Devonian phoebodont shark teeth

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Shark teeth of the phoebodont type are the most common and diverse group of Upper Devonian ichthyoliths in the pelagic facies of the Holy Cross Mountains (Poland), South Urals and Timan (Russia). They were also found in the Givetian of Kuznetsk Basin (western Siberia). The morphology and function of tooth apparatus of *Phoebodus* was possibly similar to that of the recent shark *Chlamydoselachus anguineus*. A significant loss of diversity and relative productivity has been observed among the phoebodonts in the earliest Famennian. A new genus, *Omalodus* gen. n., and three new species of *Phoebodus*, *Ph. bifurcatus* sp. n., *Ph. fastigatus* sp. n. and *Ph. turnerae* sp. n. are proposed.

Key words: sharks, phoebodonts, teeth, morphology, biostratigraphy, Devonian, Poland, Russia.

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Introduction

Shark teeth, scales and fin spines are very common among the Devonian and Carboniferous fish microfossils. They are highly diverse, usually well preserved, and easy to extract with acetic acid from calcareous deposits. The present paper is the result of studies on Devonian shark teeth from the Holy Cross Mountains, central Poland, and from several regions of Russia (see Ginter 1990; Ivanov 1992). Its main purpose is to establish distribution of the phoebodont sharks in the Late Devonian of the East European Platform margin and to describe new morphological forms of their teeth. Vast material, especially from the South Urals (Bashkiria), usually well dated by conodonts, and some findings of Middle Devonian phoebodont teeth from Kuznetsk Basin (Western Siberia) makes posible a revision of *Phoebodus* and determination of stratigraphic ranges of three previously described and three new species.

Material

During recent years new collections of phoebodont teeth from the Holy Cross Mountains have been made: a rich assemblage of ichthyoliths from Ostrówka (which complemented that collected by I. Nasiłowski; see Ginter 1990), and some dozens of specimens from Jabłonna, Łagów and Wietrznia. The other Holy Cross Mountains specimens described herein come from the localities of Tudorów, Miedzianka, Kostomłoty, Wietrznia, Karczówka and Kadzielnia (Fig. 1B). The second part of the material originates from three regions: South Urals (Bashkiria; localities of Ryauzyak, Zigan, Kuktash, Lemeza, Zuyakovo, Askyn, Popovskiy and Kuk-Karauk; Fig. 1C); Timan-Pechora province (Ukhta region, Vezha-Vozh River, borehole 2023); and Kuznetsk Basin (Lebedyanka Quarry and Mazalovskiy Kitat River).

The South Urals and Timan localities are situated on the opposite margin of the East European Platform to that of the Holy Cross Mountains and represent a similar facies development of the Late Devonian. Rhythmic, lime-marly deposits predominate; carbonate buildups or condensed pelagic limestones are developed in strictly limited uplifted areas (see Szulczewski 1971, 1981, 1989; Ulmishek 1988; Abramova & Baryshev in press; Abramova *et al.* in press).

In the Holy Cross Mountains and the South Urals, phoebodont teeth are found together with other elasmobranch remains, such as teeth of symmoriids, other cladodontiforms, few protacrodonts, scales of ctenacanths and protacrodonts, associated with acanthodian scales, and crossopterygian and paleoniscoid fragments. Macroremains of placoderms, crossopterygians and palaeoniscoids (Gorizdro-Kulczycka 1934; Kulczycki 1957; Ivanov in press) also occur. Arthrodires and ptyctodonts dominate among them, while among the ichthyoliths, elasmobranch remains strongly predominate. The optimum of phoebodont teeth occurrence coincides with that of palmatolepidid conodonts.

Frasnian conodont zonation used here is not based on the latest subdivision proposed by Ziegler & Sandberg (1990). Conodont dating of most of samples was made earlier, and since in many cases we could not see the conodonts, it was impossible for us to update it. We adapt the term 'Local Substage' to translate the Russian term 'горизонт' ('horizont').

Specimens from the Holy Cross Mountains are housed in the Institute of Geology, University of Warsaw (abbreviated as IGPUW) or in the Institute of Paleobiology, Polish Academy of Sciences (ZPAL) in Warsaw. All material from South Urals, Timan and Kuznetsk Basin is housed in the collections of the Laboratory of Paleontology, St. Petersburg University (LP) in St. Petersburg.

