

MIDDLE PALAEOZOIC CHONDRICHTHYANS AND THE ASSOCIATED ICHTHYOFAUNA FROM SOUTHERN POLAND: A REVIEW

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Abstract: During the last sixty years, large collections of ichthyofauna, mainly isolated, microscopic, skeletal remains (ichthyoliths), from the Middle–Upper Devonian and Lower Carboniferous rocks of southern Poland have accumulated in the hands of Polish palaeontologists and in palaeontological institutions. Some parts of these collections were described in unpublished dissertations and others were published in dispersed papers, dealing mostly with selected regions or taxa. This review summarises the available data from the following regions: the Holy Cross Mountains, the Cracow Upland, the Sudetes and the Lublin Coal Basin (in the latter two cases, single localities). Altogether, 29 chondrichthyan species were identified and a few more still require classification. Of the Sarcopterygii, three species of onychodontiforms and one of the actinistians were found, in addition to a collection of dipnoans that was described much earlier. A few morphological types were distinguished among actinopterygian scales; otherwise the actinopterygian fossils are not referred to any lower-level taxon, and the same applies to the acanthodians. There were several attempts in the past to apply Polish ichthyoliths in biostratigraphy and palaeoecology, but after all these years, it appears that such propositions have only limited significance.

Key words: Chondrichthyes, Osteichthyes, Devonian, Carboniferous, Poland.

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INTRODUCTION

The following review is dedicated mainly to chondrichthyan remains from the carbonate facies of the Middle Devonian to Lower Carboniferous of the Holy Cross Mountains and a few isolated localities in southern Poland. The Chondrichthyes predominated in the Devonian/Carboniferous seas of the study area and left the most diverse assemblages of fossils. However, isolated microfossils of actinopterygians, sarcopterygians and acanthodians (mostly teeth and scales) are often found in the chondrichthyan-bearing samples studied as accessory material and will be briefly described here, too. A review of placoderms, another important group in the Middle–Late Devonian of Poland, will be presented in detail in a separate monograph.

The paper is organised in the following way. First, the geographic location (Fig. 1), geology and age of the most important sites and horizons are briefly described. Then,

a systematic review of each vertebrate group is presented, showing its distribution and evolution in this area. Finally, the significance of Polish Middle Palaeozoic ichthyofauna to biostratigraphic and palaeoecological studies is discussed. In the Appendix, there is a list of samples collected from Polish localities, with the names of fish taxa identified at each of them and the probable dating. All the datings in the paper, unless otherwise stated, are based on the Standard Conodont Zonation.

The authors hope that such a comprehensive review will be helpful for future students of Palaeozoic vertebrates, because thus far all the information was dispersed in isolated publications and unpublished dissertations. The authors also hope that the ongoing works on the revision of the materials from the Lower Devonian and Silurian will soon complete the picture of the Middle Palaeozoic vertebrate fauna of Poland.

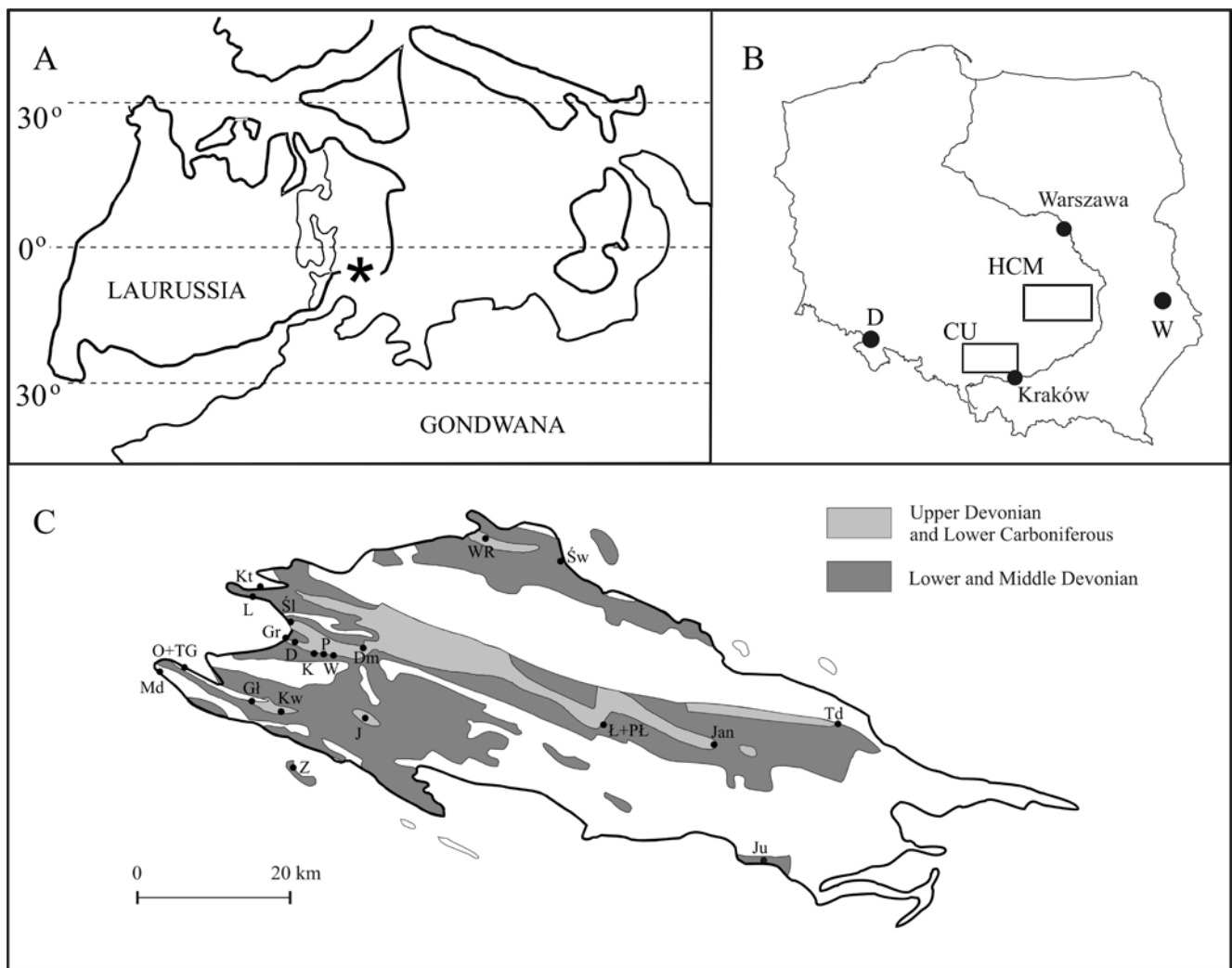


Fig. 1. Location maps. **A.** Position of the territory of Poland (marked with asterisk) against a palaeogeographic reconstruction of the Late Devonian (after Scotese and McKerrow, 1990, modified). **B.** Location of the Holy Cross Mountains (HCM), Cracow Upland (CU), Dzikowiec in Sudetes (D) and Włodawa in the Lublin Coal Basin (W) in relation to an outline of Poland. **C.** Position of studied sections in the Holy Cross Mountains. D – Dálnia, Dm – Domaszowice, Gł – Góra Łgawa, Gr – Grabina, J – Jabłonna, Jan – Janczyce, Ju – Jurkowiec-Budy, K – Kadzielnia, Kw – Kowala, L – Laskowa; L+PL – Łągów and Plucki, Md – Miedzianka, O+TG – Ostrówka and Todowa Grząba, P – Psie Górkę, Śl – Ślichowice, Św – Świętomarz, Td – Tudorów, W – Wietrzna, WR – Wzdół Rządowy, Z – Zbrza.

MATERIALS AND REPOSITORY

The major source of the material analysed in this paper is the collections accumulated during the preparation of three works: the Ph.D. dissertation by Ginter (1994) and the M.Sc. theses by Durska (2001) and Wilk (2018). The specimens used in those unpublished studies were recovered from rocks personally by the authors or obtained from other researchers, particularly those who had searched for conodonts at Polish Devonian and Carboniferous sites. Parts of these materials were published in the following papers: Ginter (1990, 1995, 2002, 2004), Ginter and Ivanov (1992, 1995a, b, 1996, 2000), Ivanov and Ginter (1996), Ginter and Turner (2010), Ginter *et al.* (2010, 2015), Turner and Ginter (2018), Ginter and Złotnik (2019). The other part of the collection was the result of scientific cooperation with a few Polish scientists: Ginter and Piechota (2004), Ginter and Niedźwiedzki (2019), Ginter and Skompski (2019); also the

specimens published in earlier studies (Kulczycki, 1957; Racki, 1985; Liszkowski and Racki, 1993) were re-examined. The collection was completed during the field and laboratory works of Polish National Science Centre (NCN) Project 2016/23/B/ST10/03262 (2017–2019).

The specimens were generally obtained by the acid leaching of carbonate rocks, sieving, and then picking them out of the residues. Many specimens, especially those from the samples collected in the years 1970–1990, were a by-product of the search for conodonts, fortunately preserved by careful researchers, especially Professors Michał Szulczewski and Stanisław Skompski (Faculty of Geology, University of Warsaw), Jerzy Dzik (Institute of Palaeobiology, Polish Academy of Sciences) and Grzegorz Racki (Faculty of Natural Sciences, University of Silesia in Katowice, Sosnowiec). All the collections mentioned above were re-studied, the taxonomy of the specimens was updated in relation to current knowledge and a few crucial

forms were re-illustrated, using the SEM at the Institute of Palaeobiology, Polish Academy of Sciences, in Warsaw.

Institutional abbreviations: GIUS, University of Silesia in Katowice, Sosnowiec, Poland; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland; and MWGUW, Museum of the Faculty of Geology, University of Warsaw, Warsaw, Poland.

THE GEOLOGY OF THE MAIN LOCALITIES

The Holy Cross Mountains

Kielce Region, western part

Góra Laskowa (Laskowa Hill): An active quarry on a hill north of the village Laskowa, near Kostomłoty, north-west of Kielce, displaying mainly dolomitised, massive Givetian limestones (Racki, 1985, 1993). Fish microfossils were recovered from the Middle *Po. varcus* through to *K. disparilis* conodont zones (Ginter, 2004).

Slichowice: A large quarry, now a protected rock reserve, in the western part of Kielce, displaying a fold, formed of Upper Devonian limestones and shales (Szulczewski, 1971). A few chondrichthyan teeth and scales were found in the lower Famennian Middle *Pa. triangularis* and *Pa. crepida* Zone.

Dalnia Hill: The only positive sample (i.e., containing fish microfossils) from the Dalnia Hill (Szulczewski, 1973, table 1, sample f; Ginter, 1990) was taken from the condensed limestone, filling a neptunian dyke within massive Givetian–Frasnian stromatoporoid-coral limestones. The conodonts found in the sample show condensation at least from the upper *Pa. expansa* Zone to the Tournaisian *S. crenulata* Zone.

Wietrznia: A large exposure, comprising three joined, inactive quarries in the south-eastern part of Kielce. The quarry is now protected and a palaeontological museum was built at its margin. The profile comprises partly dolomitised late Givetian to Frasnian detrital limestones at the bottom, covered with massive, micritic Frasnian/Famennian pelagic limestones. The Devonian section ends with Famennian thin-bedded, marly limestones intercalated with marly shales (Szulczewski, 1971, 1989). The ichthyoliths were found in more than forty samples, from the early Frasnian *M. falsiovalis* Zone to the early Famennian Middle *Pa. crepida* Zone, but the occurrences of chondrichthyan teeth begin only in the middle Frasnian (Ginter, 2004).

Kadzielnia: An inactive, protected quarry in the southern part of Kielce, exposing a Frasnian carbonate mud-mound, covered with uppermost Frasnian detrital limestone and Famennian thin-bedded, marly limestones, intercalated with marly shales (Szulczewski, 1971, 1981). Numerous ichthyoliths, but mainly of osteichthyan origin, were collected from the *Pa. hassi* to the *Pa. rhomboidea* Zone.

Psie Górki: A few limestone rocks on a hill south of the centre of Kielce (Szulczewski, 1971). The outcrop yielded a few chondrichthyan microfossils from the Frasnian–Famennian boundary beds, *Pa. linguiformis* and Early *Pa. triangularis* Zone (Ginter, 2002).

Karczówka: A now nonexistent outcrop of Frasnian limestones on a slope of Karczówka Hill in Kielce (Żaba,

1973) yielded a relatively rich collection of *Phoebodus bifurcatus* specimens (16 teeth; Ginter and Ivanov, 1992) and several sarcopterygian teeth, dated as the *rhenana* Zone. Unfortunately, the phoebodont teeth apparently had internal fissures and almost all have crumbled into minute pieces owing to the changing conditions in the collection room.

Kowala-Wola Quarry: In the Kowala-Wola Quarry, south of Kielce, the whole section represents deep, intrashelf, basal facies, from the Frasnian to the lowermost Carboniferous. Fish microremains were recorded mainly from marly limestones and shales, with chert intercalations, of the H-3 and H-4 units of Racki and Baliński (1998), representing the upper part of the *Pa. linguiformis* Zone through to the Late *Pa. triangularis* Zone (Ginter, 2002). A holocephalian tooth was recovered from the *Pa. trachytera* Zone (Ginter and Piechota, 2004) and a few cladodont teeth were found as high as the *Pa. expansa* Zone.

Jabłonna: The profile of the Devonian section at Jabłonna (Borków Syncline, south-west of Kielce) during its exploration comprised about 30 layers of Frasnian and Famennian calcirudites and micritic limestones (Żakowa *et al.*, 1983). The fish-bearing samples were collected from the Famennian part, between the *Pa. triangularis* and *Pa. postera* zones (Ginter, 2002).

Góra Łgawa (Łgawa Hill) – Jaźwica: A large quarry near the town of Chęciny, south-west of Kielce, situated in Givetian–Frasnian stromatoporoid-coral massive limestones (Racki, 1981, 1993), covered with upper Frasnian and Famennian rhythmic, medium to thin-bedded limestones and shales. A sample from the set R of Racki (1981; upper Frasnian *Pa. rhenana* Zone) yielded a few cladodont teeth and numerous sarcopterygian remains.

Ostrówka: The huge Ostrówka Quarry in the Gałęzice region, in the westernmost part of the Holy Cross Mountains, is situated in Middle/Upper Devonian stromatoporoid-coral limestones, which thus far did not yield fish remains. However, on its northern flank a few beds of condensed, micritic thin-bedded limestones of middle to late Famennian age crop out. In different sections, the age span of this member is different, probably owing to the syndimentary tectonic block movements (Szulczewski *et al.*, 1996), but its longest, recorded, stratigraphic range was from the *Pa. marginifera* through to the *Pa. praesulcata* Zone. Numerous researchers were collecting and studying samples from these condensed limestones in the past, so a large number of chondrichthyan teeth (more than 200, mainly of the phoebodontiforms) and other microscopic fish remains have accumulated (Ginter, 1990, 1994, 2000; Durska, 2001; Wilk, 2018).

Todowa Grząba: On the northern edge of Ostrówka Quarry (see above), above the Famennian beds, there are remnants of a small hill, called Todowa Grząba. The hill is mostly composed of late Viséan crinoidal limestone, probably having slumped from a nearby carbonate platform into the deeper parts of the basin. From these rocks, thus far only one shark tooth fragment has been recovered: a crown of a *Ctenoptychius*-like petalodont. However, within the calcirudite sequence, there occur two thin layers (each no thicker than 10 cm) of autochthonous, dark, biomicritic limestone (wackestone), rich in phosphatic microfossils,

juvenile goniatites, and pelagic algae. The latter layers were first described and interpreted by Belka and Skompski (1988). Unfortunately, despite the abundance of conodonts and goniatites, precise dating has not been possible. The age of the biomicrite layers falls somewhere in the *Gnathodus bilineatus* Zone. The ichthyofauna (about 100 chondrichthyan teeth and scales, mainly of the falcetid origin, associated with numerous actinopterygian and acanthodian microremains) was described by Ginter *et al.* (2015).

Miedzianka: In the westernmost part of the Holy Cross Mountains, there is a small quarry, situated in Frasnian and Famennian limestones, formerly making up the high Miedzianka Hill. Ichthyoliths were found in the uppermost Frasnian (*Pa. linguiformis* Zone) to the middle Famennian (*Pa. rhomboidea* or *Pa. marginifera* Zone). Phoeobodonts occur in the uppermost part of this interval (Ginter and Ivanov, 1992), but in the Frasnian–Famennian boundary beds only the teeth of protacrodonts, ctenacanth and numerous remains of sarcopterygians were found.

Kielce Region – eastern part

Łagów: In the northern part of Łagów, a town 40 km east of Kielce, Famennian limestones and shales crop out in several places, but the best sites are situated on the western slope of Dule Gorge (a locality already described at the beginning of the 20th century by Sobolev, 1912) and on the other side of the hill, on the eastern side of Słupska Street. The limestones yielded numerous cephalopods and conodonts, and also well preserved ichthyoliths of various kinds. All of the collected ichthyoliths were recovered from the *Pa. marginifera* Zone (Wilk *et al.*, 2019).

Plucki: An artificial trench on the eastern bank of Łagowica River, between the village of Plucki and the town of Łagów. Three samples collected from Plucki yielded ichthyoliths (Ginter, 2002). Sample P-1 comes from an unknown position within a black cephalopod limestone layer of the latest *Pa. linguiformis* through earliest Early *Pa. triangularis* age, 30 cm thick. This layer, probably of local distribution, is the only example of typical Kellwasser Limestone facies in Poland. It is highly fossiliferous, rich in goniatites, nautiloids, bivalves, entomozocean ostracods and conodonts, as well as arthrodire placoderms. Two other samples (KWK 3 and 4), the age of which is determined as the Early *Pa. triangularis* Zone (Racka, 2000), come from the top part of the lens described above and an overlying, marly, nodular bed.

Tudorów: The only positive sample from the outcrop near Tudorów (Racki, 1993), a village south of Opatów, yielded eight chondrichthyan teeth, identified as *Phoeobodus bifurcatus* and *Ph. latus*. The age of the sample was determined as the late Frasnian *Pa. rhenana* Zone.

