. 7C) are the most common in the samples. Also very numerous (especially in P-1 sample of Płucki) are acanthodian scales with diamond-shaped, smooth and glossy crowns ("*Acanthodes*" type; Fig. 7A, B).

## Preservation

Microvertebrates from Płucki and Kowala are moderately well preserved, but in chondrichthyan teeth the cusps are often broken. Much worse is the state of the specimens from Dębnik: most of the teeth are broken and partly or totally devoid of ornamentation (Fig. 4C–I). The colour of ichthyoliths
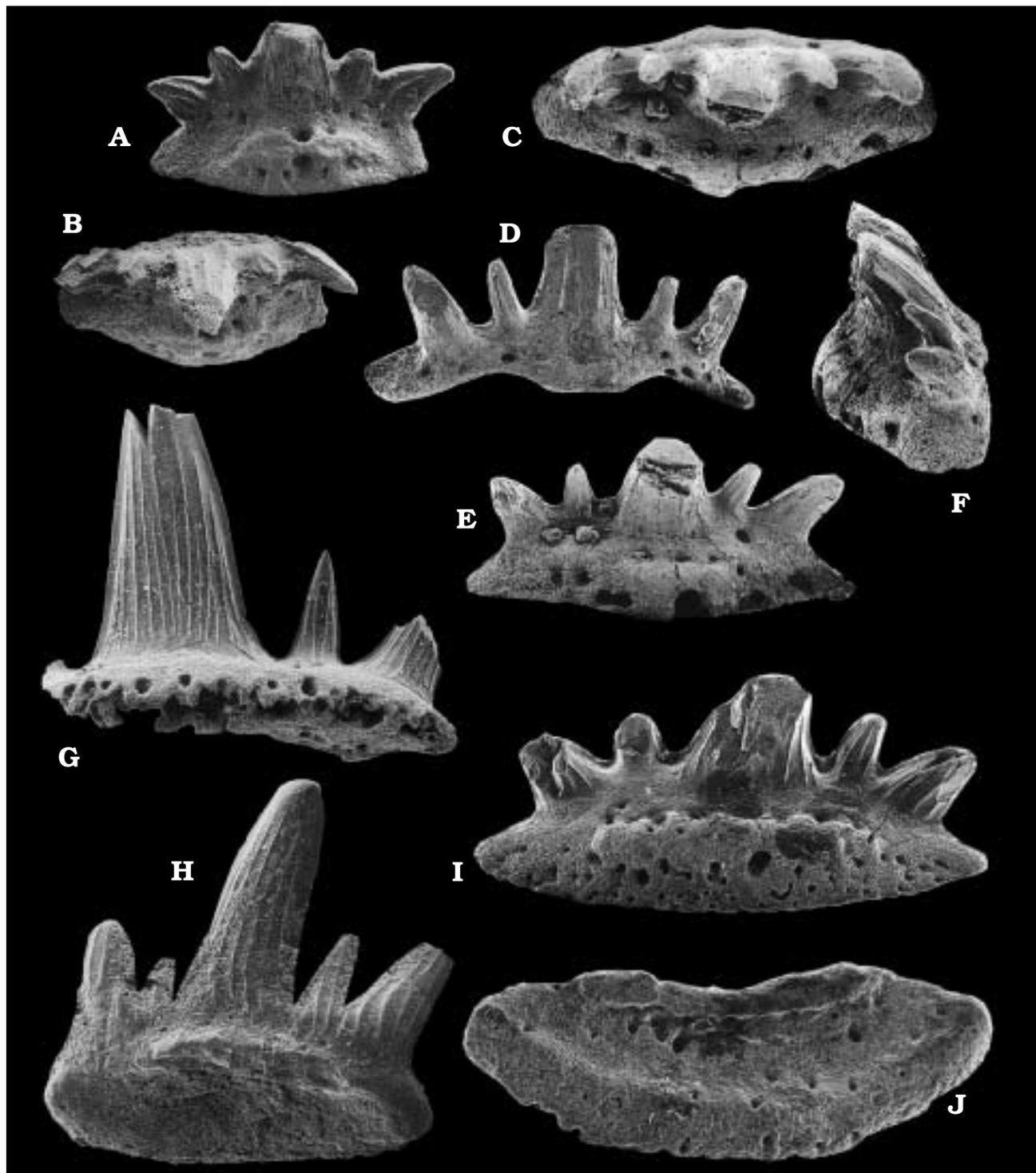
Fig. 2. *Stethacanthus resistens* sp. nov. **A**, **B**. IGPUW/Ps/1/215 from Miedzianka, sample M-EZ, Late *Pa. triangularis* Zone, lingual and occlusal views, × 40. **C–F**. Holotype, ZPAL P.IV/216 from Płucki, sample P-1, *Pa. linguiformis* Zone, occlusal, labial, lateral and lingual views, × 60. **G**. IGPUW/Ps/4/1 from Płucki, sample KWK3, Early *Pa. triangularis* Zone, lingual view, × 40. **H**. IGPUW/Ps/4/2 from Kowala, sample Kx-12, labial-basal view, × 27. **I**, **J**. IGPUW/Ps/1/216 and IGPUW/Ps/1/217 from Psie Górki, sample PG-T, *Pa. linguiformis* Zone, lingual and basal views, × 32 and × 40 respectively. All SEM micrographs.

is light-brown, with three exceptions: all the specimens from Płucki are completely black; the specimens from Dębnik, sample Dz-13, are white (the result of preparation?) or light brown; the specimens from Miedzianka (especially Md-I/1) are strongly recrystallised and haematitised, with many red spots.