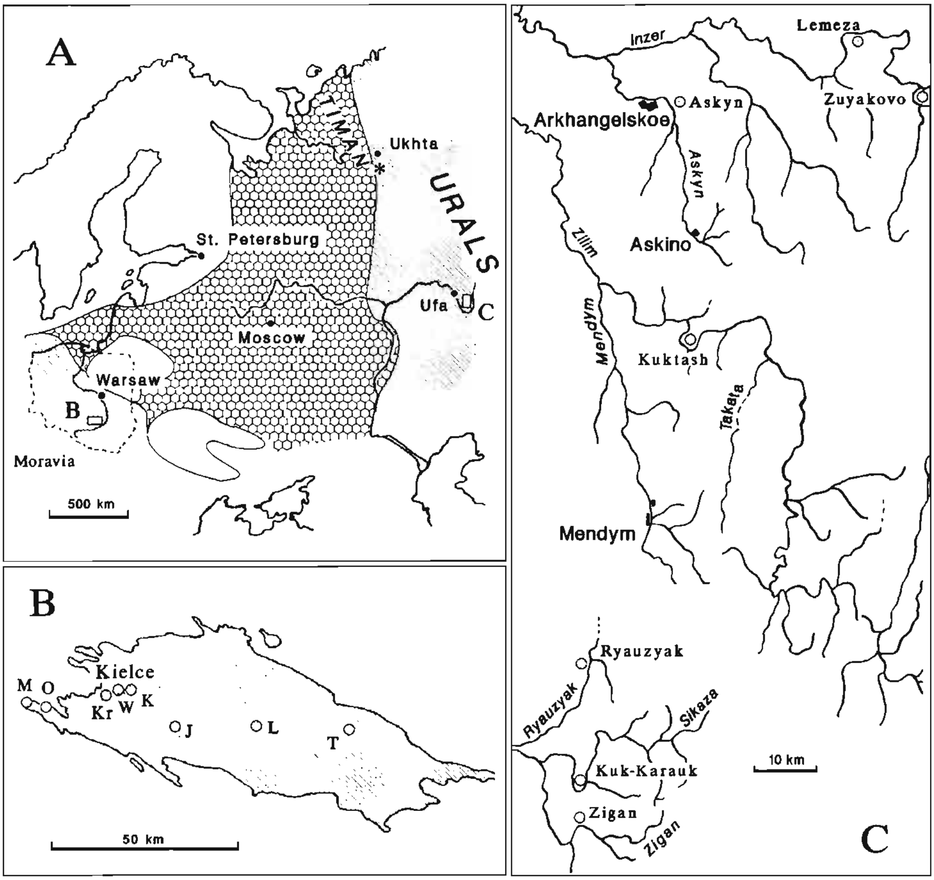

Fig. 1. ❑A. Localization of the studied areas, the Holy Cross Mts (B), and South Urals (C), asterisk - Vezha-Vozh in the Timan-Pechora province. Late Devonian area of shallow-water sedimentation represented by honeycomb pattern, pelagic sediments are hachured. ❑B: Localities in the Holy Cross Mts (shadowing shows the extend of Paleosoic outcrops): M - Miedzianka, O - Ostrówka, Kr - Karczówka, W - Wietrznia, K - Kadzielnia, J - Jabłonna, L - Łagów, T - Tudorów. ❑C: Localities on the western slope of South Urals (Bashkiria).

Dentition of phoebodonts

Three genera of fossil sharks, *Phoebodus*, *Thrinacodus* and *Omalodus* gen. n. are included here in the family Phoebodontidae. Their teeth have three main cusps in the crown and the central cusp is equal to or slightly smaller than the lateral ones. The most important feature for the systematics of phoebodonts is the nature of the tooth-base. The teeth of *Omalodus* are characterized by the base directed labiad (Fig. 3J), whereas in *Phoebodus* and *Thrinacodus* it is directed linguad. In *Thrinacodus* the tooth-base is asymmetrical and usually twisted (see, e.g., Turner 1982: Fig. 3B), and

