

The first Devonian holocephalian tooth from Poland

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A recently found “bradyodont” holocephalian tooth from bituminous shales of the Kowala Quarry, south-western Holy Cross Mountains, Poland, dated as the middle Famennian *Palmatolepis trachytera* conodont Zone, is described. In spite of its resemblance to the forms often attributed to *Helodus*, the tooth is referred to as *Psephodus cf. magnus* (Agassiz, 1838), and supposed to represent the anterior part of the dentition, based on a partly articulated specimen of *Psephodus* from the Carboniferous of Scotland. The analysis of early helodonts and psephodonts, and other Famennian chondrichthyan crushing teeth, shows numerous similarities in tooth-base structure, such as the reduction of lingual basal extension, loss of articulation devices, development of numerous nutritive foramina, and the tendency to fusion between the teeth in a tooth-family. Based on these shared characters, close phylogenetic relationships between the Protacrodontoidea, Hybodontoidea, and the Holocephali are postulated.

Key words: Chondrichthyes, Holocephali, Cochliodontiformes, teeth, phylogeny, Famennian.

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Introduction

An almost complete tooth, probably belonging to the Holocephali (Chondrichthyes), was recently found in the middle Famennian of the Kowala Quarry section, south of Kielce, Holy Cross Mountains, Poland. Judging from Stahl's (1999) review, the only earlier published, correctly dated record of Devonian holocephalians, concerns teeth from the Famennian Grassy Creek Shales of Missouri, attributed by Branson (1914, *fide* Stahl 1999) to *Helodus*. Several other records have recently been redated as the Lower Carboniferous (e.g., from Russia, Tula region, Stahl 1999; Australia, Teddy Mountains, Susan Turner personal communication 2003). This being the case, the newly found tooth brings the first confirmation of the occurrence of holocephalians in the seas of eastern Laurussia prior to the Early Carboniferous. In the present paper we provide the description of this specimen, which we refer to as *Psephodus cf. magnus* (Agassiz, 1838), and we discuss relationships of early holocephalians (“bradyodonts”) with other Famennian chondrichthyans, on the grounds of tooth morphology.

Institutional abbreviations.—AEU, Islamic Azad University, Esfahan, Iran; GIUS, Institute of Geology, Silesian University, Sosnowiec, Poland; IGPUW, Institute of Geology, Warsaw University, Warsaw; NHM, The Natural History Museum, London; NMS, The National Museums of Scotland, Edinburgh.

Geological setting

The analysed specimen was found in the active Kowala Quarry, situated in the southern limb of the Gałęzice-Kowala syncline, in the southern part of the Kielce region (Fig. 1A). The tooth was recovered from black bituminous shales with numerous bivalves (Figs. 1B, 2A), intercalated with grey and black bituminous limestones, in the eastern wall of the northern part of the quarry (Fig. 1C). Szulczewski (1971) and Berkowski (1990, *fide* Racki and Szulczewski 1996) divided the Upper Devonian succession in Kowala into the informal lithological sets A to L. The Famennian part is composed of units H-3 to L. The part of the section which yielded the studied specimen belongs to the lower part of set K.

The fossil assemblage of the bituminous shales is dominated by the pseudoplanktonic bivalves *Guerichia* (Fig. 2A) and the planktonic entomozoacean ostracodes (mainly *Richterina*) with their characteristic fingerprint-like ornament (Olempska 2002). Other fossils appear more rarely, like cephalopods belonging mostly to *Platyctyenia* (Piechota in Racka et al. in preparation, see also Berkowski 2002), and the inarticulate brachiopods *Lingula* sp. and *Barroisella* sp. (Żakowa and Radlicz 1990). The microfossil fauna is characterized by the occurrence of conodonts, miospores, tracheids, acritarchs and prasinophytes – mainly leiosphaerids (Paweł Filipiak and Małgorzata Sobstel, personal communication