Table 1. Distribution of chondrichthyan microremains and other ichthyoliths in Frasnian–Famennian boundary beds of Dębnik, Kowala, and Płucki sections.

| Sample number | Conodont zones | Stethacanthus resistens sp. nov. | Protacrodus vetustus | Chondrichthyan scaales/denticles | Acanthodian scales | Other ichthyoliths |
|---|---|---|---|---|---|---|
| **Dębnik** | | | | | | |
| Dz-19 | Early Pa. triangularis | | | | | + |
| Dz-18 | | | | | | + |
| Dz-17 | | | | | + | + |
| Dz-16 | | | | 1 | + | + |
| Dz-15 | | | | | + | + |
| Dz-14 | | 1 | | 6 | | + |
| Dz-13 | | 2 | | 13 | + | + |
| Dz-12 | | 5 | | 1 | + | |
| Dz-11 | Pa. linguiformis | | | | | + |
| Dz-10 | | | | | | + |
| Dz-9 | | | | | | + |
| Dz-8 | | | | | | + |
| Dz-7 | | | | | | + |
| Subtotal: | | 8 | 0 | 21 | | |
| **Kowala** | | | | | | |
| Ko-36 | Late | | | | + | + |
| Ko-35 | Pa. triang | 2 | | | | |
| Ko-24 | E. Pa. triang. | | | 6 | + | |
| Kx-12 | Pa. linguif. | 1 | | | | |
| Ko-SF | | 2 | 1 | | | |
| Subtotal: | | 5 | 1 | 6 | | |
| **Płucki** | | | | | | |
| P-1 | Pa. linguif. | 4 | 1? | 12 | + | + |
| KWK4 | E. Pa. triang. | 2 | | | + | |
| KWK3 | | 1 | | 2 | + | |
| Subtotal: | | 7 | 1 | 14 | | |
| Total: | | 20 | 2 | 41 | | |



Fig. 3. *Stethacanthus resistens* sp. nov., large tooth, IGPUW/Ps/4/3 from Kowala, sample Ko-SF, *Pa. linguiformis* Zone, basal (**A**) and labial (**B**) views, × 20. All SEM micrographs.

(articulation boss) is elongated laterally or subcircular, its margins are perforated by several nutritive foramina. Often the lingual median foramen is larger than the others, which makes the button look like a horizontal eight. The labio-basal thickening is single, undivided, usually rectangular and straight.

### *Stethacanthus resistens* sp. nov.

Figs. 2, 3, 4C–I, 5C.

*Stethacanthus* sp.; Ginter 1991: 75, pl. 8: 4, pl. 9: 2, 3.
*Cladodus* cf. *C. thomasi* Turner; Ivanov et al. 1992: 89, pl. 36: 3, 4.
*Stethacanthus thomasii* Turner [sic]; Derycke 1992: 39–40, fig. 14, pl. 2: 10, 11.
*Stethacanthus* cf. *thomasi* (Turner); Ginter 1995: fig. 2A.
"symmoriid with button partially divided"; Ginter and Ivanov 1996: fig. 4C.
"stethacanthid?"; Ginter and Ivanov 1996: fig. 5C, D.
*Stethacanthus* cf. *thomasi* (Turner); Ginter and Ivanov 2000: pl. 1: J.

*Holotype*: Specimen ZPAL P.IV/216 from the Holy Cross Mts, Płucki near Łagów, sample P-1, latest Frasnian, *Palmatolepis linguiformis* conodont Zone; Fig. 2C–E.

*Etymology*: Latin *resistens*, resistant.

*Material*.—27 specimens: eight specimens from Dębnik (samples Dz-13, 14, 15, Early *Pa. triangularis* Zone), five specimens from Kowala (samples Ko-35, Late *Pa. triangularis* Zone; Kx-12, and Ko-SF, *Pa. linguiformis* Zone), seven specimens from Płucki (samples KWK3 and KWK4, Early *Pa. triangularis* Zone, and P-1, *Pa. linguiformis* Zone), three specimens from Kadzielnia (samples K-150, K-151, *Pa. rhomboidea* Zone; K-164, Early or Middle *Palmatolepis crepida* Zone), two specimens from Psie Górki (sample PG-T, *Pa. linguiformis* Zone), and two specimens from Miedzianka (samples M-5, M-EZ, Late *Pa. triangularis* Zone).