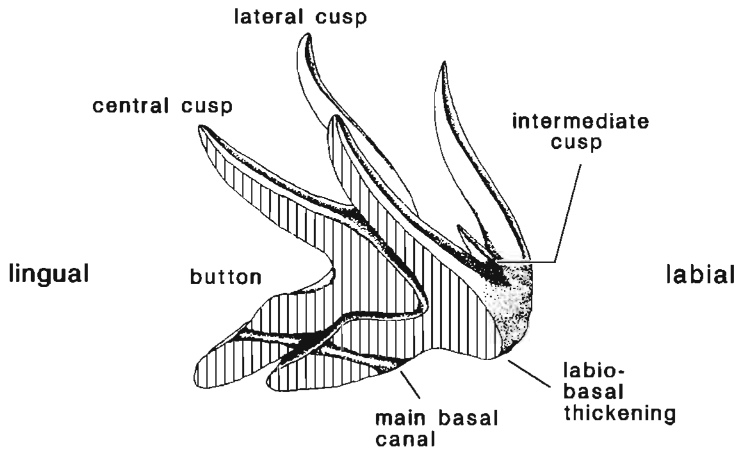

Fig. 2. Articulation between two *Phoebodus* teeth and morphological nomenclature.

in *Phoebodus* it has a symmetrical outline. Species of *Phoebodus* are defined on details of the morphology of the base and crown.

The tooth arrangement in the jaws of *Phoebodus* was probably similar to that of the recent frilled shark, *Chlamydoselachus anguineus* (see Gudger 1937; Pfeil 1983). The teeth of the latter are close in gross morphology particularly to *Ph. fastigatus* sp. n. (Fig. 3A, B) or to the juvenile stage of *Ph. bifurcatus* sp. n. (Figs 4A, 5E-H). *Chlamydoselachus* teeth are arranged in rows, separated by toothless spaces. Each tooth has a linguad extended base inserted under the labial base of the next tooth behind. In *Phoebodus*, the connection between the teeth is strengthened by a short, arcuate thickening in the ventro-labial region of the base (Fig. 2; Gross 1973: Pl. 34: 13b; Ginter 1990: Pl. 2: 1, 2b, 6b). It is probably in contact with the labiad face of the apical button in the lower, older tooth. If the underside of the base is concave, and this is usually the case, the button of the underlying tooth can be completely hidden in the concavity. In the forms characterized by a large button, the underside is, in most cases, strongly concave. Respectively, specimens with a vague button, such as the teeth of *Ph. limpidus* (see Ginter 1990: Pl. 4: 2-5) or 'juvenile' forms (Fig. 5G-H; see below), usually have a shallow concavity.

Similar basal thickening - apical button articulation between the teeth was also proposed by Hotton (1952) for the teeth of Permian xenacanths. In his model, the first, most labially situated tooth was probably functional, and the following, overlapping ones, were replacement teeth. Articulation between the teeth helped them to be carried towards the jaw margin and to become erect and functional. This model can be easily applied to the phoebodonts, but possibly more than one tooth in the row