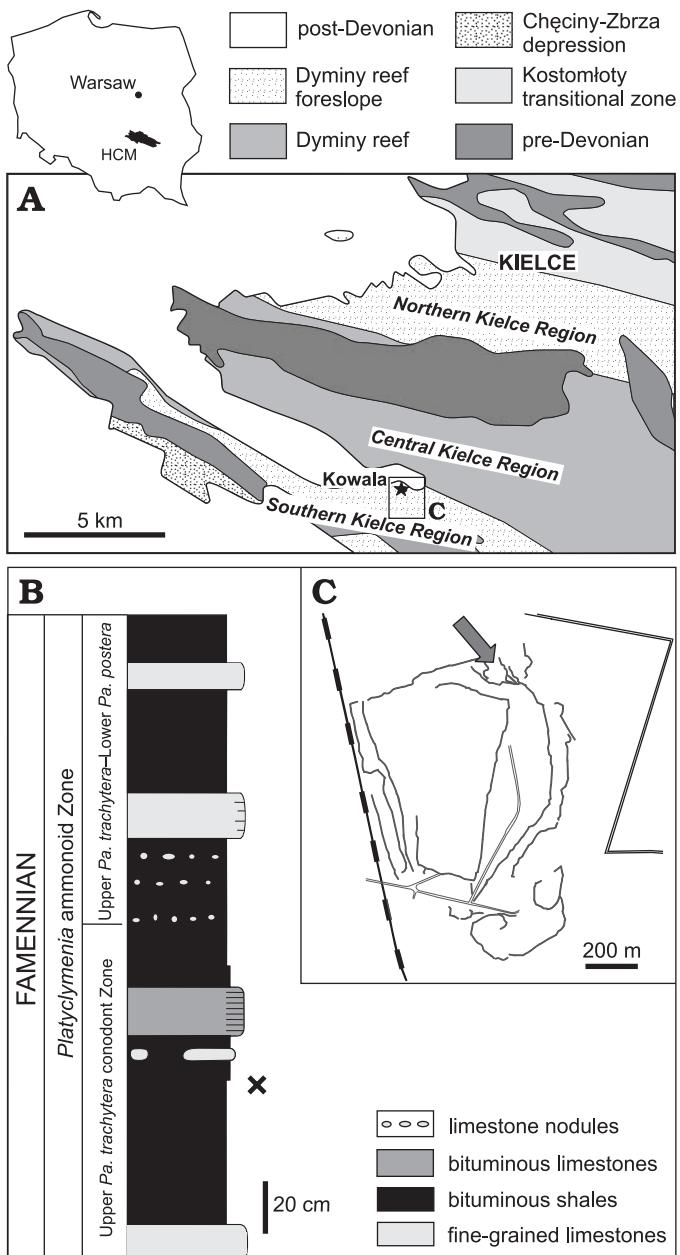


Fig. 1. A. Position of the Holy Cross Mountains massive (HCM) against the outline of Poland and the location of the Kowala section in the western Holy Cross Mountains (after Racki 1993). B. Stratigraphic column of the northern part of the Kowala Quarry, with the position of the discovered tooth (cross). C. Location of the studied section in the Kowala Quarry, indicated by an arrow.

2003). A similar assemblage to that in the black shales occurs in the limestones, where the fossils are not abundant but more diverse (see Berkowski 2002), with the addition of articulate brachiopods of the *Rozmanaria magna* assemblage (*sensu* Biernat and Racki 1986) and the trilobite *Cyrtosymbole* sp.

The presence of conodonts: *Palmatolepis glabra lepta*, *Pa. minuta minuta*, *Pa. gracilis sigmoidalis*, *Pseudopolygnathus granulosus* and *Scaphignathus velifer leptus*, enables a precise dating of the bed with the tooth (Sobstel in

Racka et al. in preparation). This conodont assemblage is typical of the Late *Pa. trachytera* Zone. The beginning of the Late *Pa. trachytera* Zone is marked by the first entry of *Ps. granulosus* (Korn and Ziegler 2002). *Pa. m. minuta* terminates in the upper part of this zone and *Pa. glabra lepta* disappears at the upper limit of this zone (Ji and Ziegler 1993). At the same time *S. velifer leptus* (Korn and Ziegler 2002) occurs, whereas *Pa. gracilis sigmoidalis* appears for the first time within the Late *Pa. trachytera* Zone (Ji and Ziegler 1993). The Late *Pa. trachytera* conodont Zone corresponds to the lower part of the *Platyclymenia* ammonoid Genozone (House 2002: 8) and spans the upper part of the *Prolobites delphinus* Zone and the lowermost part of the *Platyclymenia annulata* Zone (Korn 2002: 559).