## Systematic account

**Class Chondrichthyes Huxley, 1880**
**Order Symmoriida Zangerl, 1981**
**Family Stethacanthidae Lund, 1974**
**Genus *Stethacanthus* Newberry, 1889**

*Type species*: *Physonemus altonensis* St. John and Worthen, 1875.

*Remarks*.—Stethacanth teeth have cladodont-type crowns which means that the central cusp is the longest. The cusps are ornamented on both sides with numerous, subparallel, distinct cristae. In five-cusped specimens, which are the most common, the outer lateral pair of the cusps is higher and thicker than the intermediate ones. The lingual button
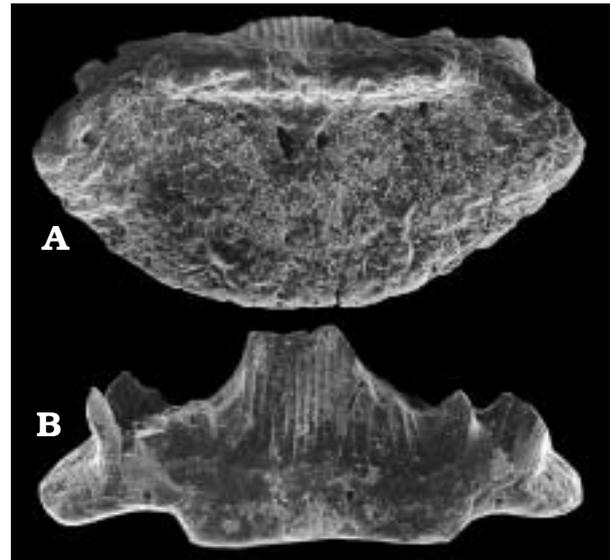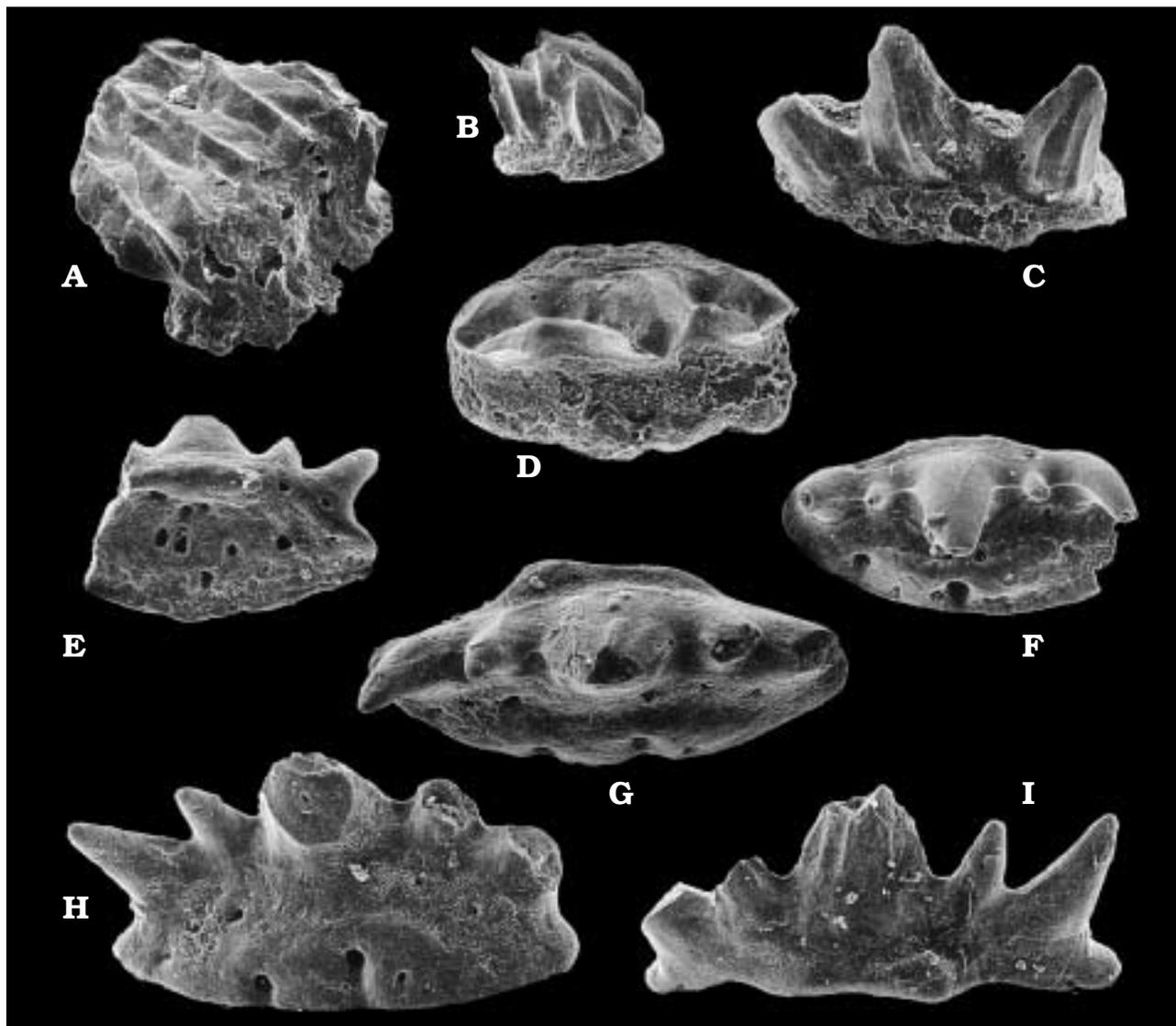
Fig. 4. Chondrichthyan microremains from Dębnik, sample Dz-13, Early *Pa. triangularis* Zone. **A**, **B**. "Ctenacanth-type" scales, IGPUW/Ps/4/4 and IGPUW/Ps/4/5. **C–I**. *Stethacanthus resistens* sp. nov. teeth. **C**, **D**. Problematic tricuspid tooth, IGPUW/Ps/4/6, labial and occlusal views. **E**. IGPUW/Ps/4/7, basal view. **F**. IGPUW/Ps/4/8, occlusal view. **G–I**. IGPUW/Ps/4/9, occlusal, lingual and labial views respectively. All × 80. All SEM micrographs.