Łysogóry Region

Świętomarz: Sparse fish microremains have been found in limestones of the Middle Devonian (Givetian) Skąły Formation (the Sitka Coral-Crinoid Limestone Member and the Sierzawy Member), Świętomarz–Śniadka section, Bodzentyn syncline, Łysogóry Region, northern Holy Cross Mountains. The fish remains are associated with conodonts of the *hemiansatus* to *ansatus* zones. Thelodont scales of

Australolepis sp. come from the area of Śniadka village, from the samples dated as *Po. hemiansatus* to *Po. rhenanus/Po. varcus* zones (Turner and Ginter, 2018).

Lublin Coal Basin

A sample of late Viséan (V3a–c) limestone from the borehole Włodawa IG 4, east of Lublin, yielded a piece of a tooth and a few hundred well-preserved scales, comparable to those of *Glencartius costellatus* (Traquair, 1884) from Glencartholm, Scotland, UK. Most of the scales are typical, compound body scales of the ctenacanthid type (Ginter and Skompski, 2019). The investigated sample is represented by wackestone microfacies with a recrystallised matrix and sporadic endothyrid foraminifers, productid spines, ostracods, and gastropods.

Cracow Upland

Czatkowice: This large, active quarry is situated between Czerna and Czatkowice, the northern suburb of Krzeszowice, west of Kraków. The major part of the Tournaisian–Viséan carbonate sequence exposed in the quarry represents the carbonate ramp and platform environments. In the entire succession, there is only one lithological unit deposited in an intra-shelf basin and composed of graded, spiculitic limestones, named the Przy Granicy Quarry Formation (Appelt, 1998).

In the four positive samples, spanning the interval from Tournaisian *G. delicatus* through to Viséan *G. beckmanni* Zone, there were found more than 20 chondrichthyan teeth, belonging mostly to *Thrinacodus*, falcetids, and unidentified euselachians with protacrodont crowns (Ginter and Złotnik, 2019). There also occur several chondrichthyan branchial denticles, chondrichthyan, actinopterygian and acanthodian scales, and a piece of actinopterygian jaw. The state of preservation of the microfossils is rather poor.

Czerna: The village of Czerna extends on the slopes of the valley of the Czernka Stream, running roughly in the NW to SE direction, north of Krzeszowice. The eastern bank of the stream is currently largely covered by forest. However, a few decades ago, there were numerous outcrops of Mississippian limestones. Sample Cz-1 (Viséan, *G. bilineatus* Zone) was collected from a limestone layer cropping out not far from the road, at the beginning of a long escarpment, in the middle part of the valley. The vertebrate assemblage from this sample contains almost 30 chondrichthyan teeth (Ginter and Złotnik, 2019). In addition, there are chondrichthyan scales and numerous actinopterygian microfossils: scales, teeth, vertebrae and other bone fragments. The ichthyoliths are usually slightly broken, which indicates that they were deposited in an environment of moderate energy.

Boreholes north of Kraków: Belka (1985, 1987) described conodonts from a few boreholes between Olkusz and Sosnowiec. Among his samples, nine contained ichthyoliths. About 15 chondrichthyan teeth (mainly of phoeobodontids) were found from the interval between late Famennian *Pa. expansa* and Viséan *G. austini* Zone.

Dębnik: The quarry at Dębnik, north-west of Kraków, is famous for its black Frasnian limestones, e.g., used for

building churches in the area. However, ichthyoliths were found in a ditch excavated near the quarry (Ginter, 2002). They were recovered from all samples of the marly limestones intercalated with micritic, detrital and graded, detrital limestones (Racka, 2000; probable *Pa. linguiformis* through the Early *Pa. triangularis* zones). Chondrichthyan microremains occur in a detrital limestone layer 40 cm thick and in the marly limestone just above, all of Early *Pa. triangularis* age.

Sudetes

Dzikowiec: In an abandoned quarry on a slope of Wapnica Hill, there crop out about 60 m of Upper Devonian limestones, a thin layer of black clay and 1.5 m of Tournaisian *Gattendorfia* limestone from the deep part of a carbonate platform. The upper Famennian part of the profile yielded only two phoebodont teeth, but in the *Gattendorfia* limestone (sample Eb-N, collected by Dieter Weyer from Berlin, Late *S. duplicata*–*S. sandbergi* zones) an excellently preserved tooth of *Thrinacodus ferox* was found, associated with several teeth of a yet unidentified falcetid. Ginter and Niedźwiedzki (2019) also reported a ctenacanthid fin spine from the overlying clastic sediments of late Tournaisian or early Viséan age.

SYSTEMATIC PALAEOONTOLOGY

For the precise information concerning the material studied, sample numbers, names of taxa, quantity of specimens, and sample datings, see Appendix.

Class Chondrichthyes Huxley, 1880

Discussion on the term “Elasmobranchii”: Traditionally, most of the non-holocephalian groups of shark-like chondrichthyans used to be classified as Elasmobranchii. This practice originated from the point of view that the division between the lineages, leading to extant Elasmobranchii and Holocephali happened very early, perhaps in the Silurian. According to this concept, such early sharks as phoebodonts, xenacanth, ctenacanth, symmoriids and hybodonts, plus modern sharks and rays, were placed together within the Subclass Elasmobranchii, whereas orodonts, petalodonts, edestids, and cochliodonts, plus modern holocephalians (chimaeroids), were treated as the Subclass Euchondrocephali (e.g., Grogan and Lund, 2004). However, independent studies on the evolution of the dentition of Palaeozoic chondrichthyans (e.g., Ginter, 2005; Ginter *et al.*, 2010, p. 25, fig. 19) and on their neurocrania (Pradel *et al.*, 2011) showed that the common ancestor of modern sharks, rays and holocephalians must have existed much later, most probably in the Middle Devonian, and that several orders, previously understood as elasmobranchs, are in fact stem chondrichthyans. Maisey (2012) went as far as to restrict Elasmobranchii to Neoselachii, excluding not only Palaeozoic groups, but even Mesozoic hybodonts. Although the present authors do not accept the latter proposition in full (identifying Elasmobranchii with a wider group, i.e., Euselachii, including Neoselachii, Hybodontiformes and

certain Late Palaeozoic forms, such as *Sphenacanthus*, *Tristychius* and *Onychoselache*), it is certain that the conventional “Elasmobranchii” is a paraphyletic grouping and not a clade. Therefore, the authors do not use this term here at all, and consider the subtitle of the Handbook of Paleoichthyology, volume 3D, “Paleozoic Elasmobranchii: Teeth” (Ginter *et al.*, 2010) to be misleading, because only a very small part actually deals with true elasmobranchs.

Order Omalodontiformes Turner, 1997

Family Omalodontidae Ginter, Liao
and Valenzuela-Rios, 2008

Genus *Omalodus* Ginter and Ivanov, 1992

Type species: *Phoebodus? bryanti* Wells, 1944.

Remarks: This genus is the only Polish representative of an interesting and still insufficiently understood order of basal chondrichthyans, the omalodontiforms. The dentition in this group is composed of teeth, the bases of which are directed labially; this is unusual in Palaeozoic sharks, which mostly have lingually directed bases. The bases of omalodont teeth, forming a tooth-family overlap and probably were firmly connected to each other with soft tissue during the animal's life. Thus far, articulated specimens of *Omalodus* have not been found, but a well-preserved anterior portion of a skeleton of an Early Devonian omalodontiform *Doliodus* from Canada, studied with the use of CT-scan (Maisey *et al.*, 2014), revealed several interesting features. There is some monognathic heterodonty in the dentition: the anterior teeth have deeper bases and more symmetrical crowns than those in the postero-lateral position. The pectoral fins are supported with spines, as in acanthodians. Of course, it is unknown whether *Omalodus*, known mainly from the upper part of the Middle Devonian, retained these special characters.

Because of its phoebodont tooth-crown, with three principal, almost equal cusps (or with the median cusp somewhat smaller), *Omalodus* was initially referred to as *Dittodus* and placed within the xenacanth (Hussakof and Bryant, 1918) or tentatively as *Phoebodus* (Wells, 1944; Gross, 1973). Ginter and Ivanov (1992) noted the unusual, labial direction of the *Omalodus* base and because of that erected a new genus but decided to retain it in the family Phoebodontidae. Only later (Ginter, 1994; Turner, 1997) did it become evident that the form of the base separates *Omalodus* from *Phoebodus* at the higher systematic level and the shape of the crown is convergent.

Omalodus grabau (Hussakof and Bryant, 1918)

Fig. 2A, B

Material: Three teeth from the Holy Cross Mountains (Laskowa Hill), GIUS-4-412/106–8.

Description and remarks: The tooth crown is of phoebodont type (*sensu* Ginter *et al.*, 2010, p. 8–9) with the median cusp slightly smaller than the two lateral main cusps. Between the main cusps there occur very small, intermediate cusplets. All the cusps are slightly curved lingually, rounded in cross-section and lacking lateral carinae. The base is directed labially at an obtuse angle to the crown. The lingual side of the base is concave, and the labial is

gently convex. Below the crown-base interface, there is a row of minute foramina.

The teeth studied are symmetrical and their shape is regular, similar to those from Morocco (Hampe *et al.*, 2004), but in contrast to certain American specimens (e.g., Gross, 1973),

in which the number of intermediate cusps varies from side to side and the angles between the cusps are different.

Stratigraphic range: In Poland, Middle Devonian, Givetian, Middle–Late *Polygnathus varcus* Zone; worldwide, middle Givetian–lower Frasnian.

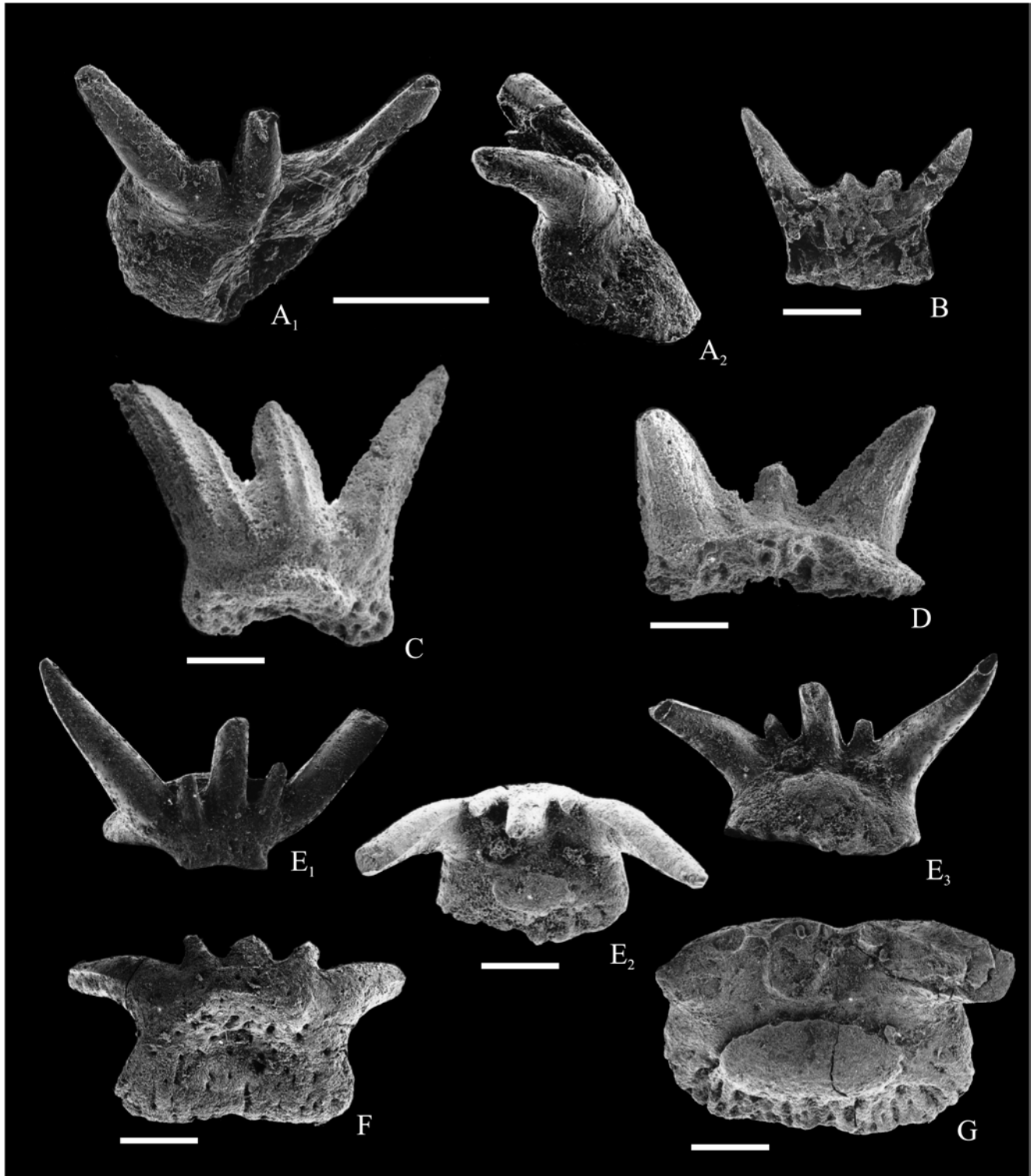


Fig. 2. Chondrichthyan teeth from the Middle Devonian of the Holy Cross Mountains. **A, B.** *Omalodus grabau* (Hussakof and Bryant, 1918) from Laskowa, sample L-II/a, Givetian, Middle–Late *varcus* Zone. A – GIUS-4-412/107 in oral and lateral views, B – GIUS-4-412/106 in labial? view. **C, D.** *Wellerodus* sp. from Wietrzna, sample W-68, late Frasnian, Early *rhenana* Zone. C – MWGUW/Ps/7/2 in labial view, D – MWGUW/Ps/7/1 in lingual view. **E, F.** *Phoebodus fastigatus* Ginter and Ivanov, 1992, from Laskowa, sample L-II/a, Givetian, Middle–Late *varcus* Zone. E – GIUS-4-412/101 in labial, oral and lingual views, F – GIUS-4-412/104 in aboral view. **G.** *Ph. sophiae* St. John and Worthen, GIUS-4-412/103, from Laskowa, sample L-II/a, Givetian, Middle–Late *varcus* Zone. Scale bars = 0.5 mm.

Order Antarctilamniiformes Ginter, Liao and Valenzuela-Ríos, 2008

Family Antarctilamnidae Ginter, Liao and Valenzuela-Ríos, 2008

Genus *Wellerodus* Turner, 1997

Type species: *Diplodus priscus* Eastman, 1899.

Remarks: The genus *Wellerodus* is known almost only from isolated diplodont teeth, found mainly in the Middle–Upper Devonian boundary beds of New York State, USA. These teeth are very similar to those of *Antarctilamna* Young, 1982, described on the basis of partly articulated specimens from Antarctica and Australia, but are characterised by a stronger median cusp and a more distinct orolingual button. Judging by the material of *Antarctilamna* and the specimens attributed to *Wellerodus* by Potvin-Leduc *et al.* (2015), the representatives of this genus most probably possessed dorsal fin spines.

Wellerodus sp.
Fig. 2C, D

Material: Three teeth from the Holy Cross Mountains (Wietrznia), MWGUW/Ps/7/1–3.

Description and remarks: The teeth have fairly well-preserved crowns, but with partly removed enameloid. The lateral main cusps are large, triangular, and labio-lingually compressed. The median cusp is smaller and reaches no more than a half of the height of the lateral ones. Remnants of spiral cristae are visible on the labial side of the larger specimen (MWGUW/Ps/7/2). The bases of the specimens are broken. Because of the size of the median cusp, the specimens most probably represent *Wellerodus* (and not *Antarctilamna*), but the specific affinity is uncertain.

Stratigraphic range: In Poland, Upper Devonian, Frasnian, Early *Pa. rhenana* Zone; worldwide, upper Givetian–upper Frasnian.

Order Phoebodontiformes Ginter,
Hairapetian and Klug, 2002

Family Phoebodontidae Williams in Zangerl, 1981

Genus *Phoebodus* St. John and Worthen, 1875

Type species: *Phoebodus sophiae* St. John and Worthen, 1875.

Remarks: For more than 125 years, this genus has been known only from its characteristic, symmetrical, tri- or pentacuspoid teeth. Only at the beginning of this century, a specimen from Alaska (still undescribed, in the collection of Cleveland Museum of Natural History), a few teeth associated with a spine, was found. Finally, Frey *et al.* (2019) published articulated specimens of *Phoebodus saidselachus* from the Famennian of Morocco, with skulls, vertebral columns, dorsal fin spines and numerous well-preserved teeth, some of them still in place, arranged in tooth families. Only the caudal fins are missing. The body shape of *Phoebodus* is elongated, almost as in recent *Chlamydoselachus*, and the jaws are long and relatively narrow, but not as much as in *Thrinacodus*. The size of the largest skull, compared to the proportions of more complete specimens, indicates that the fish could have reached three metres.

None of the phoebodont teeth found in Poland are con-specific with the Moroccan specimens, but *Phoebodus turnerae* from Miedzianka, Holy Cross Mountains, is rather close to them.

Phoebodus fastigatus Ginter and Ivanov, 1992
Fig. 2E, F

Material: 12 specimens from the Holy Cross Mountains (Laskowa Hill, Wietrznia), GIUS-4-412/101, 104, 105, 111–118, MWGUW/Ps/1/63.

Description and remarks: The three main cusps are long, slender, and smooth, rounded in cross-section. The base is trapezoid, wider lingually. The orolingual button is circular or slightly oval, situated centrally. *Ph. fastigatus* is similar to *Ph. sophiae*, but is characterised by more gentle and slender cusps, a somewhat thinner base and a more rounded, orolingual button.

Stratigraphic range: In Poland, Middle Devonian, Givetian, *varcus–disparilis* zones and Upper Devonian, Frasnian, *Pa. transitans–Pa. rhenana* zones; worldwide, Givetian–Frasnian.

Phoebodus sophiae St. John and Worthen, 1875
Fig. 2G

Material: 63 specimens from the Holy Cross Mountains (Laskowa Hill), GIUS-4-412/102, 103, 120–180.