According to several authors (e.g., Szulczewski 1971; Narkiewicz 1988; Berkowski 2002) the Famennian deposits exposed in the Kowala Quarry, mainly dark and laminated marls, bituminous claystones and nodular limestones, developed in basinal facies of the off-reef environment. The depositional environments in the Famennian are characterised by progressing transformation from anaerobic to well oxygenated conditions and accompanying shallowing of the area (Szulczewski 1995). Benthic fossils are absent from the bituminous shales. The existence of abundant planctonic fossils indicates that the surface waters remained oxygenated longer compared to the bottom waters and also suggests the presence of an oxygen depleted zone. Some planctonic animals (e.g., entomozoaceans) had a strong preference for deeper environments and were suited for living in poorly oxygenated environments (see Olempska 2002). Also, the occurrence of leiospheres often is interpreted as a result of a density stratification of the water column after a reduction in surface water salinity. Hence, a poor oxygenation of the bottom water probably resulted from density stratification of the water column and sluggish circulation in the basinal area (Olempska 1997).

Systematic palaeontology

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)

Figs. 2A, 3.

Material.—Single, partly broken and abraded tooth, GIUS-4-2314 Kow-1, from the middle Famennian, Late *Pa. trachytera* conodont Zone, of the Kowala Quarry, south-western Holy Cross Mountains, Poland.

Description.—The specimen is very dark brown, almost black, and lacks probably about a half of a lateral ramus. It broke off apparently quite soon after falling on the sea floor,

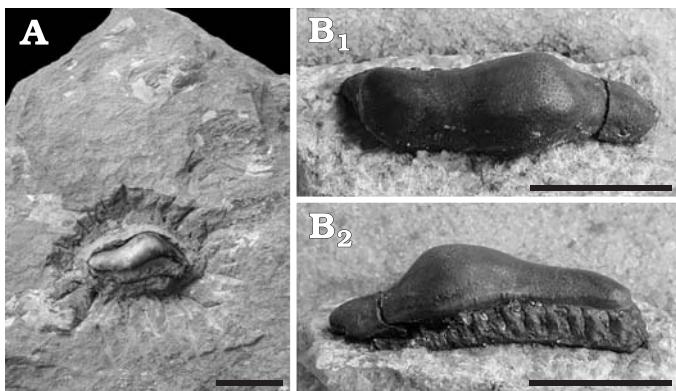


Fig. 2. A. Position of the tooth of *Psephodus* cf. *magnus* (GIUS-4-2314) from Kowala, as found on the rock. Note shells of a bivalve *Guerichia* in the upper right. B. Tooth of *Psephodus magnus* (NHM 28746) from the Viséan, Carboniferous Limestone of Armagh, Northern Ireland, in occlusal (B₁) and lingual (B₂) views; same specimen as figured by Stahl (1999: fig. 58H). Scale bars 10 mm.

because the edges of the breaking surface are rounded by abrasion (Fig. 3A₃). Before losing a piece, the tooth seems to have been virtually symmetrical mesio-distally, but the broken ramus might also have been a little shorter. In oral view the tooth is gently arched (Fig. 3A₂), with the labial side concave and the lingual side convex. The end of the preserved ramus is rounded. 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 (Fig. 3A₁), and the corresponding part of the basal surface is concave (Fig. 3A₃).

Three faces of the base, labial, lingual and basal, can be distinguished. The slightly concave shape of the labial face (Fig. 3A₃) suggests that it overlapped the lingual side of the base of a preceding (more labial) tooth in a family. There are some pores on the labial face, but they are hardly visible due to the sediment filling them. Traces of large nutritive canals can be observed on the lingual face of the base, mainly in a form of grooves (Fig. 3A₁). The basal surface is smooth and devoid of any traces of foramina (Fig. 3A₃). The crown is composed of tubular dentine, with openings of tubules present all over the crown surface (Fig. 3A₁, A₂).