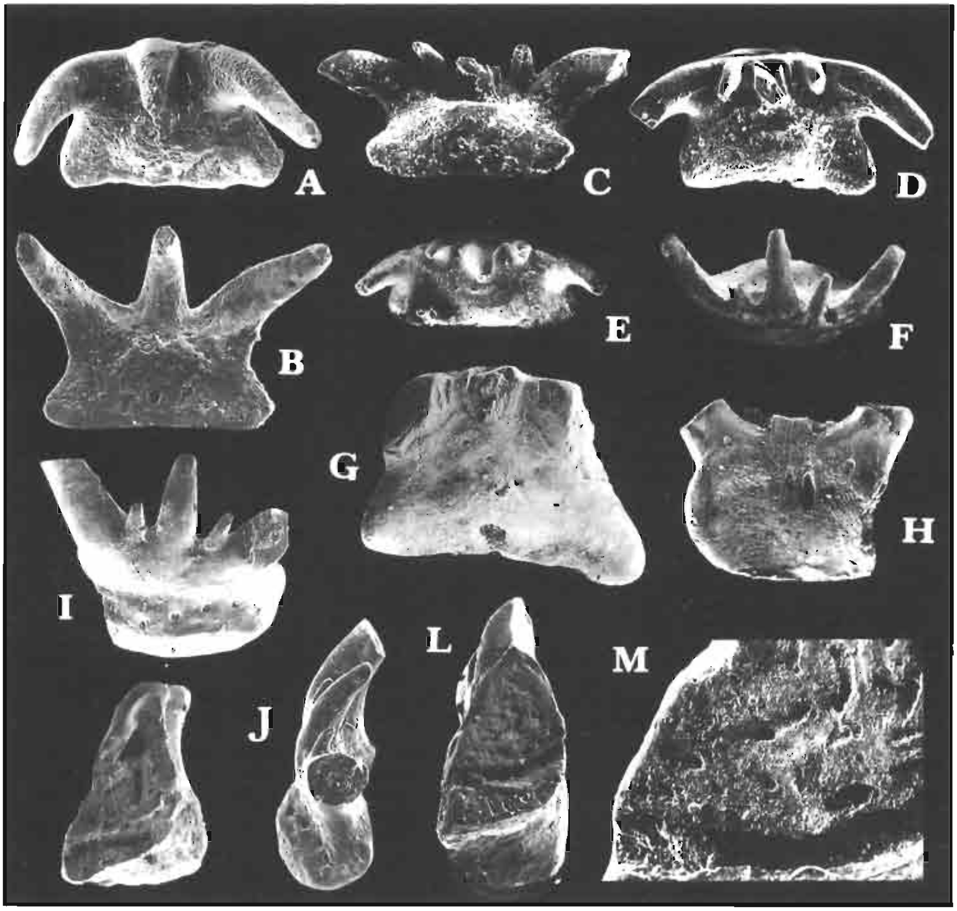

Fig. 3. ❑A, B, G. *Phoebodus fastigatus* sp. n. A, B. Holotype LP 5-1 in occlusal and lingual views, Mazalovskiy Kitat River, Givetian Mazalovskiy Kitat Substage. G. Specimen LP 7-1 in occlusal view, Alchedat Quarry, Givetian Alchedat Substage. ❑C-F. *Ph.* aff. *fastigatus*. C, D. Specimen LP 7-2 in lingual and occlusal views, Ryauzyak, Mendym Substage, *P. gigas* Zone. E, F. Specimen IGPUW Ps/1/63 in occlusal and labial views, Wietrznia, *A. triangularis* or *P. gigas* Zone. ❑H-M. *Omalodus bryanti* (Wells), Lebedyanka Quarry, Givetian Alchedat Substage. H. Specimen LP 7-3 in lingual view. I, J. Specimen LP 7-4 in labial and lateral views. K. Cross section through the base and central cusp of specimen LP 7-5. L, M. Cross sections showing canal joining two faces of the base of specimen LP 7-6. A-G, I, J × 40; H × 27; K, L × 20; M × 70.

was functional. In *Chlamydoselachus*, several teeth of the row are exposed on the jaw margin and they are used more to hold prey, than to cut, the latter function being characteristic of modern shark teeth. The cusps of phoebodont teeth are delicate, and their cutting edges are usually very weak, even if they exist. So it is more likely that they worked in a similar way to *Chlamydoselachus* teeth, than to teeth of more advanced modern sharks.

Variation in tooth morphology of *Phoebodus*

The kind of differentiation in morphology between the teeth in such rows as well as the variation from the symphysial to angular parts of *Phoebodus* jaw are so far open to speculation. Teeth assigned to *Phoebodus* usually have three or five cusps (including intermediate, smaller ones). Specimens with four cusps occur seldom (Ginter 1990: Pl. 2: 2a), and those with six or seven (Fig. 7A-B) are extremely rare. In the species in which additional cusplets are found (all except *Ph. australiensis* and *Ph. fastigatus* sp. n.), the presence of tricuspid tooth forms can also be explained by analogy with *Chlamydoselachus*. They might have been situated in the symphysial region (see Gudger 1937), or they may come from a female individual (Pfeil 1983), or may represent a juvenile stage. In this case, 'juvenile' means small teeth of a young individual. Such small teeth may also, however, represent a special position in the jaw.

'Juvenile' forms of *Phoebodus* teeth were found in *Ph. gothicus* (Ginter 1990: Pl. 3: 5a-c) and in *Ph. bifurcatus* sp. n. (Figs 4A, 5E-H). In both species such forms have very short and thin intermediate cusps or such cusps may be absent. The three main cusps make a smaller angle than usual between each other; they are ornamented only by scarce, thin striae or totally lack ornament. It is difficult to distinguish the button from the rest of the tooth-base, whereas in the fully grown tooth of both mentioned species the button is high and distinct.