Description and remarks: The specimens, found in the samples from Laskowa Hill, almost exactly conform to the original description of *Ph. sophiae* (St. John and Worthen, 1875). The main feature of this species is a thick, broad tooth base, elliptical or trapezoidal with rounded angles. A large and distinct, oval, articular boss (button) occupies the large part of the orolingual side of the base. The arcuate basolabial thickening, corresponding to the button, usually has slightly enlarged ends.

The crown is not characteristic, in most cases pentacuspoid. The three main cusps are relatively thick. In the Polish material, on several specimens, the ornamentation of the cusps with cristae on the labial face is visible and a distinct, lateral carina often occurs. However, most of the teeth have rounded, unornamented cusps, most probably due to post-mortem abrasion.

Stratigraphic range: In Poland, Middle Devonian, Givetian, Late *varcus–hermanni-cristatus* zones; worldwide, middle Givetian–early Frasnian.

Phoebodus cf. *latus* Ginter and Ivanov, 1995a
Fig. 3C

Material: Nine teeth from the Holy Cross Mountains (Wietrznia, Kadzielnia, Tudorów), MWGUW/Ps/1/89, MWGUW/Ps/14/1–8.

Description and remarks: The teeth of *Phoebodus latus* are very similar to those of *Ph. bifurcatus*, a better known and more widely encountered younger species. However, they lack the double, lingual extensions of the base, typical of *Ph. bifurcatus*, and are generally wider. In the material from the south Urals some heterodonty was observed (see

Ginter and Ivanov, 1992, “*Phoebodus* sp. A”, fig. 7A–H): several teeth have the median cusp split in two and a small, additional, intermediate cusplet in the central position (and therefore seven cusps in the crown). However, the majority of teeth have a normal, pentacuspoid crown. The specimens from Poland, tentatively referred here to *Ph.* cf. *latus*, are rather poorly preserved, with broken bases, and at least some of them might actually represent *Ph. bifurcatus*. Teeth with seven cusps were not found.

Stratigraphic range: In Poland, Late Devonian, Frasnian, *rhenana* Zone; worldwide, Early *hassi-rhenana* zones.

Phoebodus bifurcatus Ginter and Ivanov, 1992
Fig. 3A, B

Material: 21 teeth from the Holy Cross Mountains (Kostomłoty, Karczówka, Grabina, Tudorów), MWGUW/Ps/1/70, 71, MWGUW/Ps/14/11–29.

Description and remarks: The crown is composed of five cusps: three main ones and two intermediate cusplets. The main cusps are strongly curved. The labial face of the median cusp and the intermediate cusplets is covered with a few distinct, sharp, straight subparallel ridges. Such ridges on the lateral main cusps are spirally curved. The only other phoebodont species with a similar, sharp ornamentation of the crown is *Ph. latus*. The base is thick, extended far lingually, bifurcated at the lingual end. The aboral side of the base is convex, forming an almost semi-cylindrical, labio-lingual tunnel. The orolingual button is broad and oval.

Stratigraphic range: In Poland, Upper Devonian, Frasnian, *Pa. rhenana* Zone; worldwide, *rhenana-linguiformis* zones.

Phoebodus turnerae Ginter and Ivanov, 1992
Fig. 3D

Material: 3 specimens from the Holy Cross Mountains (Miedzianka and probably Łągów), MWGUW/Ps/1/102, MWGUW/Ps/14/31, ZPAL P.IV/10.

Description and remarks: The teeth are generally similar to those of *Ph. gothicus*, with the lingually pointed base, but they differ from the latter in the less sigmoidal cusps, shorter bases and the large orolingual button, situated at the lingual rim, and not in the centre of the base.

Stratigraphic range: In Poland, Late Devonian, middle Famennian, *rhomboidea* and *marginifera* zones; worldwide, early–middle Famennian, *crepida-marginifera* zones.

Phoebodus gothicus Ginter, 1990
Figs 3E, F, 4A–E

Material: 82 teeth from the Holy Cross Mountains (Jabłonna, Ostrówka, Zbrza, Łągów) and 1 from Sudetes (Dzikowiec), MWGUW/Ps/1/1–12, 46, MWGUW/Ps/14/41–96, ZPAL P.IV/77, ZPAL P.IV/201–211, 212a.

Description and remarks: This phoebodont species is characterised spectacular teeth. Their bases extend far lingually, forming the shape of a gothic shield (Fig. 3F; sometimes very narrow, resembling teeth of *Thrinacodus*, e.g., Ginter, 2000, fig. 2M; Wilk, 2018, plate1, fig. A), pointed at

the lingual end, and have a large, rounded orolingual button in the centre. However, in the material studied, there are a few teeth most probably also representing *Ph. gothicus*, but with somewhat different outlines of the bases. In some cases, they are rather wide (Fig. 3A, C), in others, the lingual end is not pointed, but rounded (Fig. 3 B, D). There are also forms with very short, coarsely cristated, straight cusps (Fig. 3E), unlike in typical specimens, in which they are relatively long, slender and sigmoidally curved. All the teeth are symmetrical; the subspecies with asymmetrical teeth, *Ph. gothicus transitans* (known from North Gondwana, Ginter *et al.*, 2002), has not been found in Poland, despite the large number of specimens analysed.

Stratigraphic range: In Poland, Late Devonian, Famennian, Early *marginifera*–Middle *praesulcata* zones; worldwide, Famennian, *crepida-praesulcata* zones.

Phoebodus limpidus Ginter, 1990
Fig. 4F

Material: 22 specimens: 17 from the Holy Cross Mountains (Jabłonna and Ostrówka), 4 from the boreholes near Olkusz, 1 from Sudetes (Dzikowiec), MWGUW/Ps/1/39–44, MWGUW/Ps/14/101–116.

Description and remarks: The cusps are very long and slender, their surface is smooth or covered with delicate cristae. The intermediate cusplets are relatively long. The base is thin, usually in a shape of a rounded triangle. The orolingual button is rather vague or obsolete.

This late Famennian species often occurs in deep-water facies, together with *Jalodus australiensis*. It is noteworthy that this is the only phoebodont found in the Upper Silesian boreholes.

Stratigraphic range: In Poland, Late Devonian, Famennian, Late *postera*–Middle *praesulcata* zones; worldwide, the same.

Phoebodus cf. *politus* Newberry, 1889

Material: Two teeth from the Holy Cross Mountains (Kadzielnia), middle or late Famennian. See: Kulczycki, 1957, plate 13, figs 7, 8.

There are two tricuspid teeth in the collection of the Museum of the Earth in Warsaw, described by Kulczycki (1957) as *Dittodus* sp., but most probably belonging to *Phoebodus*. In the discussion (Kulczycki, 1957, p. 361), the author admitted that the teeth are similar to *Ph. politus* Newberry, 1889 from the Cleveland Shale of Ohio, but for some unknown reason did not draw any taxonomic conclusion from this observation. Indeed, the teeth, although incomplete, are similar to those of *Ph. politus*, especially in their size (5 and 8 mm between the apexes of the lateral cusps) and the general shape of the crown. However, because the bases are missing, the decisive identification cannot be done.

Genus *Thrinacodus* St. John and Worthen, 1875

Type species: *Thrinacodus nanus* St. John and Worthen, 1875.

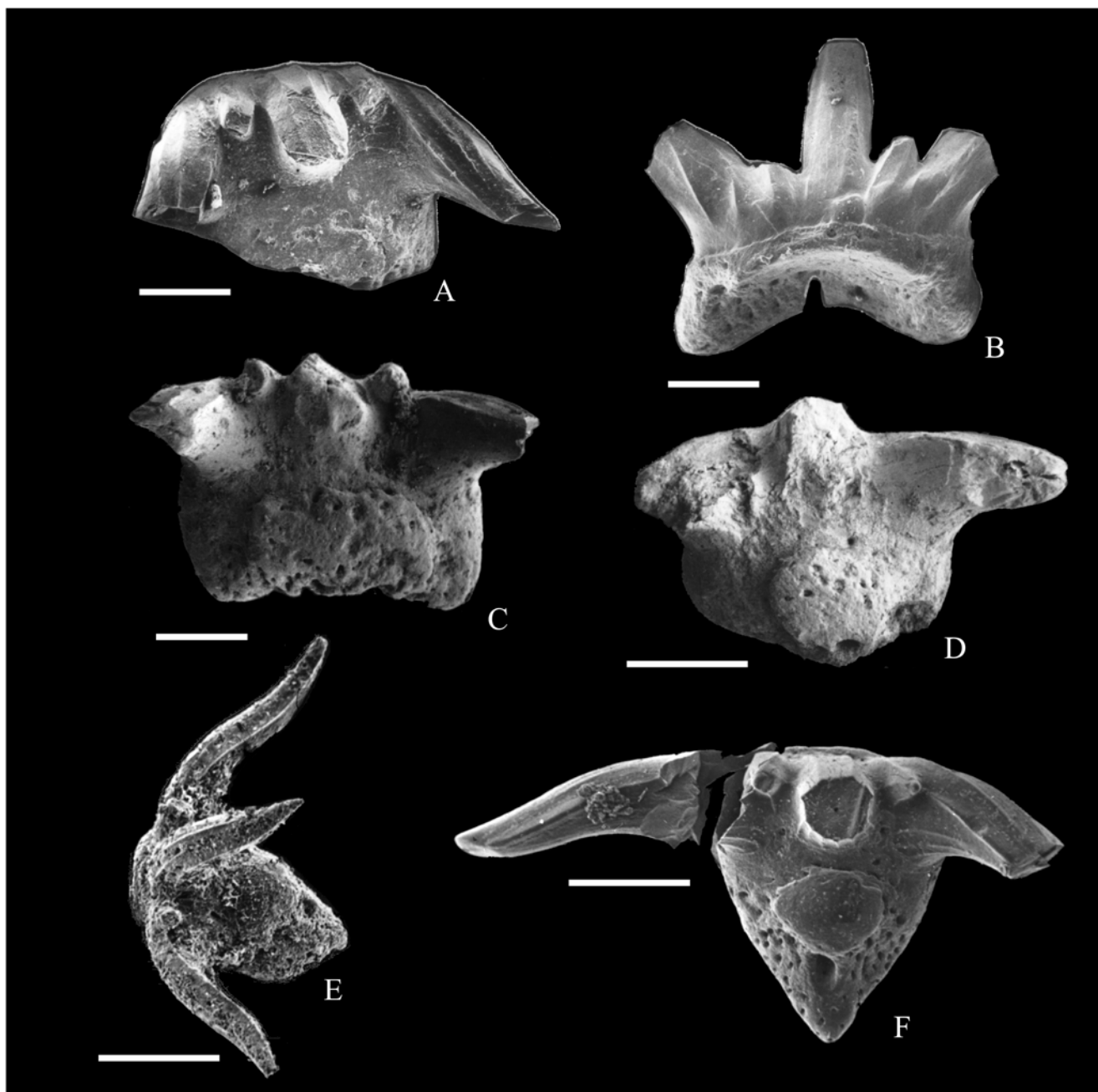


Fig. 3. Phoebodont teeth from the Upper Devonian of the Holy Cross Mountains. **A, B.** *Phoebododus bifurcatus* Ginter and Ivanov, 1992, from Karczówka, sample Kr-7, late Frasnian, *rhenana* Zone. A – MWGUW/Ps/1/70 in oral view, B – MWGUW/Ps/1/71 in aboral/labial view. **C.** *Ph. cf. latus* Ginter and Ivanov, 1995, MWGUW/Ps/1/89, in oral view; from Kadzielnia, sample K-MB, late Frasnian, *rhenana* Zone. **D.** *Ph. turnerae* Ginter and Ivanov, 1992, MWGUW/Ps/1/102, in oral view; from Miedzianka, sample Md-6, middle Famennian, *rhomboidea* or *marginifera* zones. **E, F.** *Ph. gothicus* Ginter, 1990. E – ZPAL P.IV/201 in lateral view; from Łagów, sample Ł-S59-2, middle Famennian, *marginifera* Zone, F – ZPAL P.IV/202 in oral view, from Ostrówka, sample Ost-5, late Famennian, *expansa* Zone. Scale bars = 0.5 mm.

Remarks: As in the case of *Phoebododus*, only the teeth of *Thrinacodus* were known for a long time from the second half of the 19th century (Newberry and Worthen, 1866; St. John and Worthen, 1875). Such teeth are very characteristic, tricuspid, asymmetrical, with a long and narrow base devoid of any articulation devices, looking like a handle of a grappling hook. The new discoveries of thrinacodont teeth in the late 20th century (e.g., Turner, 1982) sparked a discussion of their nature and function. Because of the general similarity of *Thrinacodus* to *Phoebododus*, Long (1990) placed them

both in the family Phoebodontidae. There were speculations, formally expressed by Ginter and Turner (2010, p. 1669), that “The occurrence of asymmetrical teeth in *Thrinacodus* could have been a dental response to the gradual changes of jaw morphology, from a typical arcuate shape, typical for most Palaeozoic sharks and presumably present in *Phoebododus* or a common ancestor of both, to narrow, V-shaped jaws”. The discovery of articulated specimens of *Thrinacodus gracila* (Grogan and Lund, 2008) in the Serpukhovian of Bear Gulch, Montana, USA revealed that at least Mississippian

representatives of this genus were eel-like fishes with pointed jaws, all fins reduced and no dorsal fin spines.

An evolution of thrinacodont teeth was observed from almost symmetrical in the middle to late Famennian *Th. tranquillus* Ginter, 2000 to extremely asymmetrical

Th. ferox (Turner, 1982), known mainly from the Tournaisian. However, there are Late Mississippian forms with a small degree of asymmetry, such as *Th. dziki* Ginter *et al.*, 2015. All these three species are present in Polish collections.

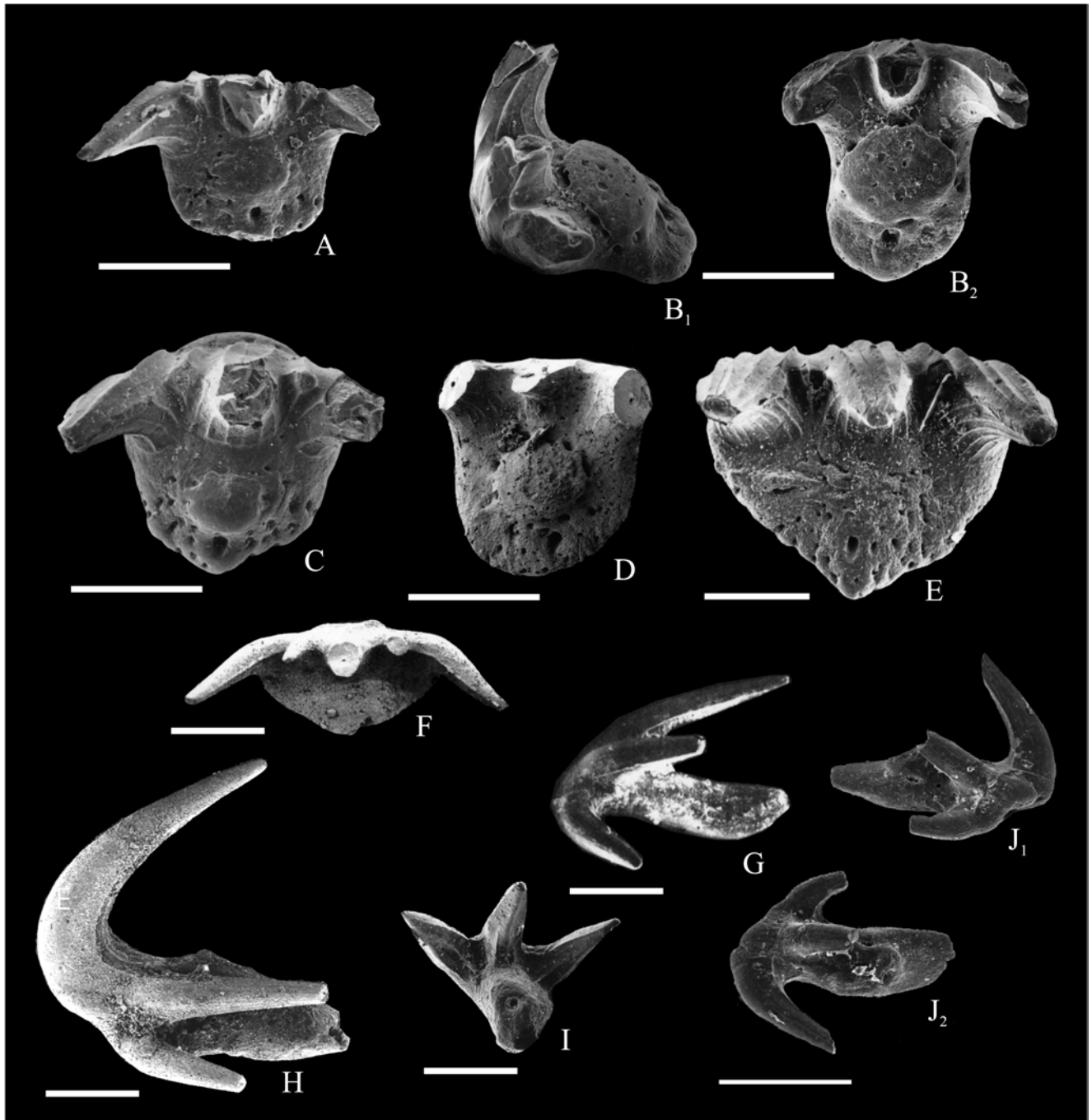


Fig. 4. Phoebodontid teeth from the Upper Devonian and Lower Carboniferous of southern Poland. **A–E.** Various shapes of teeth in *Phoebodus gothicus* from the late Famennian of Ostrówka. **A** – ZPAL P.IV/205 in oral view, sample Ost-5, *expansa* Zone, **B** – ZPAL P.IV/206 in lateral and oral views, sample Ost 284.II.293, *postera* or Early *expansa* Zone, **C** – ZPAL P.IV/207 in oral view, sample Ost-5, **D** – ZPAL P.IV/208 in oral view, sample Ost-12, *trachytera* Zone, **E** – ZPAL P.IV/212a on oral view, sample Ost-5, **F** – *Ph. limpidus* Ginter, 1990, MWGUW/Ps/1/40 in oral view; from Ostrówka, sample F-11, late Famennian, Late *expansa* or Early *praesulcata* Zone. **G.** *Thrinacodus tranquillus* Ginter, 2000, holotype, MWGUW/Ps/1/51 in lateral view, from the late Famennian of Ostrówka, sample F-14, Late *trachytera* Zone. **H.** *Th. ferox* (Turner, 1982), MWGUW/Ps/1/211, asymmetrical tooth in lateral view; from Dzikowice, sample Eb-N, Tournaisian, Late *duplicata-sandbergi* Zone. **I.** *Th. ferox*, symmetrical form, MWGUW/Ps/1/212 in lingual view; from Czatkowice, sample A, Tournaisian, *delicatus-cuneiformis* Zone. **J.** *Th. dziki* Ginter *et al.*, 2015, ZPAL P.IV/212 in labial and oral views, from Todowa Grząba, sample TG-D, Viséan, *bilineatus* Zone. Scale bars = 0.5 mm.