Remarks.—Problems with the systematics of Palaeozoic Holocephali, commonly called “bradyodonts” and known almost only from isolated teeth and tooth-plates (but see Lund and Grogan 1997), were presented in detail by Stahl (1999) in the Handbook of Paleichthyology. Of this, only a few facts need be repeated here. From a few articulated specimens and fragments of dentitions we know that bradyodonts display a very high degree of heterodonty. Their dentition can be composed of tooth-families, consisting of individual teeth (Fig. 3B, C₁, C₃) and of tooth-plates (Fig. 3C₂), probably primarily developed by fusion of teeth in a particular family and, at least in some taxa, of lateral fusion between two adjacent tooth-families. Broadly speaking, with the exception of Chondrenchelyiformes and Chimaeriformes, Devonian–Carboniferous bradyodonts are subdivided, at the ordinal level, accord-

ing to the numerical ratio of “free” tooth-families to the tooth-families with tooth-plates, the total number of tooth-families, and the shape of tooth-plates. Representatives of only two orders, Helodontiformes and Cochliodontiformes are known to have individual teeth. Of the latter group, numerous such teeth were recorded only from Psephodontidae and from two genera (*Lophodus* and *Venustodus*) treated by Stahl (1999) as *incertae sedis*. In the other cochliodontiform dentitions there are virtually only tooth-plates.

Lophodus and *Venustodus* are very characteristic and can be excluded from the comparison with our tooth from Kowala. The dentition of *Helodus*, apparently the only genus of the Helodontiformes, consists almost entirely of unfused teeth except a few tooth-plates (four in *Helodus simplex*, according to the restoration by Moy-Thomas 1936: text-fig. 4) of a *Pleuroplax*-type, i.e., with the crowns of fused teeth clearly differentiated (Stahl 1999: fig. 47). Typical individual helodont teeth are subsymmetrical, only gently elongated mesio-distally, and they have crowns with a strongly elevated median part, usually rounded but often developed into a tip, which is slightly directed labially. The crown is composed of tubular dentine and the base of trabecular dentine with numerous canal openings and grooves. From the first description of *Helodus* by Agassiz (1833–44) many more or less similar forms were ascribed to this genus. It is generally impossible to confirm or reject most of these identifications, because *H. simplex* is the only species represented by articulated specimens. Moreover, thanks to the discovery of the specimen from the Lower Carboniferous of Scotland, referred to as *Psephodus magnus* by Traquair (1885), in which a large part of the dental apparatus is preserved in a fairly undisturbed condition, it became clear that helodont-like teeth can occur in a dentition largely different from that of *H. simplex*. In *P. magnus* (Fig. 3C; Traquair 1885: figs. 1, 2; Stahl 1999: fig. 58A) only a few anterior tooth-families are composed of small helodont-like teeth with elevated median parts (Fig. 3C₁). Then, at least one large, flat tooth-plate on each jaw ramus occurs in a more distant position (Traquair 1885: figs. 1b, 2b; see also such plate, displaced and overturned, in Fig. 3C₂), probably forming a tooth-family with a few labially situated, elongated and flattened individual teeth (Traquair 1885: fig. 2d; Stahl 1999: fig. 58A). Teeth of the subsequent three or four tooth-families are smaller, but similar in form to the latter (Fig. 3C₃; Traquair 1885: fig. 2e). Unlike the *Pleuroplax*-like tooth-plates of *H. simplex*, those of *P. magnus* show no sign of fused teeth.

The bradyodont tooth from Kowala resembles the helodont-like teeth of *P. magnus* most closely. Slightly stronger mesio-distal elongation of a tooth and a less distinct elevation of the median part makes it different from typical teeth of *H. simplex*. Although many teeth, attributed formerly to *Helodus* (see e.g., Stahl 1999: fig. 57D, J), are very similar to the tooth under description, they do not necessarily belong to that genus. Moreover, a tooth from the Carboniferous Limestone of Armagh, Northern Ireland, housed in the Natural History Museum, labelled *P. magnus* (Fig. 2B), and accepted