A special feature of the *Ph. bifurcatus* 'juvenile' forms is seen in the labial part of the base which is much narrower, sometimes by half its width, than its lingual part. Bifurcation of the base is extreme in the smallest specimens (Fig. 5G-H), it diminishes in the next stages and in some 'adult' forms almost disappears (Fig. 4D). *Ph. fastigatus* and *Ph.* aff. *fastigatus* (Fig. 3A-G) display certain features of the *Ph. bifurcatus* juvenile stage: crown shape, lack of strong sculpture on the cusps, an indistinct button, and larger lingual width of the base. It seems possible that the late Frasnian species: *Ph. bifurcatus*, *Ph.* aff. *fastigatus* and *Ph.* sp. A, could be related to *Ph. fastigatus*, rather than to any other Middle Devonian form.

Some similarities can also be observed between the Famennian forms: *Ph.* sp. B (Fig. 7J-M), *Ph. turnerae* sp. n. (Fig. 8A-H) and *Ph. gothicus* (Fig. 8I-K). In this group the crown varies only slightly, but the base outline changes from short, almost rectangular (*Ph.* sp. B), through pentagonal or rounded (*Ph. turnerae*) to strongly expanded linguad, with an acute lingual angle, in typical specimens of *Ph. gothicus*. The button, not very distinct in the first species, becomes prominent in *Ph. turnerae*, and in *Ph. gothicus* has moved towards the crown.

Transitional forms between the teeth of above mentioned species are common as, e.g., squarish specimens with a prominent button close to the lingual rim (Fig. 8H) and broad, rounded ones with the button in the center of the upper surface of the base (Fig. 8F). Both forms are here tentatively included in *Ph. turnerae* sp. n.

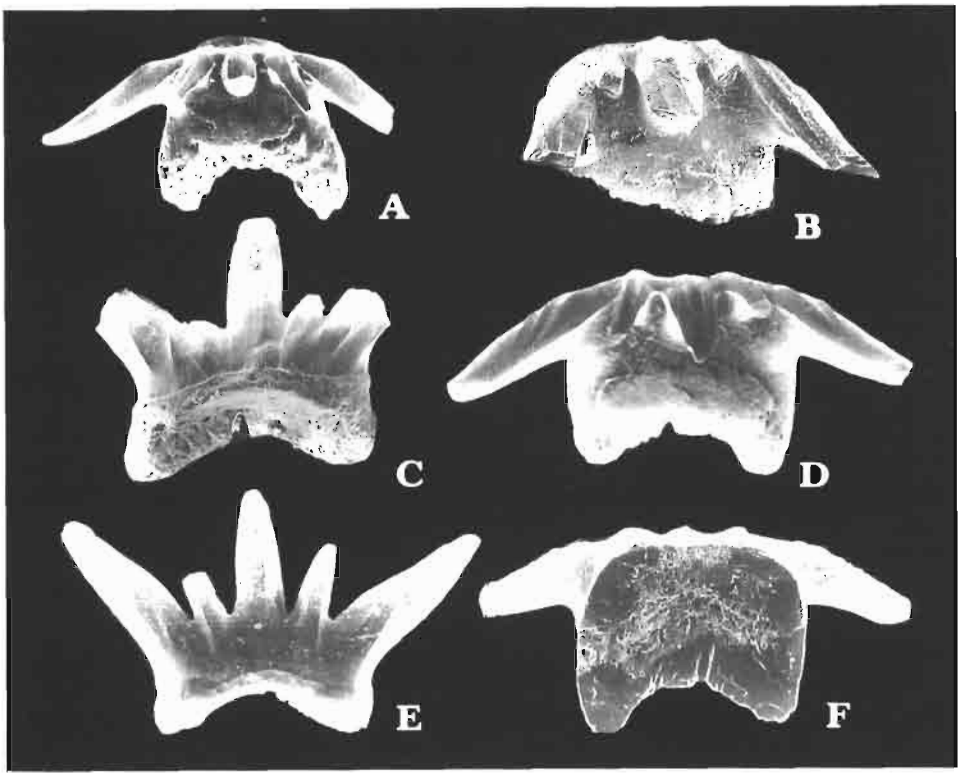

Fig. 4. *Phoebodus bifurcatus* sp. n. ❑A. Juvenile tooth LP 7-7, Vezha-Vozh River, Lyaiol Substage, *P. gigas* Zone. ❑B, C. Specimens IGPUW Ps/1/70, 71 in occlusal and labio-basal views, Karczówka, *P. gigas* or *P. linguiformis* Zone. ❑D-F. Holotype LP 7-8 in occlusal, labial, and basal views, Zigan, Mendym or Askyn Substage, *P. gigas* Zone. A × 30; B-F × 20.