*Diagnosis*.—Stethacanth teeth with no more than five cusps in the crown. The angle between the outer lateral cusps is large, almost 90°. The base is lenticular, elongated mesio-distally, with lateral angles usually extending far beyond the foot of the crown. The button and the corresponding labio-basal thickening are mesio-distally elongated and distinct.

*Description*.—The variation of *S. resistens* sp. nov. teeth is not very high. It concerns mainly the shape and dimensions of the button, whose mesio-distal to labio-lingual dimension ratio may vary from 2:1 to 5:1, and which may have a form of a straight or slightly curved ridge (Fig. 2I) or of a horizontal eight (due to perforations, Fig. 2A). Corresponding to the button outline, the shape of the labio-basal thickening varies: when the button is more oval, the projection is short (Fig. 2D, H), and when the former is elongated, so is the latter (Fig. 2J,

3). Consequently, curved buttons require curved, labially concave, projections (Fig. 2J).

The mesio-distal dimension of the base of *S. resistens* teeth from Polish collections varies from 0.5 to 3.6 mm. Bigger specimens have a larger number of cristae on the labial and lingual faces of the median cusp (up to 11–12 on each side; Figs. 2G, 3B) than the smaller ones (in some cases less than seven; Fig. 2D, E). In the latter, the cristae seem to be more prominent compared to the size of a cusp.

There is a single tricuspid specimen in the material from Dębnik, sample Dz-13 (Fig. 4C, D). Although typical teeth of *S. resistens* have five cusps, the lack of intermediate, smaller cusplets in some teeth is rather usual as a variation in stethacanths (see Zidek 1993: fig. 2A and C). Therefore, the specimen is tentatively included here in *S. resistens*.
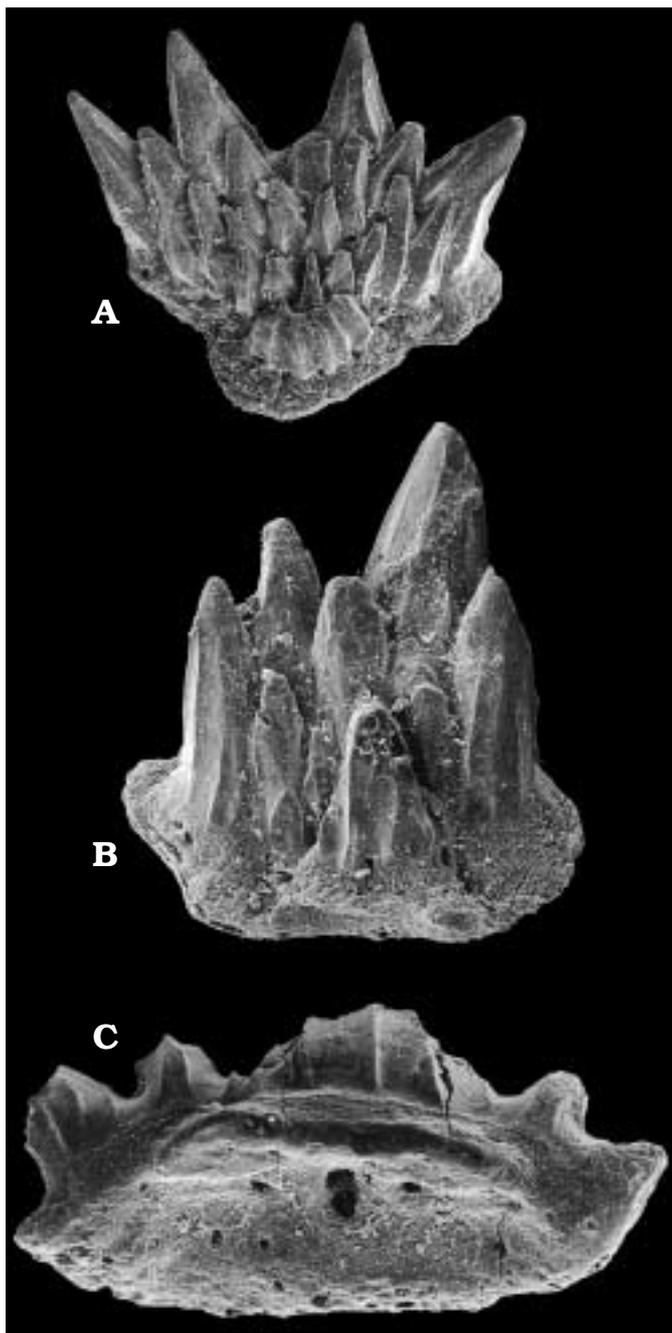
Fig. 5. Chondrichthyan microremains from Płucki. **A**, **B**. Branchial denticles?, IGPUW/Ps/4/10 and IGPUW/Ps/4/11, sample KWK3. **C**. *Stethacanthus resistens* sp. nov. tooth, IGPUW/Ps/4/12, sample KWK4, basal-labial view. All × 60. All SEM micrographs.