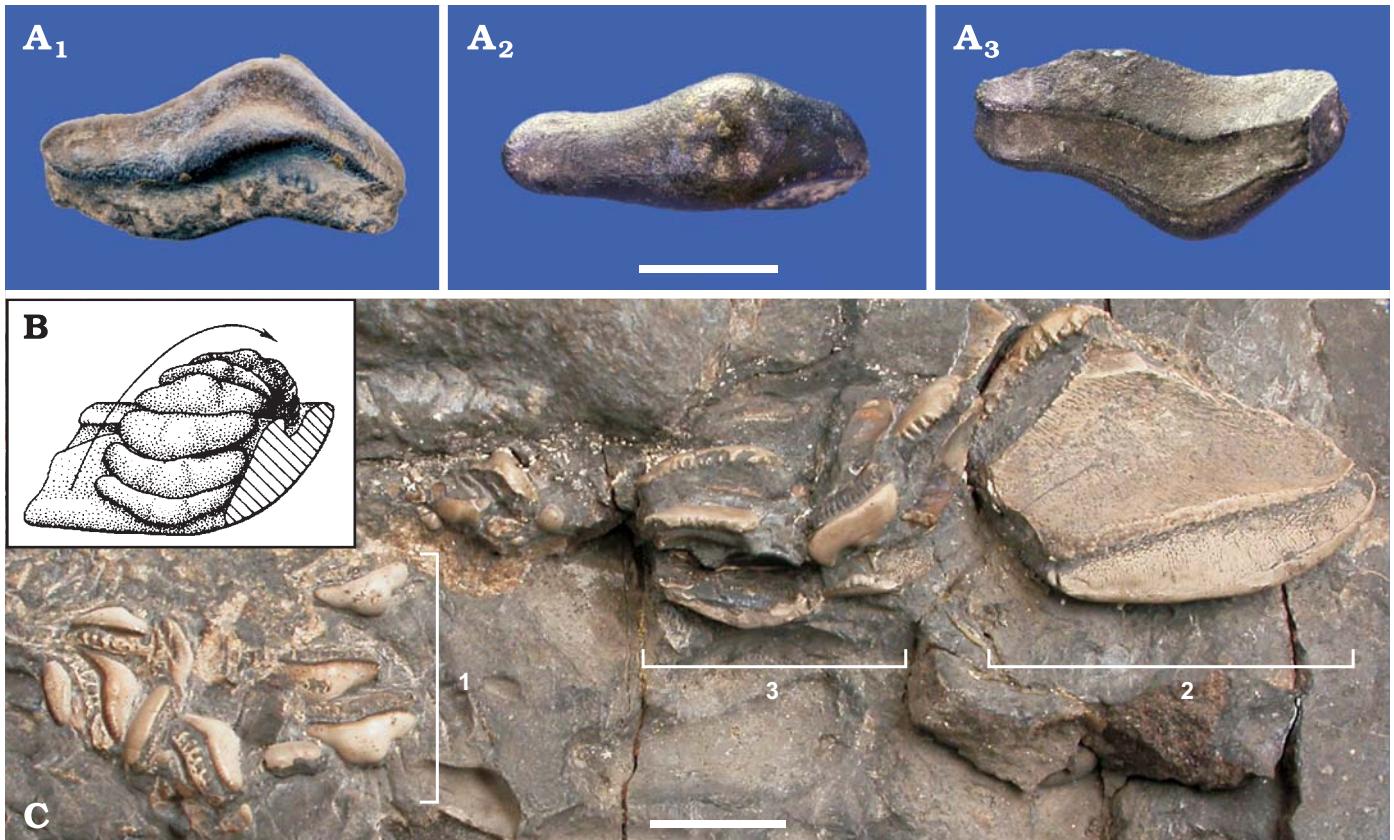


Fig. 3. A. Tooth of *Psephodus* cf. *magnus* (GIUS-4-2314 Kow-1) from Kowala, in lingual (A₁), oral (A₂), and labial/basal (A₃) views. Scale bar 5 mm. B. Arrangement and direction of replacement of helodont-like teeth in a tooth-family. Arrow indicates labial side. From Janvier (1996: fig. 4.36.G1). C. Diversity of tooth and tooth-plate morphotypes in *Psephodus magnus* (NSM 1950.38.51) from the Carboniferous Limestone, East Kilbride, Lanarkshire, Scotland; same specimen as figured by Traquair (1885: figs. 1, 2). 1, a group of helodont-like anterior teeth; 2, displaced and overturned tooth-plate; 3, flat lateral teeth. Scale bar 10 mm.