Thrinacodus tranquillus Ginter, 2000

Fig. 4G

Material: 37 teeth from the Holy Cross Mountains (Jabłonna, Ostrówka), 2 from the Cracow Upland (boreholes near Olkusz), MWGUW/Ps/1/47–53, MWGUW/Ps/14/121–149, ZPAL P.IV/104.

Description and remarks: The tooth crown of *Th. tranquillus* is composed of three equal, slender, strongly recurved cusps, covered on both sides with gentle, subparallel cristae. The base is long (labio-lingually), very narrow, subcircular in vertical section close to the crown and flattened or concave in the lingual part; it is twisted, and its long axis is slightly curved in relation to the crown (with the exception of few teeth probably of the symphyseal tooth-family). The opening of the main basal canal is usually situated half-way along the base.

Teeth of *Th. tranquillus*, because of their almost symmetrical crown with long and slender cusps, sometimes more closely resemble teeth of *Phoebodus* than those of other thrinacodonts. In particular, specimens with weakly twisted bases, such as the symphyseals, are similar to the teeth of *Ph. gothicus*, the bases of which are often very long and narrow.

Stratigraphic range: In Poland, Late Devonian, middle to late Famennian, *Pa. trachytera*–*Pa. expansa* (or Middle *Pa. praesulcata*) zones; worldwide, middle–late Famennian, *Pa. marginifera*–*Pa. praesulcata* zones.

Thrinacodus ferox (Turner, 1982)

Fig. 4H, I

Material: Ten teeth from the Cracow Upland (Czerna, Czatkowice), one tooth from Sudetes (Dzikowiec), MWGUW/Ps/1/211–214, MWGUW/Ps/13/1, 18, ZPAL P.IV/301, 302, 321–323.

Description and remarks: Most of the teeth of *Thrinacodus ferox* found in Poland are classical asymmetrical forms with the distal cusp much larger than the other two. However, in Czerna, a tooth also occurs that is somewhat similar to *Thrinacodus dziki* (Ginter *et al.*, 2015), with the size difference between the delicate, sigmoidal cusps less conspicuous. In sample A from Czatkowice, a minute, almost symmetrical tooth was found, closely resembling that illustrated by Turner (1982, fig. 3A). Such teeth most probably represent anterior, parasymphyseal tooth families.

Stratigraphic range: In Poland, Carboniferous, Tournaisian–late Viséan, *S. duplicata*–*G. bilineatus* zones; worldwide, cosmopolitan in the Tournaisian, rare occurrences in the uppermost Famennian (*Pa. expansa* Zone) and the Viséan.

Thrinacodus dziki Ginter, Duffin, Dean and Korn, 2015

Fig. 4J

Material: Nine teeth from the Holy Cross Mountains (Todowa Grząba), MWGUW/Ps/11/8–11, MWGUW/Ps/14/151–155, ZPAL P.IV/212.

Description and remarks: This thrinacodont species is characterised by the following combination of features: there are three cusps in the tooth-crown, typical for *Thrinacodus*, either equal to each other or the distal cusp may be slightly larger than the other two. The median cusp is offset from

its normal position and displaced lingually. The basal/labial part of the crown below the median cusp forms a bulge. In this bulge, there is a distinct basal canal opening.

Stratigraphic range: In Poland, Carboniferous, late Viséan, *G. bilineatus* Zone; worldwide, late Viséan.

Family Jalodontidae Ginter, Hairapetian and Klug, 2002

Genus *Jalodus* Ginter, 1999**Type species:** *Phoebodus australiensis* Long, 1990.*Jalodus australiensis* (Long, 1990)

Fig. 5A

Material: 86 teeth from the Holy Cross Mountains, one tooth from the Cracow Upland (boreholes near Olkusz), MWGUW/Ps/1/14–34, 36, MWGUW/Ps/14/161–223, ZPAL P.IV/209a–211a.

Description and remarks: The teeth of *Jalodus australiensis* possess only three cusps, entirely lacking intermediate cusplets. The cusps are triangular and labio-lingually compressed, straight or slightly recurved, but never sigmoidal. The median cusp is often much shorter than the lateral cusps, as in the xenacanthiforms. The labial face of the cusps is covered with an ornament of more or less regularly stacked lanceolate ridges, like imbricating sharp leaves. The base is thick and directed lingually. The apical button is absent or weakly differentiated from the rest of the base.

Stratigraphic range: In Poland, Late Devonian, middle to late Famennian, Late *Pa. marginifera*–Late *Pa. expansa* (or Middle *praesulcata*) zones.

Order Xenacanthiformes Berg, 1937

Family indet.

Genus *Bransonella* Harlton, 1933**Type species:** *Bransonella tridentata* Harlton, 1933.*Bransonella nebraskensis* (Johnson, 1984)

Fig. 5B, C

Material: Four teeth from the Holy Cross Mountains (Todowa Grząba), ZPAL P.IV/213–216.

Description and remarks: The teeth of *Bransonella* from Todowa Grząba have crowns, composed of three short, straight cusps, covered on the labial faces with coarse cristae, partly straight and partly wavy, joining upwards, forming a lanceolate pattern (similar to that in *Jalodus*). The lateral cusps are twice as large as the median cusp. The base is thick and compact, with a button covering almost all the orolingual side. The basolabial tubercle is heel-like, straight, and thin.

Stratigraphic range: In Poland, Carboniferous, late Viséan, *G. bilineatus* Zone; worldwide, Carboniferous, Viséan–Permian, Cisuralian.

Superorder Cladodontomorphi Ginter, Hampe and Duffin, 2010

Order Symmoriiformes Zangerl, 1981

Family Falcatidae Zangerl, 1990

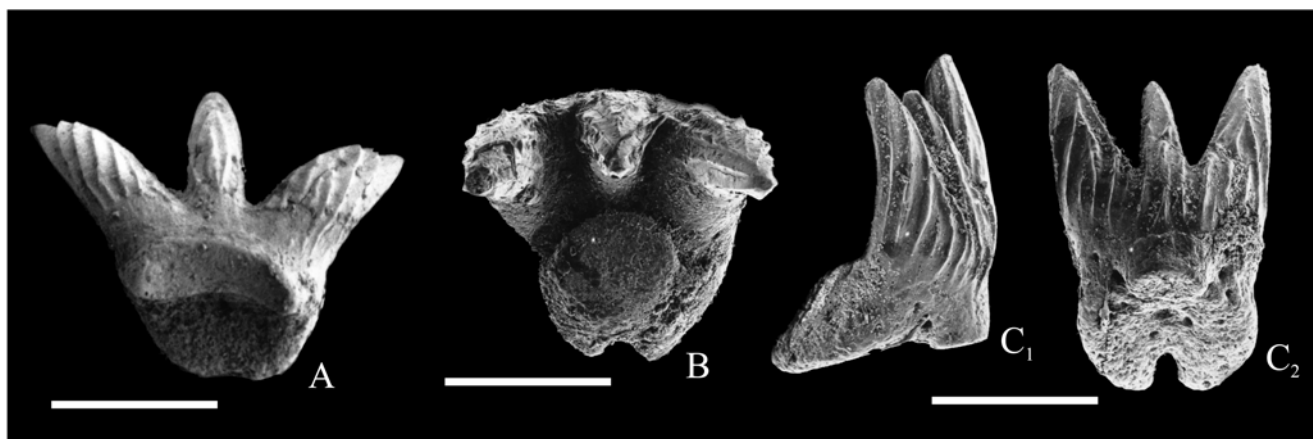


Fig. 5. Teeth of *Jalodus* and *Bransonella* from the western Holy Cross Mountains. **A.** *Jalodus australiensis* (Long, 1990), MWGUW/Ps/1/17 in labial/aboral view; from Ostrówka, sample F-11, late Famennian, Late *expansa* or Early *praesulcata* Zone. **B, C.** *Bransonella nebraskensis* (Johnson, 1984) from Todowa Grząba, sample TG-D, Viséan, *bilineatus* Zone. **B.** ZPAL P.IV/213 in oral view; **C.** ZPAL P.IV/215 in lateral and aboral/labial views. Scale bar = 0.5 mm.

Remarks: The Carboniferous members of this family are small fishes, usually 20–30 cm long, with large eyes, and having a peculiar spine attached at the back of a head (most probably only in males), curved and projecting forward (e.g., Lund, 1985, 1986). However, the recent study on a falcetid from the middle Famennian of Morocco, *Ferromirum* (Frey *et al.*, 2020) revealed that the early falcetids had a single fin spine, curved backwards, preceding the anterior fin in a normal way. The posterior fin is much smaller than the anterior one and devoid of a spine, typically of all the Symmoriiformes.

The articulated specimens of the Falcetidae are known from the Upper Devonian, middle Famennian (Frey *et al.*, 2020) through to the Upper Pennsylvanian (e.g., Williams, 1985), but their teeth also were recovered from the Permian (see the reviews in Ginter, 2018, table 1; Ginter and Złotnik, 2019, appendix 1). In Poland, the undoubted falcetid teeth, minute, characterised by long, slender, widely separated cusps, were found virtually only from the Mississippian (Tournaisian and Viséan). However, a few imperfectly preserved teeth from the Famennian, placed here among the unidentified “cladodont teeth”, might also represent this group.

Genus *Danaea* Pruvost, 1922

Type species: *Danaea fournieri* Pruvost, 1922.

Danaea cf. fournieri Pruvost, 1922
Fig. 6A

Material: 33 teeth from the Holy Cross Mountains (Todowa Grząba), MWGUW/Ps/7/5, MWGUW/Ps/11/1–5, 12–17, MWGUW/Ps/14/231–248, ZPAL P.IV/219–221.

Description and remarks: The teeth of this form, very similar to those of *Danaea fournieri* from the Viséan of Belgium (Fournier and Pruvost, 1928), were analysed and compared in detail by Ginter *et al.* (2015). The almost symmetrical tooth crown usually consists of five or seven cusps.

The median cusp is long and slender, sigmoidal in lateral view, often slightly inclined laterally, and sub-circular in cross-section. The whole cusp, except for the uppermost fifth, is ornamented with dense sub-parallel cristae. There is no distinct lateral carina; only the lateral cristae run continuously to the cusp apex. The ornamentation of the lateral cusps is similar, but usually there is no uppermost unornamented area.

The base is roughly pentagonal with rounded angles. The orolingual button is oval, sometimes almost split in two by the openings of the main basal canal, which are situated on the lingual and labial sides of the button. The basolabial projection is tubercle-like, squarish in cross-section, and not wider than the basal part of the median cusp. The size of the teeth of *D. cf. fournieri* from Todowa Grząba is 0.6–1.5 mm for the mesio-distal dimension of the base.

Stratigraphic range: In Poland, Carboniferous, late Viséan, *Gnathodus bilineatus* Zone; worldwide, Viséan, Moliniacian–Brigantian.

Danaea williamsi Ginter and Hansen, 2010

Fig. 6B

Material: Five teeth from the Holy Cross Mountains (Todowa Grząba), MWGUW/Ps/11/18, 19, MWGUW/Ps/14/251–253.

Description and remarks: The teeth of *D. williamsi* from Todowa Grząba are small (0.5 mm across the base) and have five cusps. There is a specific ornament of the median cusp, composed of cristae which, on the labial side, diverge laterally at the base and then corresponding pairs join before reaching the tip, whereas on the lingual face they converge at various heights. The outermost cusps are strongly divergent, more so than in *D. cf. fournieri*. The base is provided with a distinct button, in the shape of a horizontal figure of 8, at the lingual rim.

Stratigraphic range: In Poland, Mississippian, late Viséan, *Gnathodus bilineatus* Zone; worldwide, Viséan–Serpukhovian.

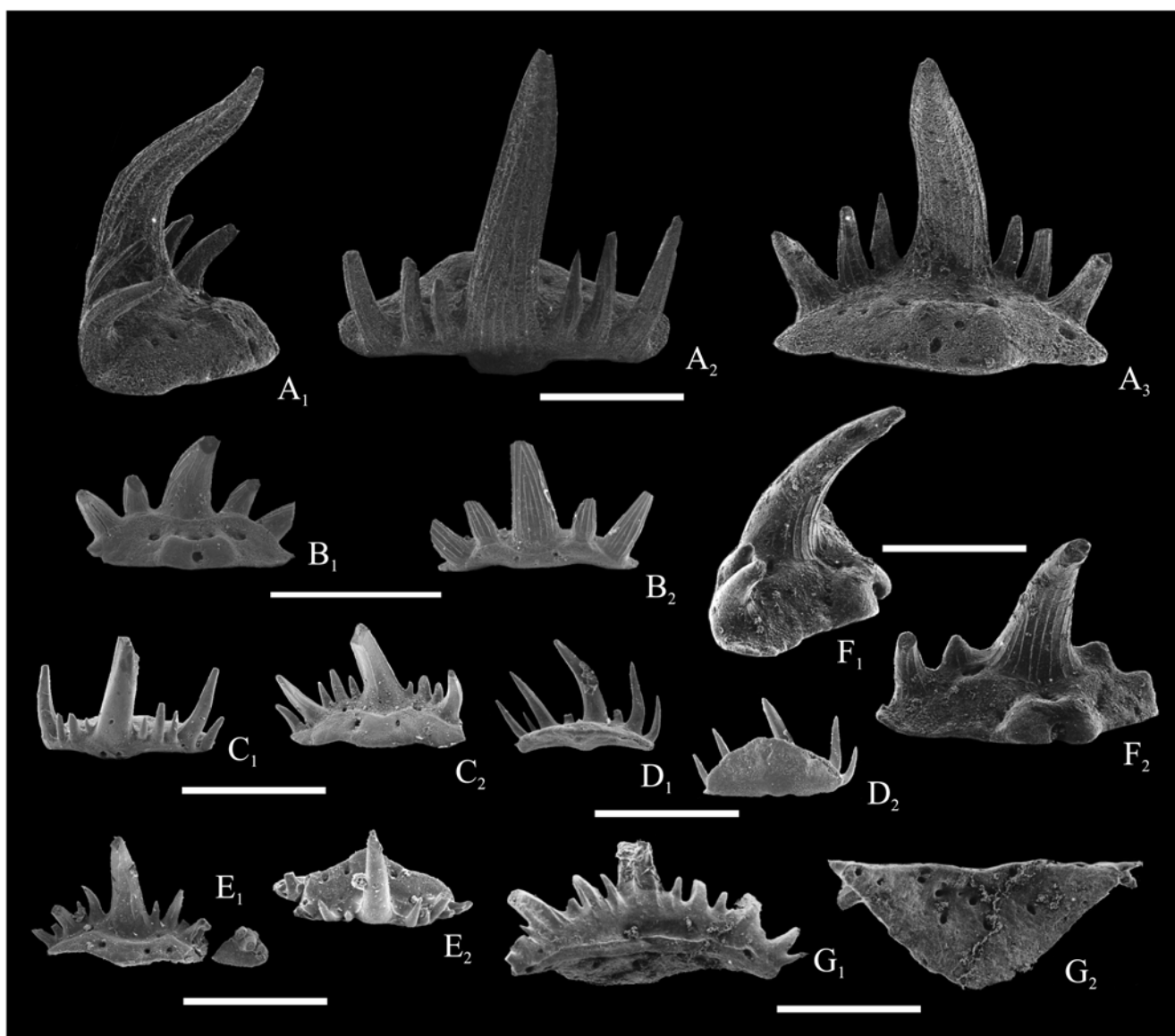


Fig. 6. Falcetid teeth from the Lower Carboniferous of the Holy Cross Mountains and the Cracow Upland. A–C. Falcatidae from Todowa Grząba, sample TG-D, Viséan, *bilineatus* Zone. A – *Denaea* cf. *fournieri* Pruvost, 1922, ZPAL P.IV/221, in lateral, labial and lingual views, B – *D. williamsi* Ginter and Hansen, 2010, MWGUW/Ps/11/18 in lingual and labial views, C – *D. wangi* Wang *et al.*, 2004, MWGUW/Ps/7/6 in labial and lingual views. D–G. Chondrichthyan teeth from Czerna, sample Cz-1, Viséan, *bilineatus* Zone. D – *D. wangi*, ZPAL P.IV/303 in lingual and oral views, E – *D. wangi*, ZPAL P. IV/306 in lingual and oral views, F – Falcatidae indet., ZPAL P.IV/226 in lateral and lingual views, G – Cladodontomorphi indet., ZPAL P. IV/255 in labial and aboral views. Scale bars = 0.5 mm.

Denaea wangi Wang, Jin and Wang, 2004
Fig. 6C–E

Material: Seven teeth from the Holy Cross Mountains (Todowa Grząba) and four teeth from the Cracow Upland (Czerna), MWGUW/Ps/7/6, MWGUW/Ps/14/261–266, ZPAL P.IV/222–224, 303–306.

Description and remarks: The Polish material of *D. wangi* was described by Ginter *et al.* (2015; here also is an extensive discussion on the validity of this species and its similarity to “small *Damocles*” from the Serpukhovian of Bear Gulch, Montana) and Ginter and Złotnik (2019). The teeth of *D. wangi* are minute, 0.4–0.7 mm mesio-distally. The tooth-crown is cladodont, asymmetrical, with seven to eight delicate cusps inclined distally. The highest cusp is situated not exactly in the median position, but slightly

displaced in the mesial direction. There is a different number of lateral cusps on the mesial and distal (3–4) sides. The difference in size between the cusps is moderate. The base is thin and flat, triangular in the oral view, with a tiny basolabial tubercle.