*Remarks*.—The Late Devonian *Stethacanthus resistens* sp. nov. is very close to the Early Carboniferous *S. thomasi* (Turner, 1982). The only difference is the number of lateral cusps; in *S. resistens* sp. nov. there are no more than two cusps on each side, and the number of cusps in *S. thomasi* is usually greater, sometimes different on each side (Turner 1982: figs. 6C, 8J; Ginter 1995: fig. 5E). *Stethacanthus* cf. *altonensis* from the lower Chesterian (= late Viséan) of Caney Shale, Oklahoma (Zidek 1993: fig. 2A–D) is another

very similar form. However, two differences may be pointed out: first, the base of *S*. cf. *altonensis* is more lingually extended than that of *S. resistens* and therefore, its outline is rather triangular than lenticular; second, the angle between the lateral cusps of the younger form is much smaller. The problem with diagnosing *S. resistens* teeth is that their characters, although probably unique for the species in the late Frasnian and early Famennian, are general for the genus and they tend to repeat in younger stethacanthids in different configurations.

After having submitted the final version of the manuscript I had an opportunity to examine original specimens of "*Cladodus*" *wildungensis* Jaekel, 1921, in the Museum für Naturkunde der Humbodt-Universität, Berlin. These specimens come from a latest Frasnian Kellwasserkalk layer of Bad Wildungen, Germany. Teeth of the latter species, preserved as natural moulds together with well preserved jaws (Gross 1938), seem to be very similar to those of *S. resistens* sp. nov. This suggests that "*C.*" *wildungensis* and *S. resistens* are closely related or perhaps even conspecific, but further detailed morphological study is necessary before any taxonomic decision is taken. Thus far "*C.*" *wildungensis* used to be considered as a relative of either xenacathiforms (e.g., Maisey 2001) or ctenacanthoids (Coates and Sequeira 2001). However, in his recent study, Alexander Ivanov (personal communication 2002) suggested its stethacanthid affinity.

*Stratigraphic range in Poland*.—Frasnian–Famennian, *Pa. linguiformis–Pa. rhomboidea* zones.

*Distribution in the world*.—Russia (South Urals, *Palmatolepis rhenana*–?*Pa. rhomboidea* zones; Kuznetsk Basin, *Pa. triangularis* Zone), Morocco (Famennian), Moravia (*Pa. triangularis* through *Pa. crepida* zones).

## Cohort Euselachii Hay, 1902
## Superfamily Protacrodontoidea Zangerl, 1981
## Genus *Protacrodus* Jaekel, 1921

*Type species*: *Protacrodus vetustus* Jaekel, 1921.

### *Protacrodus vetustus* Jaekel, 1921
Fig. 6.

*Protacrodus vetustus* Jaekel; Gross 1938: 131–141, figs. 3–5, pl. 2.
*Protacrodus vetustus* Jaekel; Glikman 1964: fig. 20.
*Protacrodus vetustus* Jaekel; Zangerl 1981: 62, figs. 64, 65.
*Protacrodus* cf. *vetustus* Jaekel; Ginter 1991: 75, pl. 8: 5.
*Protacrodus* cf. *vetustus* Jaekel; Ginter 1995: figs. 2B [?], 4B.
*Protacrodus* cf. *vetustus* Jaekel; Ginter and Ivanov 2000: pl. 1F.