as such by Stahl (1999: fig. 58H), seems the closest to the tooth from Kowala of all the specimens examined by us, both as far as the crown and the base features are concerned. Therefore, we decided tentatively to assign our tooth as *P. cf. magnus*, leaving it in open nomenclature due to the lack of diagnostic tooth-plates and a large stratigraphical distance.

The deep water, oxygen depleted facies in which the tooth was found is rather unusual for Lower Carboniferous coeliodonts, typically occurring in bright limestones, rich in benthic fauna, such as the Mountain Limestone of Armagh (Agassiz 1833–44). We therefore presume that the tooth might have been deposited as a gastric residue of a larger predator which had preyed in some neritic area and later travelled through the surface waters of the Kowala basin. Such an interpretation was provided by Williams (1990) for the rare occurrence of orodont crushing teeth in the Cleveland Shale of Ohio.

Discussion

Thanks to the recent studies on the shallow water chondrichthyan fauna from western USA and North Gondwana

(Ginter 2001; Ginter et al. 2002), quite a few new forms of Famennian chondrichthyan teeth, some of which used to be considered characteristic of the Carboniferous and later times, have been revealed. Their common feature is that they are elongated mesio-distally and that their crowns are low, which suggests that they might have served not only for catching prey, as most Devonian chondrichthyan teeth did, but also (or only) for crushing hard, shelly organisms. In earlier works, Devonian teeth of this type were attributed to the genera *Protacrodus* and *Orodus* only, the best known of which is *Protacrodus vetustus* Jaekel, 1925 (Gross 1938; see also Ginter 2002). Samples from the Famennian of Iran (Ginter et al. 2002) yielded several orodonts, two new protacrodontid species, viz. *Protacrodus serra* and *Deihim mansureae*, and a new, yet unnamed species of *Lissodus* (Hybodontoidea). The bradyodont tooth of *Psephodus* cf. *magnus* from the Famennian of Kowala, presented herein, brings a new value to the list.

Differences between the above mentioned taxa lie in the characteristics of their tooth-crowns. Protacrodontids have all the cusps clearly differentiated, with only basal parts fused, covered with coarse vertical ridges joining at the tips. Orodonts have the cusps fused up to their tips or almost, but it

is easy to distinguish their position by the relative thickness of the crown. Most orodonts are coarsely cristated (Long and Hairapetian 2000: fig. 5; Ginter 2001: fig. 6H). Their coronal tissue can be composed of tubular dentine or not. Tooth-crowns of *Lissodus* have all the cusps fused and usually an almost smooth surface, but in addition they have a special projection, called “labial peg”, probably taking part in the interconnection between the adjacent teeth in a tooth-family (Ginter et al. 2002: fig. 12). And, last but not least, teeth of *Psephodus* have no trace of cusps, only a broad bulge probably indicates the former position of the highest, median cusp (Figs. 2B₂, 3A₁). The crown is smooth and its outer layer is entirely composed of tubular dentine.

It may be important to add here that the protacrodontids, at least *P. serra* and *D. mansureae*, are supposed to display a substantial degree of monognathic heterodonty. They probably have few smaller, symmetrical teeth with a distinct, high median cusp, in a cladodont manner (Fig. 4A; Ginter et al. 2002: pls. 4J, K, 5D–F) or even cutting teeth (Ginter et al. 2002: fig. 11A–E), at the symphyseal region, and more elongated, lower and perhaps more asymmetrical teeth postero-laterally. Unfortunately, although a jaw with teeth of *P. vetustus* is preserved, this condition cannot be checked, because the whole anterior part is missing. Teeth of *Lissodus* sp. also show certain amount of variability, concerning mainly the mesio-distal elongation of an element.