Stratigraphic range: In Poland, Carboniferous, late Viséan, *Gnathodus bilineatus* Zone; worldwide, Viséan–Serpukhovian.

Falcatidae indet.

Fig. 6F

There are several teeth of the falcetid design, but still unclassified, in the Mississippian and probably also in the Famennian of southern Poland. They are usually in many

respects similar to those of *Denaea furnieri*, but the minor differences in the crown or base features indicate that they represent some other taxa. Such teeth are particularly numerous (about 20 specimens) in the Tournaisian and Viséan of the Cracow Upland (Czatkowice and Czerna; Ginter and Złotnik, 2019, figs 3B–H, 4D, E). The present authors hope that in future, when a good comparative material is found, at least some of these teeth will receive formal names.

Order Ctenacanthiformes Glikman, 1964
 Family Ctenacanthidae Dean, 1909
 Genus *Ctenacanthus* Agassiz, 1837

Type species: *Ctenacanthus major* Agassiz, 1837.

Ctenacanthus spp.

In the Famennian of Ostrówka there were found two large teeth and three fragments of fin spines, which may be attributed to ctenacanthids (Wilk, 2018, plate 5). The teeth, about 15 mm wide, are generally similar to *Ctenacanthus concinnus* (Newberry, 1875). One of the spine fragments (Wilk, 2018, plate 5A), showing only the interface between the ornamented and unornamented part, is 6 cm long. This indicates that the complete spine was originally extremely large, at least 50 cm long.

Genus *Cladodoides* Maisey, 2001

Type species: *Cladodus wildungensis* Jaekel, 1921.

Cladodoides wildungensis (Jaekel, 1921)
 Fig. 8A, B

Material: 19 teeth from the Holy Cross Mountains (Kowala, Płucki, Kadzielnia, Psie Górki, Miedzianka) and 8 from the Cracow Upland (Dębnik), MWGUW/Ps/1/215–217, MWGUW/Ps/4/1–3, 6–9, 12, MWGUW/Ps/14/271–285, ZPAL P.IV/216.

Description and remarks: The teeth of this species from Poland were described by Ginter (2002) as a new species *Stethacanthus resistens*. However, re-examination of the original material from Bad Wildungen revealed that they are identical to those of *Cladodoides wildungensis* (Jaekel, 1921).

The teeth are cladodont, almost always pentacuspoid. Two tooth morphotypes can be distinguished. The first and larger form (base width about 3 mm) is characterised by a long and slender, median cusp, with a flat labial and strongly convex lingual face. About 8–10 distinct, but not very coarse vertical cristae occur on the labial side; there are apparently slightly more numerous and less pronounced cristae on the lingual face. The cristae terminate at around two thirds of the way up the cusp and the apical part is smooth. The outer lateral cusps, strongly laterally divergent, are much shorter than the median cusp. The second, smaller morphotype (base width up to 2 mm) has a thinner and relatively shorter, median cusp than in the large form, with similarly developed but fewer cristae. Because the teeth are smaller, the cristae seem to be relatively coarser. The base outline is elongated mesio-distally, with the lateral ends sticking beyond the crown foot.

Stratigraphic range: In Poland, Late Devonian, latest Frasnian–middle Famennian, *Pa. linguiformis*–*Pa. rhomboidea* zones; worldwide, the same.

Genus *Glencartius* Ginter and Skompski, 2019

Type species: *Ctenacanthus costellatus* Traquair, 1884.

Glencartius costellatus (Traquair, 1884)
 Fig. 7

Material: One tooth from the Holy Cross Mountains (Todowa Grząba) and one tooth from Lublin Coal Basin (Włodawa), MWGUW/Ps/12/1, ZPAL P.IV/256. Additionally, more than 200 scales from Włodawa.

Description and remarks: The teeth of *G. costellatus* associated with the articulated specimens, described by Traquair (1884) and Moy-Thomas (1936) from Glencartholm in Scotland, are symmetrical and very regular in shape. The median cusp is wide, slightly compressed at the base and rounded in cross-section at the tip. Two or three lateral cusps may be developed on each side. All of the cusps are ornamented on both sides with rather coarse, often slightly wavy cristae. Some of the cristae bifurcate at the base. The base is lenticular in the oral view. On the labial side, there is a shallow depression, framed by thick, elliptical, or semi-elliptical basolabial projections, and there are two pad-like, rounded buttons on the orolingual surface.

In the tooth from Todowa Grząba, half of the crown is preserved; the base is completely destroyed. The crown is cladodont, with four lateral cusps on each side. The labial side of the crown is covered with strong cristae, converging at various heights, and the lingual side bears more delicate cristae. The shallow depression at the base of the labial side of the median cusp indicates that there might also have been a basolabial depression in the base. In the tooth from Włodawa, only a piece of the median part is preserved. The median cusp is somewhat compressed labio-lingually and its labial side is covered with strong cristae, two of which bifurcate at the base. Similar ornamentation continues on the lateral cusp.

Despite the incompleteness of Polish teeth of *G. costellatus*, the preserved features are so spectacular and unique that there is no doubt as to their identification. The tooth from Włodawa is associated with more than 200 body scales of the ctenacanthid type *sensu* Reif (1978), very similar to those on the articulated Scottish specimens. There are also a few other types of scales, probably from the head region (Ginter and Skompski, 2019, fig. 7). Many scales are perfectly preserved, better than those on the holotype, and give an interesting overview of the squamation of this species.

Stratigraphic range: In Poland, Carboniferous, late Viséan, *Gnathodus bilineatus* Zone; worldwide, early to late Viséan.

Order Squatinactiformes Zangerl, 1981
 Family Squatinactidae Cappetta, Duffin and Zidek, 1993
 Genus *Squatinactis* Lund and Zangerl, 1974

Type species: *Squatinactis caudispinatus* Lund and Zangerl, 1974.

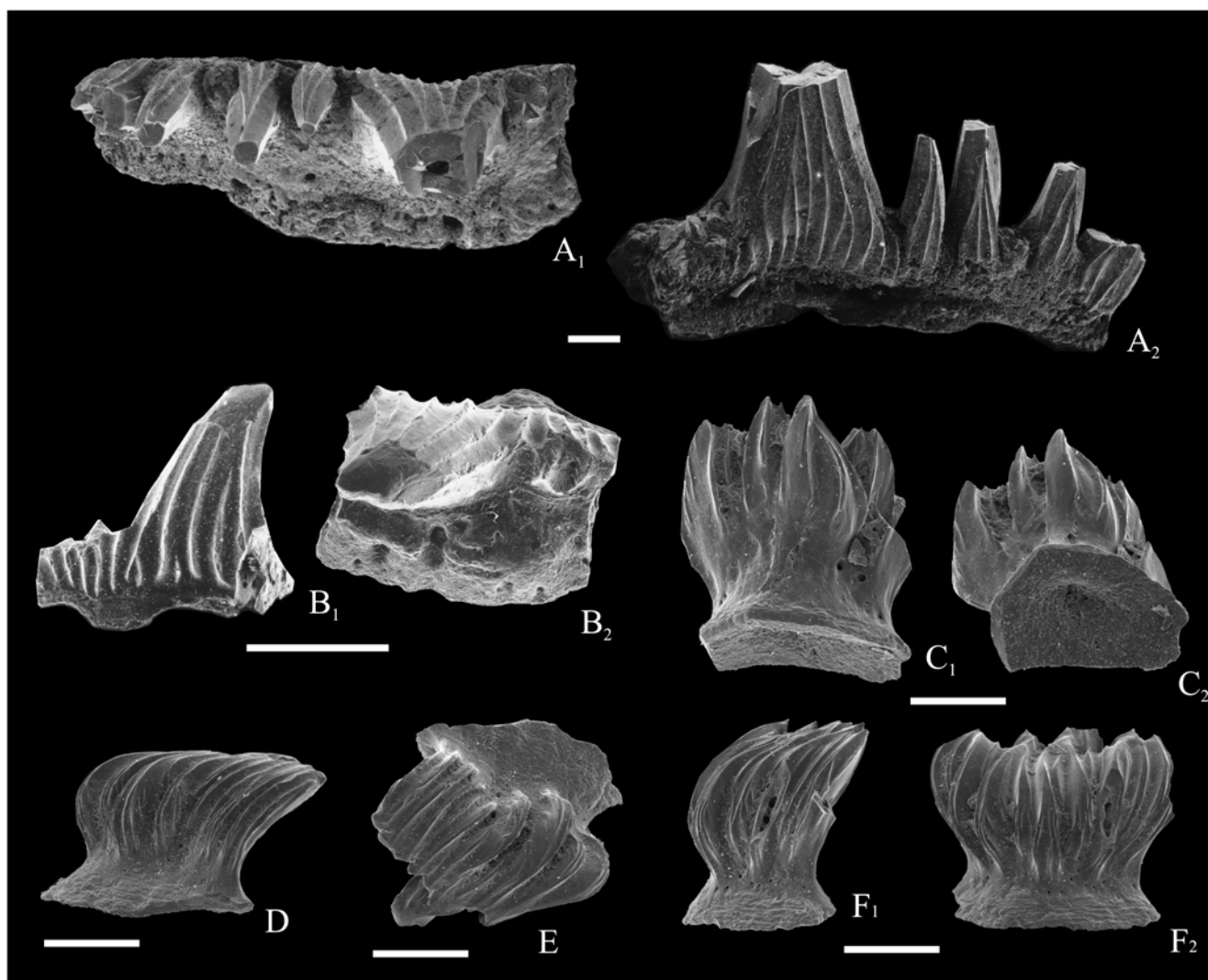


Fig. 7. Ctenacanthid teeth and scales from the Lower Carboniferous of southern Poland. **A, B.** Teeth of *Glencartius costellatus* (Traquair, 1884). **A** – ZPAL P.IV/256, in oral and labial views; from Todowa Grząba, sample TG-D, Viséan, *bilineatus* Zone, **B** – MWGUW/Ps/12/1, in labial and oral views; from the Włodawa IG 4 borehole, late Viséan. **C–F.** Body scales, probably of *G. costellatus*, from the Włodawa IG 4 borehole. Scale bars = 0.5 mm.

Squatina glabrum (Ginter, 1999)

Fig. 8F

Material: 31 teeth from the Holy Cross Mountains (Ostrówka, Miedzianka, Łagów), MWGUW/Ps/14/291–319, ZPAL P.IV/127, 218.

Description and remarks: At the beginning, the teeth of *S. glabrum* were identified as belonging to *Symmorium*, but after a restudy of the original material of the latter genus and the observation on the teeth of *Squatina* from the Bear Gulch of Montana, the species was transferred to its current position. The most important feature is the deep basolabial sulcus below the median cusp and the double orolingual button. The teeth are cladodont, generally very delicate, with slender, almost smooth cusps. In the Polish material, they are always pentacuspoid, although elsewhere, e.g., in Thuringia (Ginter, 1999), they can have seven cusps.

Stratigraphic range: In Poland, Late Devonian, middle–late Famennian, *Pa. marginifera*–*Pa. expansa* zones; worldwide, middle Famennian–Tournaisian.

Order indet.

Family indet.

Genus *Clairina* Ginter, 1999

Clairina marocensis (Derycke, 1992)

Fig. 8G

Material: 1 tooth from the Holy Cross Mountains (Kadzielnia), MWGUW/Ps/1/226.

Description and remarks: Only four teeth of this species have been found in the world thus far: one in the Anti-Atlas, Morocco (Derycke, 1992), two in Thuringia, Germany (Ginter, 1999) and one in the Holy Cross Mountains, Poland. They have five cusps, distributed in a fan-like manner, with a peculiar ornamentation of both sides. On the labial side the cristae are arranged as overlapping leaves (Fig. 8G₂), and on the lingual side they form a Christmas-tree pattern (Fig. 8G₁).

Stratigraphic range: In Poland, Late Devonian, early Famennian, *Pa. crepida* Zone; worldwide, Famennian, *Pa. crepida*–*Pa. expansa* zones.

Cladodontomorphi indet. 1

Fig. 6G

Description and remarks: There are many unclassified cladodont teeth in the studied material, but one of them deserves special attention. In the sample from Czerna (Cz-1, *G. bilineatus* Zone), there is a tooth 1 mm wide (ZPAL P.IV/255), very delicate and brittle, virtually symmetrical.

Its crown is multicuspid, comb-like, of the cladodont design. The median cusp is very slender, covered with only a few cristae, rather strong in comparison to the width of the cusp. There are seven lateral cusplets on each side of the median cusp, of which the fourth are the highest. The smaller cusplets often grow on a side of the larger one. The base

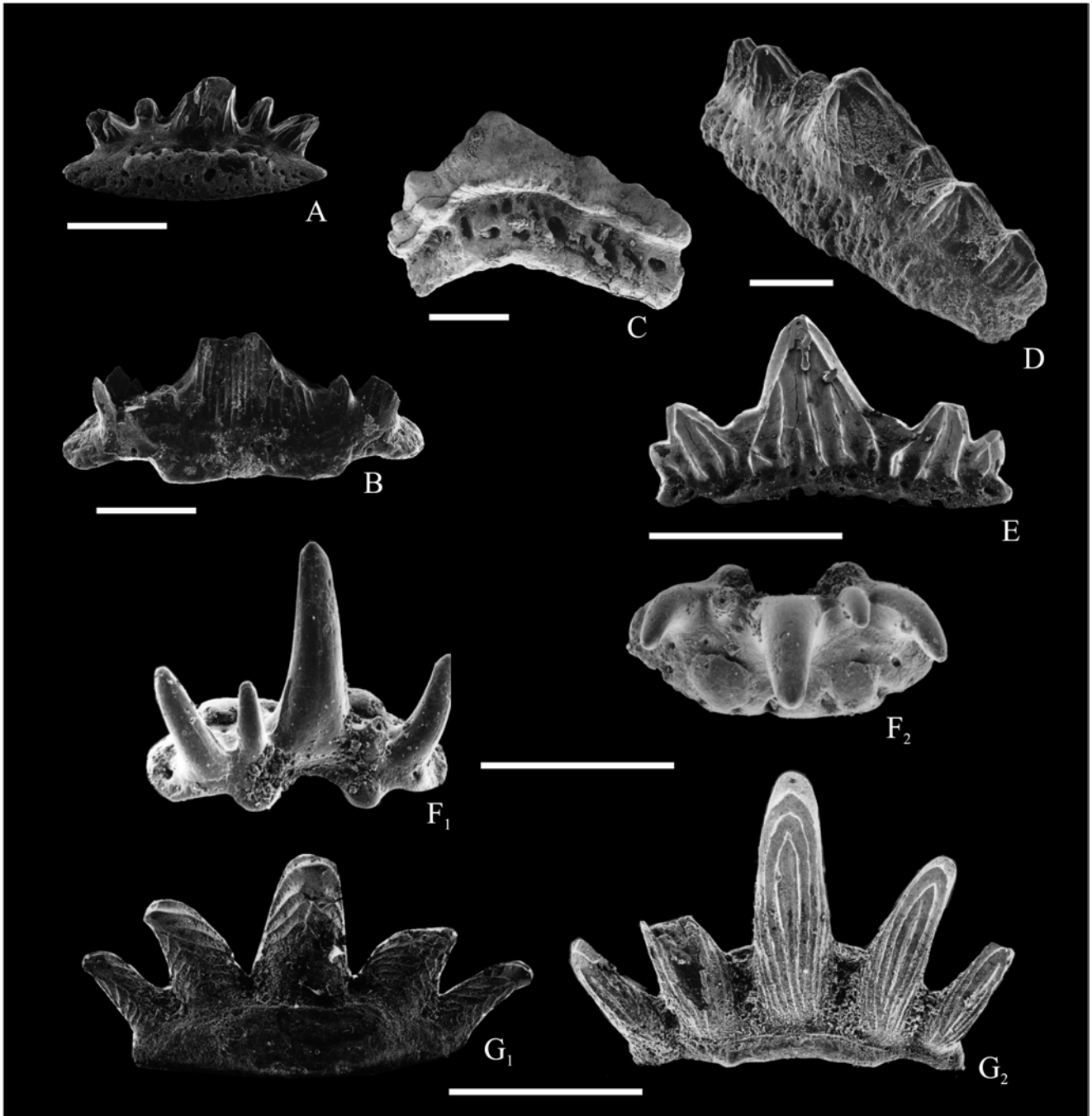


Fig. 8. Chondrichthyan teeth from the Upper Devonian and Lower Carboniferous of southern Poland. **A, B.** *Cladodooides wildungensis* (Jaekel, 1921). **A** – MWGUW/Ps/1/217 in lingual view; from Psie Górki, sample PG-T, late Frasnian, *linguiformis* Zone, **B** – MWGUW/Ps/4/3 in labial view; from Kowala, sample Ko-SF, *Pa. linguiformis* Zone. **C.** *Cassisodus margaritae* Ginter and Sun, 2007, ZPAL P. IV/232 in lingual view; from Czerna, sample Cz-1, Viséan, *bilineatus* Zone. **D.** *Protacrodus vetustus* Jaekel, 1925, MWGUW/Ps/4/13 in oblique lingual view; from Kowala, sample Ko-SF, *Pa. linguiformis* Zone. **E.** *P. serra* Ginter *et al.*, 2002, ZPAL P.IV/229 in labial view; from Ostrówka, sample Ost Am VII/185, late Famennian, Early *expansa* or Middle *praesulcata* Zone. **F.** *Squatinactis glabrum* (Ginter, 1999), ZPAL P.IV/127 in labial and oral views; from Łagów, sample Ł-09, middle Famennian, Early *marginifera* Zone. **G.** *Clairina marocensis* Derycke, 1992, MWGUW/Ps/1/226 in lingual and labial views; from Kadzielnia, sample K-462 w 50, early Famennian, *crepida* Zone. Scale bars: A–D = 1 mm, E–G = 0.5 mm.

is triangular in the oral view, the basolabial rim is slightly elevated, forming a kind of a parapet.