*Material*.—Six teeth from the Holy Cross Mts: one specimen from Kowala (sample Ko-SF, *Pa. linguiformis* Zone), two specimens from Wietrznia (samples W-37, Middle *Pa. crepida*, W-47, Late *Pa. triangularis* Zone), two specimens from Jabłonna (sample J-IIIs, Middle *Pa. triangularis* Zone), and one specimen from Miedzianka (sample Md-I/1, *Pa. crepida* Zone). Ginter (1995: fig. 2B) figured a *Protacrodus* tooth, allegedly the only specimen of this genus found thus far from Płucki (sample P-1, *Pa. linguiformis* Zone).
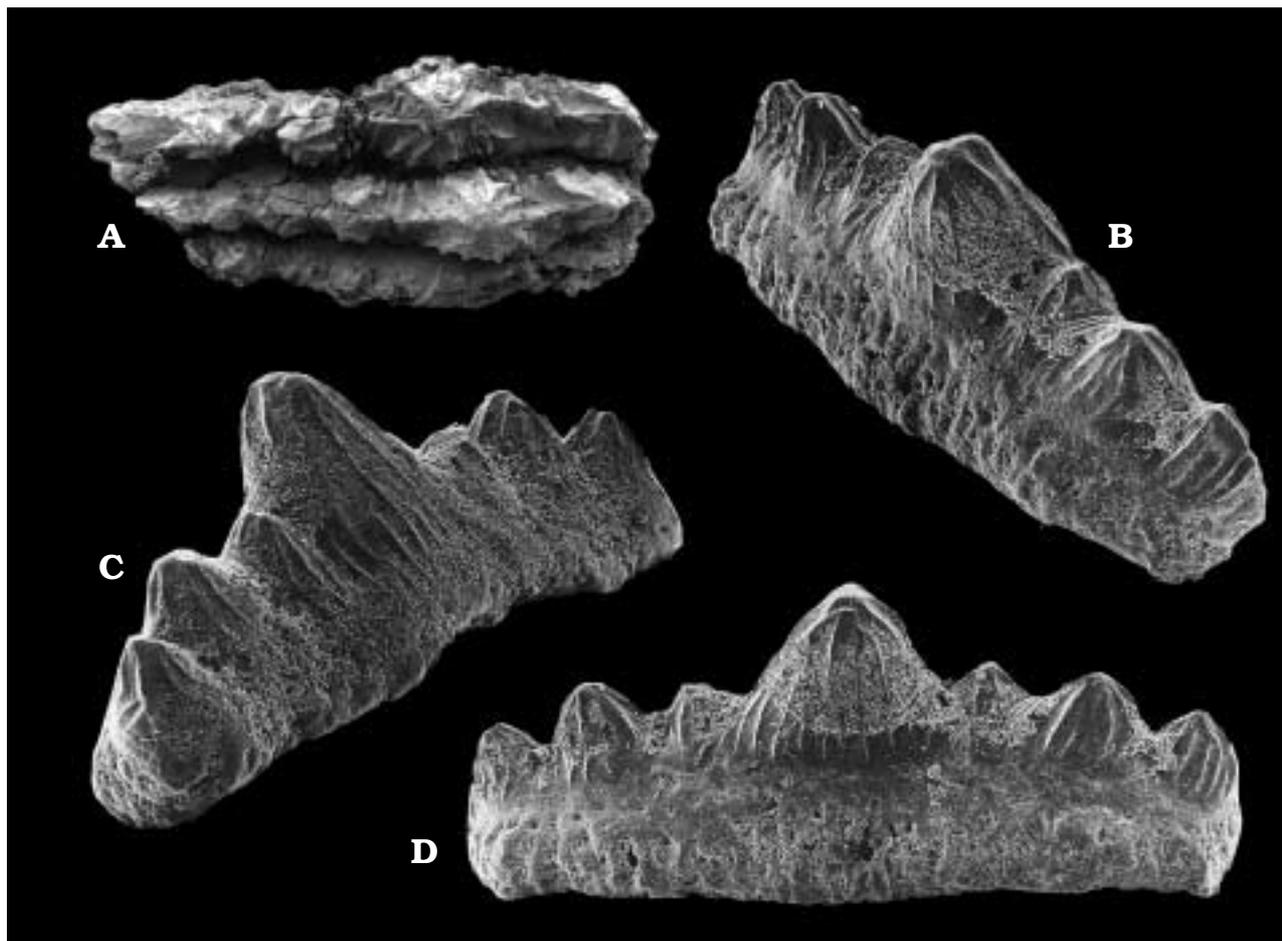
Fig. 6. *Protacrodus vetustus* Jaekel, 1921. **A**. Tooth-whorl composed of three teeth, right side incomplete, IGPUW/Ps/1/222, sample Md-I/1, Late *Pa. triangularis* Zone, occlusal view, × 30. **B–D**. Large, almost completely preserved tooth, IGPUW/Ps/4/13, sample Ko-SF, *Pa. linguiformis* Zone, oblique lingual, oblique labial and lingual views, × 17. All SEM micrographs.