In contrast to this diversity of crowns, characteristics of the base remain stable throughout all the group of forms. The major shared characters, using an Upper Devonian cladodont, *Stethacanthus resistens* Ginter, 2002, possibly conspecific with *Cladodoides wildungensis* (Jaekel, 1921), as an outgroup, are as follows:

- considerable reduction of lingual basal extension;
- loss of articulation devices, i.e., buttons and labio-basal projections;
- development of at least one, horizontal row of numerous nutritive foramina both on the upper-lingual and basal-labial faces of the base;
- development of an area absolutely devoid of foramina on the basal-lingual face of the base;
- tendency to fusion between the teeth in a tooth-family.

The position and number of horizontal rows of pores varies from species to species and also probably can be different in different teeth of the same species or even same individual. Unfortunately, as stated above, the labio-basal row of pores is not visible on the specimen of *Psephodus* from Kowala, but observation of other helodont and psephodont teeth shows that such foramina are restricted to the concave, clearly differentiated basal-labial face, unlike in *Protacrodus serra*, where the pores are apparently present only in the narrow area just below the crown (Ginter et al. 2002: fig. 11D, K). In *Deihim* it seems that this group of basal canals have their openings both below the crown (Fig. 4D) and in the basal-labial concavity (Fig. 4C); the same can be seen in a protacrodont from Utah (Ginter 2001: fig. 6C) and it resembles the relative position of “specialised foramina” and “ir-

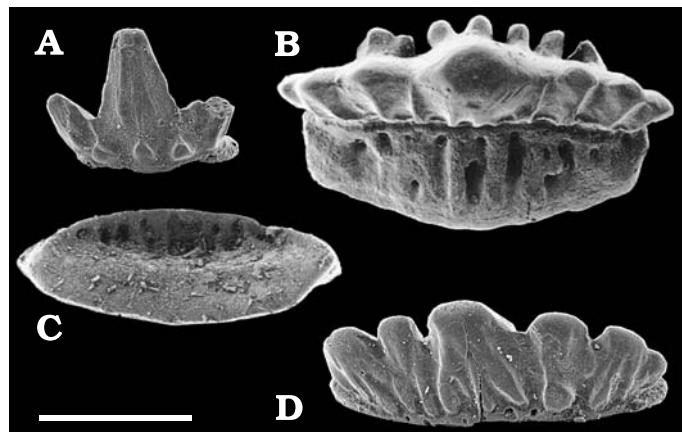


Fig. 4. Teeth of *Deihim mansureae* from the Famennian of Iran. **A, D.** From Hodjedk, Middle or Late *Pa. crepida* zones. **A.** Clutching anterior tooth, AEU 239, labial view. **D.** Postero-lateral tooth, AEU 238, labial view. **B, C.** From Huk, Early *Pa. crepida*–Late *Pa. marginifera* zones. **B.** Holotype, IGPW/Ps/5/1, occlusal view. **C.** IGPW/Ps/5/3, basal view. Scale bar 0.5 mm.

regular foramina” in certain Permian hybodontoids (Johnson 1981: figs. 1, 16, 58). However, since the basal tissue has no protective enameloid and, therefore, is vulnerable to abrasion and other destruction, it is always uncertain if all the pores which we see now were open during the animal’s life or they were actually blind endings of vascular canals.

This reservation particularly concerns the upper-lingual face of the base. In all species considered here the main horizontal row of foramina lies just beneath the crown or it is separated from the latter only by a narrow groove (Fig. 4B). However, in a great number of specimens, these pores continue lingually and downwards as wide, often anastomosing, uncovered canals which give this part of the base a spongy appearance (Figs. 2B₂, 3A₁, 4B). Thus, were these canals grooves from the very start, or was there a thin upper layer of osteodentine which disappeared, for instance, due to resorption prior to shedding or due to later abrasion? Such uncovered canals are found less often in *Protacrodus* than in the other considered taxa. On the other hand, their presence is typical of bradyodonts. Therefore, it can depend on the degree of fusion between the bases of teeth in a tooth-family during the animal’s life.