With its numerous slender cusplets and the base devoid of any articulation devices, this tooth resembles those of *Danaea wangi*. However, its almost complete symmetry, the ornamentation of the larger cusps and the specific type of growth of the intermediate cusplets are the features which combined preclude its belonging not only to *Danaea*, but also to Falcatidae and even Symmoriiformes.

Cohort Euselachii Hay, 1902

Superfamily Protacrodontoidea Zangerl, 1981

Family Protacrodontidae Cappetta, Duffin and Zidek, 1993

Genus *Protacrodus* Jaekel, 1925

Type species: *Protacrodus vetustus* Jaekel, 1925.

Protacrodus vetustus Jaekel, 1925

Fig. 8D

Material: Six teeth from the Holy Cross Mountains (Kowala, Wietrznia, Jabłonna, Miedzianka, Plucki), MWGUW/Ps/1/222, 223, MWGUW/Ps/4/13, MWGUW/Ps/14/321–322, ZPAL P.IV/227.

Description and remarks: Teeth of this species 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. 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.

There are fragments of protacrodont tooth whorls in the material from Miedzianka Hill and Jabłonna. In the specimen from Miedzianka (Ginter, 2002, 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 indicates 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.

Stratigraphic range: In Poland, Late Devonian, latest Frasnian–early Famennian, *Pa. linguiformis*–*Pa. crepida* zones; worldwide, late Frasnian–early Famennian.

Protacrodus serra Ginter, Hairapetian and Klug, 2002

Fig. 8E

Material: 27 teeth from the Holy Cross Mountains (Jabłonna, Ostrówka, Łagów), MWGUW/Ps/14/331–354, ZPAL P.IV/228–230.

Description and remarks: The teeth of this protacrodont teeth are characterised by a labio-lingually compressed, slightly recurved crown, composed of three to seven cusps, connected by a distinct occlusal blade. The crown may be

strongly asymmetrical with all the cusps inclined distally. The median cusp is often much larger than the others and probably served as a cutting blade. This is one of the earliest cases of potentially cutting dentitions in chondrichthyans.

Stratigraphic range: In Poland, Late Devonian, late Famennian, *Pa. marginifera*?, *Pa. trachytera*–*Pa. expansa* zones; worldwide, late Famennian.

Order Hybodontiformes Maisey, 1975

Family indet.

Genus *Cassisodus* Ginter and Sun, 2007

Type species: *Cassisodus margaritae* Ginter and Sun, 2007.

Cassisodus margaritae Ginter and Sun, 2007

Fig. 8C

Material: Three teeth from the Cracow Upland (Czerna), ZPAL P.IV/232, 309, 334.

Description and remarks: The teeth of *C. margaritae* from Czerna are composed of a low, crushing crown and a typical euselachian base. The crown is asymmetrical and consists of a main, pyramidal cusp, not in the median position. On the shorter side of the crown, there are two lateral cusps and on the longer one, there are three cusps in smaller specimens (Ginter and Złotnik, 2019, fig. 5E), but in the larger specimen the respective numbers are three and four (Fig. 8C). The bases of the cusps are fused. There are tubercles on both labial and lingual sides of the cusps. In the larger tooth (4 mm mesio-distally) the main part of the crown is strongly elevated.

Stratigraphic range: In Poland, Carboniferous, late Viséan, *G. bilineatus* Zone; worldwide, middle Tournaisian–late Viséan.

Subclassis Euchondrocephali Lund and Grogan, 1997

Order Petalodontiformes Zangerl, 1981

Family Belantseidae Lund, 1989

Genus *Ctenoptychius* Agassiz, 1838

Ctenoptychius sp.

Material: One tooth from the Holy Cross Mountains (Todowa Grząba), MWGUW/Ps/14/361; see Ginter (2010, fig. 7A).

Description and remarks: Only one fragmentary chondrichthyan tooth, a serrated, triangular crown blade, and a crushed base, was found in the crinoid calcirudites at the Todowa Grząba hill. It is a petalodont similar to specimens (GSL 1190 and 1191) from the collection of British Geological Survey at Keyworth, England, UK, probably found in the Viséan Mountain Limestone of Armagh (Northern Ireland, UK), and labelled as *Ctenoptychius serratus* Agassiz, 1838 (Ginter, 2010, fig. 7B).

Stratigraphic range: Carboniferous, Viséan.

Superorder Holocephali Bonaparte, 1831

Order Cochliodontiformes Obruchev, 1953

Family Psephodontidae Zangerl, 1981

Genus *Psephodus* Morris and Roberts, 1862

(ex Agassiz ms. 1859)
Psephodus cf. magnus (Agassiz, 1838)

Material: One tooth from the Holy Cross Mountains (Kowala). See Ginter and Piechota (2004, figs 2A and 3A).

Description and remarks: This single holocephalian tooth from the Devonian of Poland is very dark brown, almost black, and lacks probably about a half of a lateral ramus. Before losing a piece, the tooth seems to have been virtually symmetrical mesio-distally. The tooth has a wavy outline in lingual and labial views. The central part of the tooth is elevated, in the form of a broad swelling and the corresponding part of the basal surface is concave. The basal surface is smooth and devoid of any traces of foramina. The crown is composed of tubular dentine, with openings of tubules present all over the crown surface.

The tooth was described in detail and its identity was discussed by Ginter and Piechota (2004). It is somewhat similar to some of the teeth of *Psephodus magnus* from the Viséan of Scotland, but there is doubt that it can be conspecific, because of the large stratigraphic distance.

Stratigraphic range: Upper Devonian, middle Famennian, Late *Pa. trachytera* Zone.

Chondrichthyan scales and branchial denticles

All the shark scale types established by Reif (1978), viz. the protacrodontid, ctenacanthid and hybodontid types are present among the Devonian ichthyoliths from southern Poland. The ctenacanthid and hybodontid scales also occur in the Carboniferous, but protacrodontid type scales

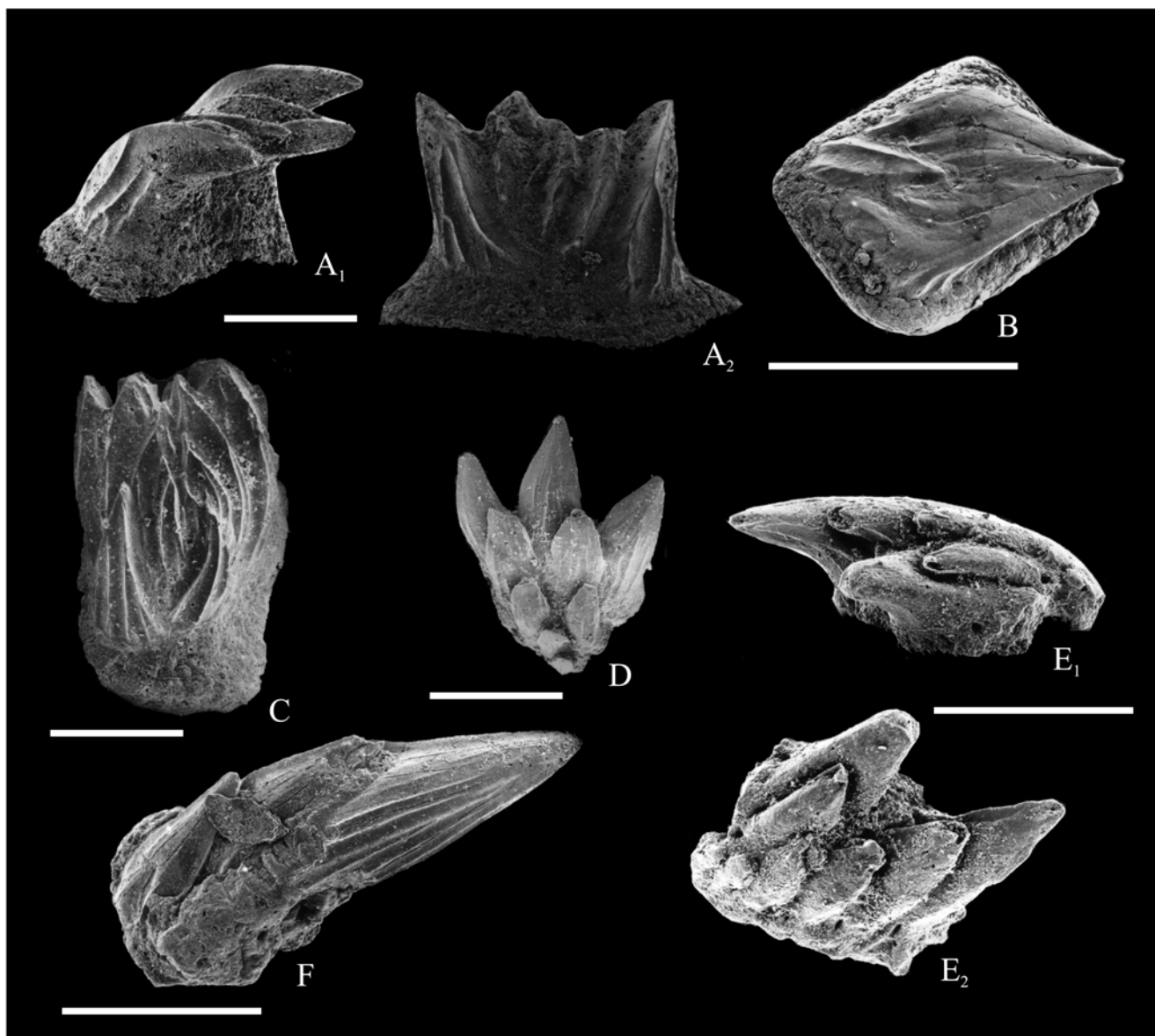


Fig. 9. Chondrichthyan scales and branchial denticles from the Famennian and Tournaisian of southern Poland. **A.** Hybodontid scale, ZPAL P.IV/234 in lateral and anterior views; from Łagów, sample Ł-blok, middle Famennian, *marginifera* Zone. **B.** Protacrodontid scale, ZPAL P.IV/236 in oblique lateral view; from Ostrówka, sample Ost-7, late Famennian, *postera* or *Early expansa* Zone. **C.** Ctenacanthid scale, MWGUW/Ps/1/234 in coronal view; from Kadzielnia, sample K-MB-45, early Famennian, Late *crepida* Zone. **D.** Branchial denticle with triple rows of cusps, MWGUW/Ps/1/233; from Łagów, sample Łd 2a+3, middle Famennian, *marginifera* Zone. **E.** Branchial denticle with double row of cusps, MWGUW/Ps/1/230; from Dzikowiec, sample Eb-N, Tournaisian, Late *duplicata-sandbergi* Zone. **F.** Branchial denticle with single row of cusps, MWGUW/Ps/1/231, from Dzikowiec, same sample. Scale bars = 0.5 mm.

do not. The protacrodontid type was first found with the remnants of *Protacrodus vetustus* in the upper Frasnian of Bad Wildungen (Gross, 1938). Such scales are very regular, somewhat similar to those of the acanthodians, with a rhomboidal, almost flat crown surface and a bulbous base (Fig. 9B). The ctenacanthid type has loosely arranged, posteriorly directed odontodes in the crown (Fig. 9C) and usually a concave ventral side of the base. Such scales are typical of *Glencartius* (originally *Ctenacanthus*) *costellatus* (Fig. 7C–F). In the hybodontid scales (the type was based on Mesozoic representatives of *Hybodus*), the lower parts of odontodes are vertical and only the ends are directed backwards (Fig. 9A; compare Reif, 1978, fig. 2).

Both in the Famennian and the Mississippian, numerous branchial denticles, probably of the symmoriiform origin,

were found. Among them there are denticles with a single row of cusps ("*Stemmatias simplex*", Fig. 9F), a double row of cusps ("*Stemmatias bicristatus*", Fig. 9E), and there is even one element with three rows of cusps, looking like a fan (Fig. 9D). Rare irregular mucous membrane denticles, similar to those described by Liao *et al.* (2007, fig. 5D–G) also were observed.

Sarcopterygian remains

The most common group of Sarcopterygii in the Late Devonian of Poland are the Onychodontiformes. Their teeth, with a characteristic ornament composed of parallel ridges with a secondary Christmas-tree pattern (Fig. 10E) are particularly abundant in the early Frasnian strata, in



Fig. 10. Acanthodian and sarcopterygian remains from the Upper Devonian of the Holy Cross Mountains. **A, B.** Acanthodian remains. **A** – *Acanthodes* type scale, unnumbered specimen, from Plucki, late Frasnian, *linguiformis* Zone, **B** – Tooth whorl, ZPAL P.IV/252, sample Ost-5, *expansa* Zone. **C–H.** Sarcopterygian remains. **C.** *Onychodus jaekeli* Gross, 1933, tip of a parasymphyseal tooth, MWGUW/Ps/1/235; from Kadzielnia, sample K-137, Frasnian, Late *hassi-rhenana* Zone. **D, E.** *Strunius rolandi*, lateral teeth, MWGUW/Ps/1/238–239, from Wietrzna, sample WTR-5, late Frasnian, *rhenana* Zone. **F.** *Strunius rolandi* (Gross, 1936), parasymphyseal tooth, MWGUW/Ps/1/236, sample WTR-5. **G.** *S. rolandi*, close-up of the surface of MWGUW/Ps/1/236. **H.** Cosmine lepidotrichium, MWGUW/Ps/1/237, from Wietrzna, sample WTR-7, early Frasnian, Early *falsiovalis*–*E. hassi* Zone. Scale bars: A, B, G = 0.1 mm, C–F, H = 0.5 mm.

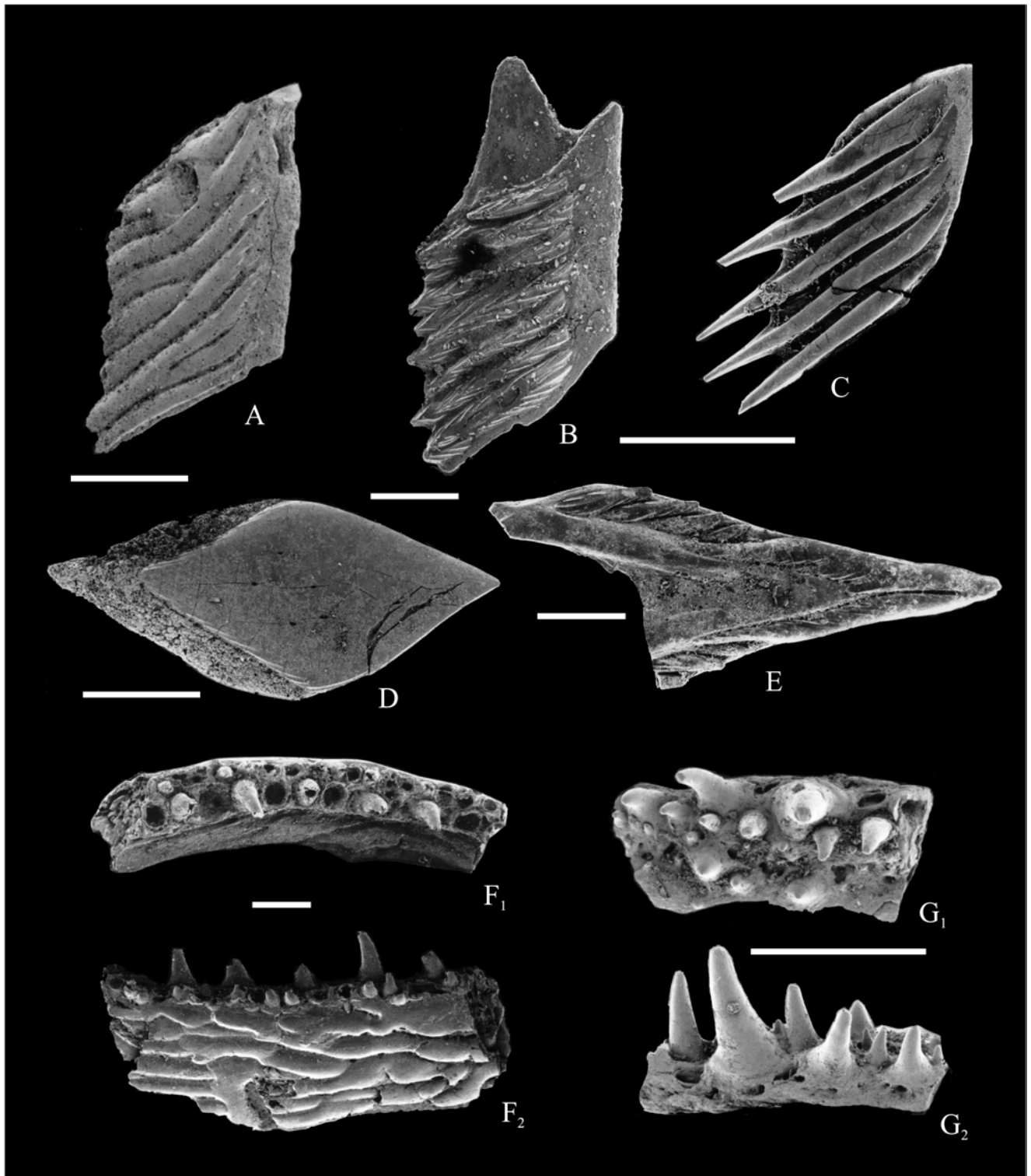


Fig. 11. Actinopterygian remains from the Upper Devonian of the Holy Cross Mountains. **A.** *Mimia*-type scale, ZPAL P.IV/242, from Wietrznia, sample WTR-5, late Frasnian, *rhenana* Zone. **B.** *Moythomasia*-type scale, ZPAL P.IV/239, from Wietrznia, sample W V, early Frasnian, *punctata* zone. **C.** *Grossator*-type, juvenile scale, ZPAL P.IV/241, from Wietrznia, WTR-9, early Frasnian, Early *falsiovalis*–*E. hassi* Zone. **D.** *Kentuckia*-type scale, MWGUW/Ps/1/238, from Góra Łgawa, sample R-2, late Frasnian, Late *rhenana* Zone. **E.** Fulcral scale, ZPAL P.IV/245, from Ostrówka, sample Ost-12, middle Famennian, *trachytera* Zone. **F–G.** Pieces of actinopterygian jaws. **F** – MWGUW/Ps/1/241, from Domaszowice, sample Dm 1–2, late Frasnian, *rhenana* Zone, **G** – ZPAL P.IV/247, from Wietrznia, sample WTR-9, early Frasnian, Early *falsiovalis*–*E. hassi* Zone. Scale bars = 0.5 mm.

the facies connected with carbonate buildups. There were noted numerous teeth of *Strunius rolandi* (Gross, 1936) from the parasymphyseal tooth whorls, long and slender, with two minute accessory cusplets (Fig. 10F), as well as short, simple, conical lateral teeth (Fig. 10E, D). A single, harpoon-like tip of a parasymphyseal tooth of *Onychodus jaekeli* Gross, 1933 was encountered in a sample from Wietrzna (Fig. 10C). In the collection of the Institute of Palaeobiology in Warsaw, there also is a yet undescribed fragmentary jaw of *Onychodus sigmoides* Newberry, 1857 (M. Ginter, pers. obs.). All these fossils are comparable to the sarcopterygian material described by Jessen (1966).