Actually, that specimen might have come from some other sample and, therefore, the occurrence of protacrodonts in Płucki remains uncertain.

*Description*.—Teeth of this form have pyramidal crowns, with the lower parts of the cusps fused together. The median cusp is subcircular in cross section and bears strong, straight or slightly wavy ridges, joining at the tip. The lateral cusps, usually three on each side, are smaller than the median cusp and generally similar in form. However, in some specimens they can be slightly labio-lingually compressed. There are also some differences in the relative height of the lateral cusps: in some forms (Fig. 6B–D) the cusps of the second lateral pair are higher than, and in the other, almost equal to those of the first pair.

The teeth have laterally elongated bases, almost without lingual extensions and lacking any articulation devices. Usually a horizontal row of irregular, large pores perforates the lingual and labial faces of the base, and another row of smaller, rounded foramina goes a little higher, along the crown-base interface (the best visible in Fig. 6D, left side). Possibly, the lower row of pores was used by the nutritive

vessels connecting the teeth in a tooth-whorl, and the vessels going directly from the covering soft tissue entered a tooth through the upper row of pores.

There are fragments of protacrodont tooth-whorls in the material from the Miedzianka Hill and Jabłonna. In the specimen from Miedzianka (Fig. 6A), bases of three teeth are fused together, with only very little overlapping. The teeth differ in size: the smallest (presumably the oldest) tooth is about 3/4 as high and wide as the largest (youngest) one. This suggests that the tooth replacement in *P. vetustus* was rather slow, and that these three teeth, or probably even more, were functional for crushing at the same time.

*Remarks*.—Protacrodont teeth described above (especially IGPUW/Ps/4/13, Fig. 6B–D) are generally similar to the teeth of the holotype of *P. vetustus* from Bad Wildungen (housed in the Museum für Naturkunde, Humboldt Universität, Berlin), thoroughly described and illustrated by Gross (1938) and then reillustrated by Zangerl (1981: figs. 64, 65). However, the teeth of the type specimen are rather uniform, all of them having conical lateral cusps without any labio-lingual compression. Thus, the teeth which possess slightly

flattened lateral cusps are assigned here only tentatively to *P. vetustus*. Later in the Famennian very similar teeth appear, but with all the cusps compressed, the median cusp included, and bent lingually. I have previously referred to them as *P.* cf. *vetustus* (Ginter 2000), but they probably belong to another species of *Protacrodus*.

*Stratigraphic range in Poland.*—Latest Frasnian–early Famennian, *Pa. linguiformis–Pa. crepida* zones.

# Chondrichthyans and the Kellwasser Event

In spite of extensive processing of conodont samples during recent years, the number of investigated teeth of chondrichthyan origin from the Frasnian–Famennian boundary beds in Poland is very low (less than 40 specimens), and so is the species diversity (apparently only two species). This low diversity and poor representation is in contrast to at least eight species found from the late Famennian. The absence of phoebodonts, whose teeth usually are the most numerous in the material from the older and younger rocks of this area (compare Liszkowski and Racki 1993; Ginter and Ivanov 2000) is one of the reasons of the situation observed. The phoebodonts were apparently highly vulnerable to the environmental changes related to the Kellwasser Event (Ginter and Turner 1999). However, it is difficult to find out which factor could have had the greatest influence on their partial extinction and/or migration, especially in the light of controversies concerning the extinction of the other faunal groups during that time interval and the nature of the Kellwasser Event itself (Copper 1998). The analysis of late Famennian pelagic shark assemblages in relation to facies (Ginter 2000) shows that the most favourable niche for phoebodonts was an open, moderately shallow to moderately deep shelf, with well oxygenated waters. Late Famennian protacrodonts, probably closely related to *P. vetustus*, are found mainly in the rocks of shallow water origin, while stethacanthids are uniformly distributed in all the analysed environments, from deep seas to slopes of peritidal carbonate platforms. The occurrence of stethacanthids and protacrodonts alone in the Frasnian–Famennian boundary beds might suggest that it was the shallowing of the basin that destroyed phoebodont communities. However, at least two of the sections described herein (Kowala and Płucki) do not represent shallow water facies, but moderately deep intrashelf basins. Therefore, changes in depth do not seem a direct cause of the phoebodont crisis. Similarly, the anoxic or hypoxic conditions which allegedly caused the development of typical, black Upper Kellwasser Limestone, were apparently present only in some parts of the region (Płucki). Moreover, protacrodonts, probably slow-moving bottom feeders which in the late Famennian did not enter areas characterised by a thick anoxic bottom water layer (e.g., Cleveland Basin; Williams 1990), were found from the latest Frasnian of Bad Wildungen, Germany (Gross
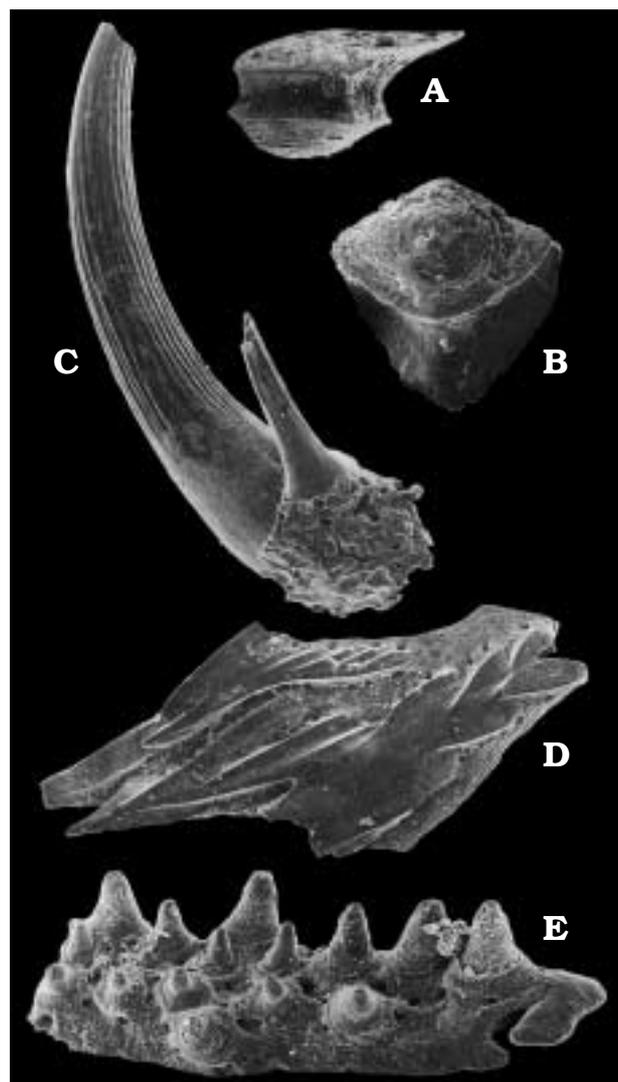