The tendency to at least partial fusion of bases occurred rather early in this group of Chondrichthyes. It is known from quite a few findings of fragments of tooth-families, composed of two or even three protacrodont teeth, in the lower Famennian of Poland (Ginter 2002: fig. 6A) and Iran (Vachik Hairapetian, personal communication 2003). Non-protacrodont teeth of that age are never found in such associations in the acid-processed residues. The interconnection between the teeth by numerous and dense vesicles, and slight overlapping of bases, probably provided good conditions for interstitial secretion of mineral tissue and, consequently, strengthening the “pavement” for crushing. This initial capa-

bility could have been used in future in bradyodonts to form tooth-plates.

From the discussion up to this point, it becomes clear that there are deep affinities between the dentition of primitive holocephalians and protacrodontids. Whereas the tooth-crown in chondrichthyans is a highly adaptive structure, the general structure of the base is much more conservative and can be a diagnostic feature at a higher systematic level. Shared characters of the tooth-bases in the groups considered are unlike any other Late Devonian ones: ctenacanthoids, symmoriforms, *Cladoselache*, phoebodontiforms, *Antarctilamna–Wellerodus* or omalodontiforms. Moreover, a gradual transition from the protacrodont morphotype towards the psephodont/helodont condition can be traced. The general motives of this transition are as follows: increase of a basal-labial area for canal openings; more and more extensive fusion between tooth-bases; fusion of cusps; fusion between crowns at least in a few tooth-families, forming of tooth-plates; development of tubular dentine.

On the other hand, close relationships between the Protacrodontoidea and Hybodontoidea, already proposed by Zangerl (1981), lie beyond doubt. Here, if we consider for instance such post-Devonian hybodont forms as *Sphenacanthus* (Dick 1998: fig. 3) and *Polyacrodus* (e.g., Duffin and Delsate 1993), it is really difficult to find any difference at all. They display the same style of bases, low and coarsely cristated cusps, no tubular dentine, and similar heterodonty, as in protacrodonts. In *Hybodus* and *Acrodus*, the best known hybodonts (see e.g., Woodward 1889: pls. 10–14), we see two opposite tendencies, towards the increase of the area occupied by frontal-type, clutching teeth (*Hybodus*) or towards the complete fusion of cusps (*Acrodus*). Both, however, could have been easily derived from the basal, protacrodont *Bauplan*. Note that for *Acrodus* it is even suggested by the name of *Protacrodus*, given by Jaekel (1925).

This being the case, it seems quite probable that hybodonts (with neoselachians?) form a sister group to helodontid/psephodontid bradyodonts (and all other holocephalians?). Protacrodontids should best be treated as a stem group of the hybodont-bradyodont clade. Position of the “orodonts” is unresolved, because they do not display any unique character; some of them possess tubular dentine and some do not. Most probably some are closer to bradyodonts, and some to hybodonts, and some perhaps to eugeneodontids (Zangerl 1981). However, it is quite possible that a lot of them derived from chondrichthyans characterised by a protacrodont-like dentition (Lebedev and V'yushkova 1993).

This phylogenetic proposition is not new. Actually, the similarities of dental features between hybodonts and bradyodonts were well known to 19th century authors. Traquair (1888: 417) noted that “it is difficult to draw any line between the Hybodontidae and Orodontidae”, regarding the latter group as comprising also *Helodus* and *Psephodus*. Later, the idea of such close relationships between these groups was abandoned, when it became clear that bradyodonts are stem-group holocephalians and, on the other hand, when many

palaeichthyologists came to an opinion that the morphology of chondrichthyan teeth is unimportant for phylogenetic analyses. However, as there does not seem today to be any generally accepted, skeleton-based proposition for the relationships between the Elasmobranchii and Holocephali, the concept presented here deserves to be brought back into life, in the light of new evidence. In any case, from the point of view of the evolution of the chondrichthyan dentition and tooth morphology, it seems to be more parsimonious than the idea of Coates and Sequeira (2001) who placed Holocephali as a sister group to stethacanthids. The work on a completely new collection of perfectly preserved bradyodont teeth from the middle Tournaisian of the Muhua section (South China; Ginter and Sun, in preparation) is currently underway. We hope that it will bring new arguments to the discussion.

Acknowledgments

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