Remains of the Dipnoi from the Holy Cross Mountains were described by Gorizdro-Kulczycka (1950) and those of the rare actinistians (*Diplocercides* Stensiö, 1922) recently have been studied by Szrek (2007).

Actinopterygian remains

The teeth and scales of primitive Actinopterygii, commonly called “palaeoniscoids”, were often found in the Devonian and Carboniferous samples studied from all regions, without any recognisable pattern of occurrence. Generally, the Devonian teeth are simple, smooth cones made of dentine and those from the Mississippian possess transparent acrodine tips. A few morphotypes of rhomboid, ganoid body scales were proposed by Ginter (1994), following suggestions from the late Russian palaeontologist, Dmitry Esin (pers. comm. with M. Ginter, Moscow, 1993). The names refer to scales found on the bodies of articulated specimens from Australia and Ohio, USA (e.g., Gardiner, 1984). The *Moythomasia* type is covered with strong ridges, secondarily ornamented with the Christmas-tree pattern (Fig. 11B); the *Mimia* type has closely packed, wavy ridges (11A); the *Grossator* type has straight, separate ridges, in the small (juvenile?) scales sticking out from the scale in its posterior part (Fig. 11C); and the *Kentuckia* type is almost completely smooth (Fig. 11D).

Occasionally, particularly in the Frasnian of the Holy Cross Mountains, fragments of actinopterygian jaws with teeth were found (Fig. 11F, G).

Acanthodian scales

Only one type of acanthodian scales was found thus far in the material studied: with a diamond-shaped, completely smooth crown and a bulbous base (*Acanthodes* type; Fig. 10A; Ginter, 1995, fig. 3G, H). Such scales occur both in the Devonian and Carboniferous part of the collection. A single piece of an acanthodian, symphyseal tooth whorl was recovered from the Famennian of Ostrówka (sample Ost-5; Fig. 10B), similar to the one illustrated by Ginter *et al.* (2002, plate 6, fig. S).

Thelodont scales and teeth

A few elongated scales, probably representing the thelodont genus *Australolepis* Turner and Dring, 1981 from the Givetian of Świętomarz area were recently described by Turner and Ginter (2018).

SIGNIFICANCE OF POLISH MIDDLE PALAEOZOIC ICHTHYOFAUNA IN BIOSTRATIGRAPHY AND PALAEOECOLOGY

There have been several attempts in the past to apply Middle Palaeozoic fish microfossils and especially chondrichthyan teeth, as tools in biostratigraphy and the reconstruction of palaeoenvironments. However, thus far most of such endeavours were of rather limited success. Ginter and Ivanov (1995a) published the proposition of a subdivision of a part of the Middle and Late Devonian, based on the evolution of teeth in *Phoebodus*, a chondrichthyan genus, commonly occurring in the seas surrounding the Laurussia. Six zones were established; the lower boundary of each zone is based on the first appearance of a species of *Phoebodus*. However, already a few years after publication of this zonal scheme, it became obvious that not all of the proposed zones are of the same fidelity, quality, and usefulness. For example, the upper part of the *Ph. sophiae* Zone (lower Frasnian) should be reconsidered, using richer and more diverse microvertebrate material from some other region preserving pelagic deposits. As well, the first appearance of *Ph. gothicus* in the other regions of the world, e.g., in Iran, is much earlier than in Poland (Ginter *et al.*, 2002). Moreover, further studies on Middle and Late Devonian shark communities from all over the world have shown that many phoebodont shark index species are restricted to the carbonate platforms, developed along continental margins, and are very rarely found in deep water or nearshore facies.

Investigation of pelagic chondrichthyan assemblages from the late Famennian (*Pa. expansa*-*Pa. praesulcata* Zone) of the regions between Laurussia and Gondwana (including the Holy Cross Mountains) has shown that the relative abundances of certain chondrichthyan tooth forms differ in relation to depth and/or distance from land. The definitions of three distinct biofacies based upon these differences have been proposed by Ginter (2000, with later modifications, summarised by Ginter *et al.*, 2010). The chondrichthyan biofacies were named after the most common representative of a predominating category. According to the presumed water depth, from the deepest to the shallowest, the biofacies are:

1. *Jalodus* biofacies: more than 25% of *Jalodus*, less than 25% of *Phoebodus* and *Thrinacodus tranquillus*, and less than 10% protacrodontids and other crushing teeth.
2. *Phoebodus* biofacies: more than 25% of *Phoebodus* and *Th. tranquillus*.
3. *Protacrodus* biofacies: more than 25% protacrodontids, less than 25% *Phoebodus* and *Th. tranquillus*.

In this model, the southern part of the Holy Cross Mountains in the late Famennian, and perhaps also a large part of southern Poland, generally represented the intermediate *Phoebodus* biofacies. The typical assemblage, e.g., from Ostrówka, consists of *Ph. gothicus*, *Ph. limpidus*, *Jalodus australiensis*, *Thrinacodus tranquillus* and *Squatina glabrum*, with the predominance of the phoebodontids.

However, shark's teeth can be useful tools in the palaeoecological analysis of upper Famennian rocks, only if a statistically valid number of precisely dated specimens is

available. Therefore, there are several general limitations to the method, especially when it is compared to the identification of palaeoenvironments by conodonts. First of all, the number of shark teeth, extracted from a typical sample, is usually less than 30 specimens, which makes the usefulness of such assemblages in statistics problematic. Furthermore, the distribution of shark teeth in rocks is very irregular. Samples, collected from the same locality and horizon, separated by a distance of ten metres might yield vastly different results in terms of both the number of specimens and, to some extent, taxonomic representation and diversity.

One interesting observation, though still insufficiently studied, can be added to the above analysis. In the samples from the earlier parts of the Frasnian, i.e. the times of the still important influence of carbonate buildups in the study area, the relative abundance of chondrichthyan teeth is low and the osteichthyans, especially the onychodonts, play the major role. There are several samples, e.g., from Kadzielnia, with quite a few ichthyoliths, but completely devoid of sharks' teeth. In the late Frasnian and especially in the Famennian, after the drowning of the carbonate platforms (Szulczewski *et al.*, 1996), the situation and the chondrichthyans begin to predominate in the assemblages. In the Mississippian, the place occupied earlier by the phoebodonts in the open-marine, relatively deeper environments, was taken over by the Falcitidae (Ginter *et al.*, 2015; Ginter and Złotnik, 2019).

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List of studied samples from the localities in southern Poland containing fish remains.

Abbreviations: E – early, M – middle, L – late, *Ph.* – *Phoebodus*,
denticles - chondrichthyan mucous membrane denticles.

Sites and samples	Ichthyofauna	Number of specimens	Age: conodont zones
HOLY CROSS MOUNTAINS			
Laskowa Hill			
L-II/a	<i>Ph. sophiae</i> <i>Ph. fastigatus</i> <i>Omalodus grabaui</i> onychodont teeth <i>Moythomasia</i> scales	25 4 3 >10 5	M.–L. <i>varcus</i>
L-II/14	<i>Ph. sophiae</i> protacrodont scales <i>Grossator</i> scales onychodont teeth Agnathan (?) scales “ <i>Ohioaspis</i> ”	4 5 2 1 2	<i>hermanni-cristatus-disparilis</i>
L-II/18	<i>Ph. sophiae</i> <i>Ph. fastigatus</i> protacrodont scales Agnathan (?) scale “ <i>Ohioaspis</i> ”	1 2 14 1	?M. <i>varcus-disparilis</i>
L-II/19	<i>Ph. sophiae</i> protacrodont scales palaeoniscoid jaw fragments and teeth	19 10 3	<i>hermanni-cristatus-disparilis</i>
L-II/26	<i>Ph. sophiae</i> protacrodont scales palaeoniscoid teeth	3 1 2	L. <i>hermanni-cristatus-disparilis</i>
L-II/29	ctenacanth scales	2	<i>disparilis</i>
L-II/32	ctenacanth scales	2	?
L-IV/18a	<i>Ph. sophiae</i>	11	<i>hermanni-cristatus</i>
Kostomloty			
Km-E	protacrodont scale	1	<i>linguiformis?</i>
Km-W	<i>Ph. bifurcatus</i>	2	<i>rhenana</i>
Kt-4/23, 24	ctenacanth scales	3	E. Famennian
	<i>Acanthodes</i> scales	2	
	<i>Moythomasia</i> scale?	1	
Ślichowice			
S-6A	ctenacanth tooth (<i>Cladodoides?</i>)	1	M. <i>triangularis</i>
	ctenacanth scale	1	
S-8	ctenacanth tooth (<i>Cladodoides?</i>)	1	E. <i>crepida</i>
	<i>Protacrodus</i> sp. cladodont tooth	1 2	
S-8A	cladodont tooth	1	E. <i>crepida</i>
	<i>Protacrodus</i> sp.	1	
S-10	ctenacanth scales	2	E. <i>crepida</i>
S-255	<i>Protacrodus</i> sp.	1	?
Dalnia			
D-F	<i>Jalodus australiensis</i>	10	condensed L. <i>expansa-crenulata</i>
Wietrznia			
W-23	fragment of <i>Protacrodus?</i>	1	M. <i>crepida</i>
	ctenacanth scale	1	
	hybodont scale (?)	1	
W-29	osteichthyan tooth	1	<i>linguiformis</i>
W-31	<i>Ph. fastigatus</i>	2	L. <i>hassi</i> –E. <i>rhenana</i>
W-33	ctenacanth scales	2	L. <i>triangularis</i>
W-35	palaeoniscoid tooth	1	M. <i>crepida</i>
W-36	ctenacanth scales	2	M. <i>crepida</i>
W-37	<i>Protacrodus vetustus</i>	1	M. <i>crepida</i>
	palaeoniscoid tooth	1	

Sites and samples	Ichthyofauna	Number of specimens	Age: conodont zones
W-45	<i>Acanthodes</i> scale	1	<i>L. triangularis</i>
W-46	osteichthyan jaw fragment	1	<i>L. triangularis</i>
W-47	<i>Protacrodus vetustus</i>	1	<i>L. triangularis</i>
	ctenacanth scales	2	
	denticle	1	
	jaw fragment?	1	
W-48	ctenacanth scale	1	<i>L. triangularis</i>
W-62	ctenacanth scales	3	<i>M. crepida</i>
	spine fragments?	3	
W-66	onychodont tooth	1	<i>punctata</i>
W-67	<i>Ph. fastigatus</i> or <i>Ph. latus</i>	1	<i>E. rhenana</i>
	phoebodont?	1	
W-68	<i>Wellerodus</i> sp.	2	<i>E. rhenana</i>
	<i>Grossator</i> scale	1	
W-72	jaw fragment	1	<i>E.-M. crepida</i>
W-B	dipodont shark tooth	1	<i>E. rhenana</i>
W-C	<i>Phoebodus</i> sp.	1	<i>E. rhenana</i>
	<i>Strunius</i> sp.	1	
W-D	<i>Ph. latus</i>	1	<i>E. rhenana</i>
W-E	onychodont teeth	2	<i>E. rhenana</i>
W-F	cladodont tooth base	1	<i>L. rhenana</i>
W III	<i>Ph. fastigatus</i>	1	<i>transitans</i>
	<i>Strunius rolandi</i>	5	
	skeletal fragments		
W IV	palaeoniscoid jaw fragments and teeth	5	<i>punctata</i>
W V	<i>Moythomasia</i> scale	1	<i>punctata</i>
W VI	<i>Strunius rolandi</i>	1	<i>punctata</i>
	protacrodont scale	1	
W VIa	<i>Ph. fastigatus</i>	1	<i>hassi-jamieae?</i>
5	palaeoniscoid teeth	5	<i>falsiovalis</i>
8	onychodont teeth	3	<i>falsiovalis</i>
	<i>Mimia</i> scales	2	
9	cosmine fragment	1	<i>falsiovalis?</i>
	palaeoniscoid jaw fragments and teeth	3	
19	<i>Strunius rolandi</i>	2	<i>hassi-jamieae?</i>
20	cosmine fragment	1	<i>hassi-jamieae?</i>
	osteichthyan teeth	5	
27a	osteichthyan teeth	3	<i>L. falsiovalis</i>
29	<i>Strunius rolandi</i>	2	<i>L. falsiovalis</i>
	<i>Moythomasia</i> scale	1	
34	<i>Grossator</i> scale	1	<i>transitans</i>
37	palaeoniscoid teeth	3	<i>hassi-jamieae?</i>
38	sarcopterygian lepidotrichium	1	<i>hassi-jamieae?</i>
39	onychodont teeth		<i>hassi-jamieae?</i>
40	<i>Ph. fastigatus</i>	1	<i>hassi-jamieae?</i>
	onychodont teeth	3	
43	onychodont teeth	2	<i>hassi-jamieae?</i>
47	onychodont teeth	2	<i>E. rhenana</i>
	palaeoniscoid teeth	3	
WTR-4	<i>Strunius rolandi</i>	1	<i>rhenana</i>
	onychodont teeth	3	
WTR-5	<i>Ph. latus</i>	1	<i>rhenana</i>
	protacrodont scales	8	
	hybodont scales	5	
	ctenacanth scale	1	
	<i>Grossator</i> scales	>10	
	<i>Strunius rolandi</i>	5	
	palaeoniscoid jaw fragments and teeth	8	
small spines	2		
WTR-7	ctenacanth scales	>10	<i>E. falsiovalis</i> – <i>E. hassi</i>
	<i>Strunius rolandi</i>	3	
	<i>Moythomasia</i> and <i>Grossator</i> scales	>10	
	osteichthyan bone fragments and teeth	>10	

Sites and samples	Ichthyofauna	Number of specimens	Age: conodont zones
WTR-8	hybodont scale	1	<i>E. falsiovalis</i> – <i>E. hassi</i>
	onychodont tooth	1	
	<i>Mimia</i> scales	2	
WTR-9	cosmine fragment	1	<i>E. falsiovalis</i> – <i>E. hassi</i>
	<i>Grossator</i> scale	1	
	<i>Moythomasia</i> scale	1	
	osteichthyan teeth	2	
	palaeoniscoid jaw fragments and teeth	3	
Kadzielnia			
K-137	<i>Strunius</i> sp.	3	<i>L. hassi-rhenana</i>
	<i>Onychodus jaekeli</i>	1	
K-138II	<i>Strunius</i> sp.	1	<i>rhenana</i>
K-150	<i>Cladodooides wildungensis</i>	1	<i>rhomboidea</i>
K-151	<i>Cladodooides wildungensis</i>	1	<i>rhomboidea</i>
K-161ś	onychodont tooth	1	<i>rhomboidea</i>
K-164	<i>Cladodooides wildungensis</i> (?)	1	<i>E.</i> – <i>M. crepida</i>
K-165	onychodont tooth	1	<i>E. rhenana-linguiformis</i>
K-202	palaeoniscoid jaw fragments and teeth	>10	<i>punctata</i> – <i>E. hassi</i>
Kd-13	<i>Grossator</i> scale fragments	3	<i>E. rhenana</i>
	palaeoniscoid tooth	1	
K-MB-Mantic.	<i>Ph. latus</i>	1	<i>rhenana</i>
	protacrodont scales	>10	
	<i>Grossator</i> scales	2	
	palaeoniscoid scales	3	
K-MB-45	protacrodont scales	2	<i>L. crepida</i>
	palaeoniscoid teeth	3	
K-MB-68	“ <i>Cladodus</i> ”	2	<i>rhomboidea</i>
K-MB-69	<i>Symmorium</i> sp.	1	<i>rhomboidea</i>
	“ <i>Cladodus</i> ” typ E	1	
K-MB-85	<i>Strunius rolandi</i>	6	<i>crepida</i>
	<i>Grossator</i> scales	2	
K-462 w 50	<i>Clairina marocensis</i>	1	<i>crepida</i>
Psie Górki			
P-25	chondrichthyan scale	1	<i>E. triangularis</i>
P-29	ctenacanth scale	1	<i>E. triangularis</i>
P-30	ctenacanth scale	1	<i>E. triangularis</i>
PG-T	<i>Cladodooides wildungensis</i>	2	<i>linguiformis</i>
	protacrodont scale	1	
PG-4	Stethacanthidae indet.	1	<i>E. triangularis</i>
Karczówka			
Kr-7	<i>Ph. bifurcatus</i>	16	<i>rhenana</i>
	<i>Strunius rolandi</i>	7	
Kowala-Wola			
Ko-SF	<i>Cladodooides wildungensis</i>	2	<i>linguiformis</i>
	<i>Protacrodus vetustus</i>	1	
Kx-12	<i>Cladodooides wildungensis</i>	1	<i>linguiformis</i>
Ko-24	chondrichthyan scales	2	<i>E. triangularis</i>
	acanthodian scales	2	
Ko-35	<i>Cladodooides wildungensis</i>	2	<i>L. triangularis</i>
Ko-36	acanthodian scales	3	<i>L. triangularis</i>
Kow-1	<i>Psephodus</i> cf. <i>magnus</i>	1	<i>L. trachytera</i>
KI-50	<i>Squatinactis</i> sp.	1	<i>E. expansa</i>
KI-51	cladodont tooth	1	<i>E. expansa</i>
	chondrichthyan scale	1	