Fig. 7. Non-chondrichthyan ichthyoliths from the Frasnian–Famennian boundary beds. **A**. Acanthodian scale, ZPAL P.IV/313, from Płucki, sample P-1, *Pa. linguiformis* Zone, lateral view, × 90. **B–E**. Specimens from Dębnik, sample 13, Early *Pa. triangularis* Zone. **B**. Acanthodian scale, IGPUW/Ps/4/14, basal view, × 80. **C**. Sarcopterygian *Strunius rolandi*, parasymphysial tooth, IGPUW/Ps/4/15, lateral view, × 40. **D**. Actinopterygian scale, IGPUW/Ps/4/16, × 60. **E**. Osteichthyan jaw fragment, IGPUW/Ps/4/17, × 60. All SEM micrographs.

1938), from the uppermost part of the *Pa. linguiformis* Zone in Poland (Kowala, possibly Płucki), as well as from the Middle *Pa. triangularis* Zone (Jabłonna). Thus, when the conditions of epibenthic life were favourable enough to provide oxygen (and shelly prey) for protacrodonts, it seems unlikely that the phoebodonts, living higher in water column, suffered from its insufficiency.

The long lasting disappearance of *Phoebodus* from the margins of southern Laurussia (the *Pa. linguiformis* through Latest *Pa. crepida* zones) is even more enigmatic when we compare it with the other groups of ichthyofauna. It seems that all taxa of acanthodians, palaeoniscoid-like actinopterygians and struniiform sarcopterygians (distribution of

placoderms is still only superficially known) which lived here before the Event persisted into the Famennian. So, no simple cause can be applied to this problem. The crisis in phoebodonts must have been a result of a coincidence of negative factors which influenced their special mode of life or their prey. However, it is interesting that the "non-phoebodont gap" is apparently longer in the areas between the Laurussia and NW Gondwana than on the north-eastern (Urals) and northern (Canada) rims of the former (see reconstruction in Fig. 1A). In the latter two regions, the earliest Famennian phoebodonts were found from the Late *Pa. triangularis* Zone and from the Early *Pa. crepida* Zone, respectively (Ginter and Ivanov 2000; Ginter and Turner 1999), that means, at least three conodont zones earlier than in Poland. This might support the idea that global cooling, proposed by Copper (1998) as the most probable cause of the extinction of atrypid brachiopods by the end of the Frasnian, should be taken into account as well. It is possible that late Frasnian phoebodonts (*Ph. bifurcatus* group) were extremely stenotermic, warm water-dependent animals, which could not survive sudden cooling of subtropical areas. A new wave of cold-resistant phoebodont species (*Ph. typicus* group) could then have come from northern seas during the early Famennian, gradually migrating southward, adapting to new conditions and step by step refilling old phoebodont niches on Laurussian and NW Gondwanan shelves.

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