Sites and samples	Ichthyofauna	Number of specimens	Age: conodont zones
Jablonna			
J-63, 90	<i>Ph. limpidus</i> cladodont teeth	1 3	<i>trachytera-postera</i>
J-III l	cladodont tooth ctenacanth scales	1 2	<i>M. triangularis</i>
J-III ł	ctenacanth scales	2	<i>M. triangularis</i>
J-III o (1843)	Stethacanthidae indet.	1	<i>M. triangularis</i>
J-III s (1846)	<i>Protacrodus vetustus</i> , tooth and whorl	2	<i>M. triangularis</i>
J-IVe (1679)	<i>Ph. gothicus</i>	1	?
J-1632	<i>Protacrodus serra</i> (?)	1	<i>L. marginifera</i> – <i>E. trachytera</i>
J-03	cladodont tooth ctenacanth scale <i>Acanthodes</i> scale	2 1	<i>triangularis</i>
J-07	ctenacanth scales	2	<i>E. –M. crepida</i>
J-24	phoebodont teeth <i>Jalodus australiensis</i> <i>Thrinacodus tranquillus</i> cladodont teeth <i>Protacrodus serra</i> ctenacanth scale branchial denticle palaeoniscoid tooth	2 3 4 2 6 1 1 1	<i>trachytera</i>
J-38	ctenacanth scales palaeoniscoid bone fragments	3	<i>triangularis</i> ?
Łgawa Hill			
set R2	fragment of cladodont tooth <i>Strunius rolandi</i> <i>Kentuckia</i> scale	2 7 1	<i>L. rhenana</i>
Grabina			
Grab	fragment of <i>Ph. bifurcatus</i> ? <i>Protacrodus</i> sp. protacrodont or ctenacanth scale <i>Strunius rolandi</i>	1 2 1 2	<i>L. hassi</i> – <i>E. rhenana</i>
Domaszowice			
Dm 1, 2	protacrodont scale <i>Strunius rolandi</i> fragment of <i>Mimia</i> jaws?	1 7 2	<i>rhenana</i>
Ostrówka			
Ost 1A	<i>Ph. gothicus</i> <i>Squatina</i> sp. cladodont tooth protacrodont scale <i>Mimia</i> ? scales <i>Acanthodes</i> scale palaeoniscoid jaw fragments	4 2 1 1 7 1	<i>trachytera</i>
Ost 2	<i>Ph. gothicus</i> <i>Ph. limpidus</i> <i>Ph. cf. typicus</i> <i>Jalodus australiensis</i> M2 <i>Squatina glabrum</i> cladodont teeth protacrodont scales denticles <i>Moythomasia</i> scales	1 2 1 2 1 4 3 2 3	<i>E. expansa</i> – <i>M. praesulcata</i>

Sites and samples	Ichthyofauna	Number of specimens	Age: conodont zones
Ost 5	<i>Ph. gothicus</i> <i>Jalodus australiensis</i> M1 and M2 <i>Th. tranquillus</i> <i>Squatinactis glabrum</i> cladodont teeth <i>Protacrodus serra</i> protacrodont scales denticles fin spines <i>Acanthodes</i> scales ischnacanthiform tooth whorl <i>Moythomasia</i> scales <i>Kentuckia</i> scales palaeoniscoid bone fragments problematic plates – Agnatha?	24 10 5 11 5 4 >10 >10 2 3 1 2 5 >10 3	<i>expansa</i>
Ost 7	<i>Ph. gothicus</i> <i>Jalodus australiensis</i> phoebodont teeth <i>Thrinacodus tranquillus</i> (?) <i>Squatinactis glabrum</i> cladodont teeth <i>Protacrodus serra</i> protacrodont scales <i>Stemmatias</i> branchial denticles denticles <i>Acanthodes</i> scales <i>Kentuckia</i> scales	1 4 3 1 3 2 2 >10 5 3	<i>postera</i> –E. <i>expansa</i>
Ost 11	<i>Jalodus australiensis</i> <i>Squatinactis glabrum</i> protacrodont scales? denticles Grossator scales	2 1 1 2 6	<i>trachytera</i> – <i>postera</i>
Ost 12	<i>Ph. gothicus</i> <i>Thrinacodus tranquillus</i> <i>Symmorium</i> aff. <i>reniforme</i> <i>Protacrodus serra</i> Grossator scales palaeoniscoid fulcral scales <i>Acanthodes</i> scales	8 6 3 1 >10 2	<i>trachytera</i>
Ost 284.II.265	<i>Jalodus australiensis</i> <i>Thrinacodus tranquillus</i> cladodont teeth <i>protacrodont scales</i> branchial and other denticles	11 5 6 4 >10	<i>postera</i> –M. <i>praesulcata</i>
Ost 284.II.293	<i>Ph. gothicus</i> <i>Ph. limpidus</i> <i>Jalodus australiensis</i> <i>Thrinacodus tranquillus</i> <i>Squatinactis</i> sp. cladodont teeth ctenacanth scales protacrodont scales denticles <i>Acanthodes</i> scales	4 1 5 1 1 3 3 5 2 3	<i>postera</i> –E. <i>expansa</i>
Ost Am VII/185	<i>Ph. limpidus</i> <i>Jalodus australiensis</i> <i>Thrinacodus tranquillus</i> cladodont teeth <i>Protacrodus serra</i> protacrodont scales branchial and other denticles unidentified plates	6 3 2 6 4 7 >10 3	E. <i>expansa</i> –M. <i>praesulcata</i>
F-8	„Cladodus” typ B <i>Protacrodus serra</i> palaeoniscoid jaw fragments	1 3	L. <i>expansa</i> –M. <i>praesulcata</i>

Sites and samples	Ichthyofauna	Number of specimens	Age: conodont zones
F-9	<i>Ph. gothicus</i>	1	<i>L. expansa</i> – <i>E. praesulcata</i>
	<i>Ph. limpidus</i> (holotyp)	1	
	“Cladodus” typ D	1	
	<i>Protacrodus serra</i>	1	
	“Cladodus” typ B	1	
F-10	“Cladodus” typ C	1	<i>L. expansa</i> – <i>E. praesulcata</i>
	<i>Protacrodus</i> (?)	2	
F-11	<i>Ph. gothicus</i>	3	<i>L. expansa</i> – <i>E. praesulcata</i>
	<i>Ph. limpidus</i>	5	
	<i>Jalodus australiensis</i>	11	
	<i>Thrinacodus tranquillus</i>	3	
	<i>Squatina</i> sp.	1	
	cladodont teeth	5	
denticles	2		
F-13I	<i>Jalodus australiensis</i>	1	<i>E.</i> – <i>M. expansa</i>
F-13II	<i>Ph. gothicus</i>	2	<i>E. postera</i> – <i>E. expansa</i>
F-14	<i>Ph. gothicus</i>	2	<i>L. trachytera</i>
	<i>Thrinacodus tranquillus</i> (holotype)	1	
	Moythomasia scales (<i>Grossator</i> ?)	3	
	fulcral scale	1	
F-16	palaeoniscoid jaw fragment	1	<i>L. trachytera</i>
F-17	palaeoniscoid jaw fragment	1	<i>L. trachytera</i>
A-2	<i>Thrinacodus tranquillus</i>	1	<i>L. trachytera</i> ?
	cladodont tooth	1	
A-3	<i>Ph. gothicus</i>	1	<i>L. trachytera</i>
	<i>Grossator</i> scale	1	
D-3	<i>Jalodus australiensis</i>	1	<i>L. marginifera</i>
	<i>Squatina</i> <i>glabrum</i>	1	
	cladodont teeth	2	
O.W.1	<i>Jalodus australiensis</i>	9	<i>M.</i> – <i>L. expansa</i>
	acanthodian scales	5	
O.W.2	<i>Ph. gothicus</i>	1	<i>M.</i> – <i>L. expansa</i>
	<i>Jalodus australiensis</i>	9	
	<i>Thrinacodus tranquillus</i>	1	
	acanthodian scales	3	
	palaeoniscoid scales	1	
O.W.3	<i>Ph. gothicus</i>	1	<i>marginifera</i> – <i>trachytera</i>
	<i>Thrinacodus tranquillus</i>	1	
	branchial denticle	1	
	acanthodian scales	11	
O.W.4	<i>Ph. gothicus</i>	3	<i>marginifera</i> – <i>trachytera</i>
	<i>Thrinacodus tranquillus</i>	2	
	acanthodian scales	3	
	palaeoniscoid scales	7	
O.W.5	palaeoniscoid scale	1	<i>marginifera</i> – <i>trachytera</i>
O.W.6	<i>Ph. limpidus</i>	1	<i>marginifera</i> – <i>trachytera</i>
	palaeoniscoid scales	5	
O.W.7	<i>Ph. gothicus</i>	1	<i>E. expansa</i>
	<i>Jalodus australiensis</i>	1	
	acanthodian scales	2	
O.W.9	<i>Ph. gothicus</i>	1	<i>M.</i> – <i>L. expansa</i>
	<i>Jalodus australiensis</i>	5	
	ctenacanthid scale	1	
O.W.10	acanthodian scales	5	<i>M.</i> – <i>L. expansa</i>
	<i>Ph. gothicus</i>	1	
	<i>Thrinacodus tranquillus</i>	1	
P.81	<i>Protacrodus serra</i>	1	<i>M.</i> – <i>L. expansa</i>
	acanthodian scales	2	
	<i>Ph. gothicus</i>	1	
P.81	<i>Jalodus australiensis</i>	1	<i>M.</i> – <i>L. expansa</i>
	<i>Squatina</i> <i>glabrum</i>	1	
	palaeoniscoid scales	1	
		3	

Sites and samples	Ichthyofauna	Number of specimens	Age: conodont zones
P.83	<i>Ph. gothicus</i> <i>Jalodus australiensis</i> <i>Squatinactis glabrum</i> <i>Protacrodus serra</i> cladodont teeth branchial denticles acanthodian scales	10 3 3 2 2 1 25	M.–L. <i>expansa</i>
Todowa Grząba			
TG-CP	<i>Thrinacodus tranquillus</i> <i>Denaea</i> sp.	3 1	late Famennian– Tournaisian mixed fauna
D-TG	<i>Thrinacodus dziki</i> <i>Bransonella nebraskensis</i> <i>Denaea</i> cf. <i>fournieri</i> <i>Denaea wangi</i> <i>Denaea williamsi</i> Falcatae indet. euselachian teeth branchial denticles <i>Stemmatias</i> chondrichthyan scales palaeoniscoid scales palaeoniscoid teeth	11 4 33 7 5 4 2 6 >10 >10 >10	Viséan 3c, <i>Gn. bilineatus</i>
Miedzianka			
Md-I/1	<i>Protacrodus</i> sp. tooth whorl fragment <i>Strunius rolandi</i> <i>Strunius rolandi</i> , tooth whorl fragment	1 10 1	<i>crepida</i>
Md-I/5	acanthodian jaw fragment?		?
Md-2	<i>Protacrodus</i> sp.? chondrichthyan scale	1 1	<i>linguiformis</i>
Md-3	cladodont teeth Osteichthyes bone fragment	2 1	?
Md-6	<i>Ph. turnerae</i> <i>Squatinactis glabrum</i> hybodont scale	2 2 1	<i>rhomboidea-marginifera</i> ?
MB	<i>Strunius rolandi</i>	2	<i>linguiformis</i>
M-5	<i>Cladodoides wildungensis</i>	1	M. <i>triangularis</i>
M-EZ	<i>Cladodoides wildungensis</i> ctenacanth scale	1 1	L. <i>triangularis</i>
Zbrza			
GR-Z	<i>Ph. gothicus</i>	5	L. <i>trachytera</i> –E. <i>expansa</i> mixed fauna
Łagów			
Ł-04-10–24	<i>Ph. turnerae-gothicus</i> palaeoniscoid scales	1 2	<i>marginifera</i>
Ł-05	<i>Ph. gothicus</i> <i>Squatinactis</i> sp. cladodont tooth protacrodont scales hybodont scale? branchial denticle <i>Acanthodes</i> scales <i>Moythomasia</i> scale	2 1 1 5 1 1 2 1	E. <i>marginifera</i>
Ł-09	<i>Ph. gothicus</i> <i>Squatinactis glabrum</i> cladodont teeth ctenacanth scales branchial denticle? <i>Acanthodes</i> scales palaeoniscoid jaw fragment	1 1 2 2 1 2 1	E. <i>marginifera</i>
Ł-S59-1	protacrodont scale hybodont scale palaeoniscoid teeth	1 1 >10	E.–L. <i>marginifera</i>
Ł-S59-2	<i>Ph. gothicus</i>	3	E.–L. <i>marginifera</i>

Sites and samples	Ichthyofauna	Number of specimens	Age: conodont zones
Ł-24-26	<i>Squatina glabrum</i>	6	<i>E. marginifera</i>
	<i>Protacrodus serra</i>	2	
	hybodont scales	5	
	<i>Strunius</i> sp.?	1	
	<i>Grossator</i> scales	>10	
Ł-blok	<i>Squatina glabrum</i>	1	<i>marginifera</i>
	hybodont scales	2	
	<i>Grossator</i> scales	7	
Łd 2a+3	branchial denticle	1	<i>marginifera</i>
Plucki			
P-1	<i>Cladodoides wildungensis</i>	4	<i>linguiformis</i> , upper part
	<i>Protacrodus vetustus</i>	1	
	<i>Moythomasia</i> scales	2	
	<i>Acanthodes</i> scales	>10	
	acanthodian spines?	3	
KWK-3	<i>Cladodoides wildungensis</i>	1	<i>E. triangularis</i>
	chondrichthyan scales acanthodian scales	2	
KWK-4	<i>Cladodoides wildungensis</i> acanthodian scales	2	<i>E. triangularis</i>
Jancyce			
Jan-1	ctenacanth scales	2	<i>M. crepida</i>
Jan-4	chondrichthyan scale	1	<i>M. crepida</i>
	palaeoniscoid jaw fragm.	1	
Tudorów			
Td-II/7a	<i>Ph. bifurcatus</i>	2	<i>rhenana</i>
	<i>Ph. latus</i>	6	
Wzdół Rządowy			
P-13	<i>Phoebodus</i> sp.	1	<i>E. trachytera</i>
P-A-12	<i>Jalodus australiensis</i> M2	1	<i>E. trachytera</i>
Świętomarz			
42/38	thelodont scales – <i>Australolepis</i> ?	3	Givetian
16/15	chondrichthyan scale?	1	Givetian
43/41	<i>Acanthodes</i> scales	3	Givetian
51/55	thelodont scales – <i>Australolepis</i> ?	3	Givetian
LUBLIN AREA			
Włodawa IG 4 borehole			
Sample	<i>Glencartius costellatus</i> tooth <i>Glencartius costellatus</i> scales <i>Bransonella nebraskensis</i>	1 >100 1	late Viséan
CRACOW UPLAND			
Dębnik			
Dz-7-Dz-11	osteichthyan teeth, scales and jaw fragments		<i>linguiformis</i>
Dz-12-Dz-19	<i>Cladodoides wildungensis</i>	8	<i>triangularis</i>
	chondrichthyan scales and denticles osteichthyan teeth, scales and jaw fragments	13	
Czatkowice			
A	<i>Thrinacodus ferox</i>	4	Tournaisian, <i>delicatus-cuneiformis</i>
	<i>Thrinacodus ferox</i> (symmetr.)	1	
	<i>Jalodus</i> sp.	1	
	Falcatidae indet.	8	
	cladodont teeth	2	
	protacrodont teeth	2	
	ctenacanth scales	2	
	hybodont scales	5	
	branchial denticles	2	
	acanthodian scales	1	
	palaeoniscoid scales, bone fragments and teeth	>10	

Sites and samples	Ichthyofauna	Number of specimens	Age: conodont zones
2K	<i>Thrinacodus ferox</i> hybodontid?	1 1	?
11	<i>Thrinacodus ferox</i> cladodont tooth eugeneodontid? palaeoniscoid scales	1 2 1 5	Viséan, <i>M. beckmanni</i> (? <i>texanus</i>)
Czat-1	<i>Thrinacodus ferox</i> palaeoniscoid teeth	2	Tournaisian, <i>delicatus-cuneiformis</i>
Czerna			
Cz-1	<i>Thrinacodus ferox</i> Falcatidae indet. <i>Denaea wangi</i> ctenacanth tooth Cladodontomorphi indet. <i>Cassiodorus margaritae</i> ctenacanth scales palaeoniscoid scales and teeth palaeoniscoid vertebrae and bone fragments	5 12 3 1 3 3 10 >10 >10	Viséan, <i>bilineatus</i>
Olkusz area boreholes			
BO-150/575a	<i>Ph. limpidus</i> <i>Thrinacodus tranquillus</i>	1 1	<i>expansa</i> – <i>M. praesulcata</i>
BO-150/579	<i>Ph. limpidus</i> <i>Thrinacodus tranquillus</i>	1 1	<i>expansa</i> – <i>M. praesulcata</i>
BO-150/580	<i>Jalodus australiensis</i> cladodont tooth palaeoniscoid teeth	1 1 2	<i>expansa</i> – <i>M. praesulcata</i>
BK-318/661	<i>Ph. limpidus</i> Falcatidae indet.	1 1	<i>L. expansa</i> – <i>M. praesulcata</i>
BK-318/663,5	<i>Ph. limpidus</i>	1	<i>M. expansa</i> – <i>M. praesulcata</i>
BE-75/466,2	cladodont tooth orodont tooth?	1 1	Viséan, <i>austini</i>
Sosnowiec IG 1 borehole			
1813	<i>Thrinacodus ferox</i> (symmetr.) branchial denticle	1 1	Tournaisian, <i>anchoralis</i>
1815,7	Falcatidae indet.	1	Tournaisian, <i>anchoralis</i>
1999	cladodont tooth	1	Famennian
SUDETES			
Dzikowiec			
Dz-4	<i>Ph. limpidus</i> <i>Ph. gothicus</i> ?	1 1	L. Famennian
Eb-N	<i>Thrinacodus ferox</i> Falcatidae indet. branchial denticles	1 12 4	<i>L. duplicata-sandbergi</i>