Systematics

Class Chondrichthyes Huxley 1880

Subclass Elasmobranchii Bonaparte 1838

Family Phoebodontidae Williams 1985

Remarks.– While establishing the family Phoebodontidae, Williams (1985, p. 124) included in it sharks having 'teeth with an outer pair of lateral cusps which are equal to or exceed the height of the main cusp' and 'two dorsal fins (...), both bearing rhombic to subrhombic fin spines'. Then, he included in the same family a new species of ctenacanthiform shark, based on almost complete skeleton, which he named *Phoebodus heslerorum*. However, the central cusp of the teeth of *Ph. heslerorum* is usually higher than the others. The lateral cusps vary from about three quarters of the height of the central cusp to about the same height' (Williams 1985: p. 127, Pl. 16: 1, 2, 8). This character makes *Ph. heslerorum* different from the type species of *Phoebodus* (*Ph. sophiae* St. John & Worthen 1875) and excludes it from the Phoebodontidae, as defined by Williams (1985).

All species of fossil sharks, whose teeth have three main cusps in the crown and the central cusp is equal to or slightly smaller than the lateral ones (among them the type species for *Phoebodus*), are thus far based only on isolated teeth. It is unknown whether these sharks possessed other parts of the skeleton similar to each other and to *'Ph'. heslerorum*. This being the case, it may appear that none of known shark genera, even the genus *Phoebodus*, may fulfill both parts of this diagnosis.

Genera included: *Phoebodus, Thrinacodus*, and *Omalodus* gen. n.

Genus *Omalodus* gen. n.

Type species: *Phoebodus? bryanti* Wells 1944

Derivation of the name: Greek ομαλος - flat, even, and οδους - tooth.

Diagnosis.– Three main cusps in the crown. The central cusp is slightly smaller than the lateral ones. The number of intermediate, smaller cusps is irregular (two to four). All cusps are inclined linguad. The base, directed labiad, forms an obtuse angle with the crown.

Omalodus bryanti (Wells 1944)

Fig. 3I-M.

Phoebodus? bryanti sp. n.; Wells 1944: p. 140-141, Pl. 3: 24-27.

Phoebodus? bryanti Wells; Gross 1973: p. 131, Pl. 34: 23a-b.

Phoebodus floweri Wells; Gross 1973: Pl. 35: 8a-b, non 7a-b.

Phoebodus sp.; Gupta & Janvier 1979: pp. 163-164, Pl. 1: 2, 3, non 5.

Remarks.– The specimens of *O. bryanti* differ from all species of *Phoebodus* by the labiad direction of the base. The material figured by Gross (1973) and that described here are characterized by a rather regular row of pores in a shallow groove on the labial side at the base-crown interface. Cross sections show that the pores are openings of canals perforating the base from the labial to the lingual side (Fig. 3K-M). In many cases there are three small intermediate cusplets which rise directly from the side of lateral main cusps. The cusps are always smooth and rounded in cross section. Maximum lateral width of base: 1.8 mm, maximum heigth of tooth along the central cusp: 1.45 mm. According to Janvier (personal communication), the specimen illustrated in Gupta & Janvier (1979: Pl. 1: 2, 3) comes probably from the United States, not from India.

Material and occurrence.– Eight teeth from Lebedyanka Quarry, Kuznetsk Basin, Western Siberia, Late Givetian, Alchedat Substage.

Genus: *Phoebodus* St. John & Worthen 1875

Type species: *Phoebodus sophiae* St. John & Worthen 1875.

Remarks.– From the original description of the type species by St. John & Worthen (1875), the following features seem to be the most important and diagnostic for the genus: the teeth have three main cusps in the crown; these cusps are equal in size or the central one is a little smaller;

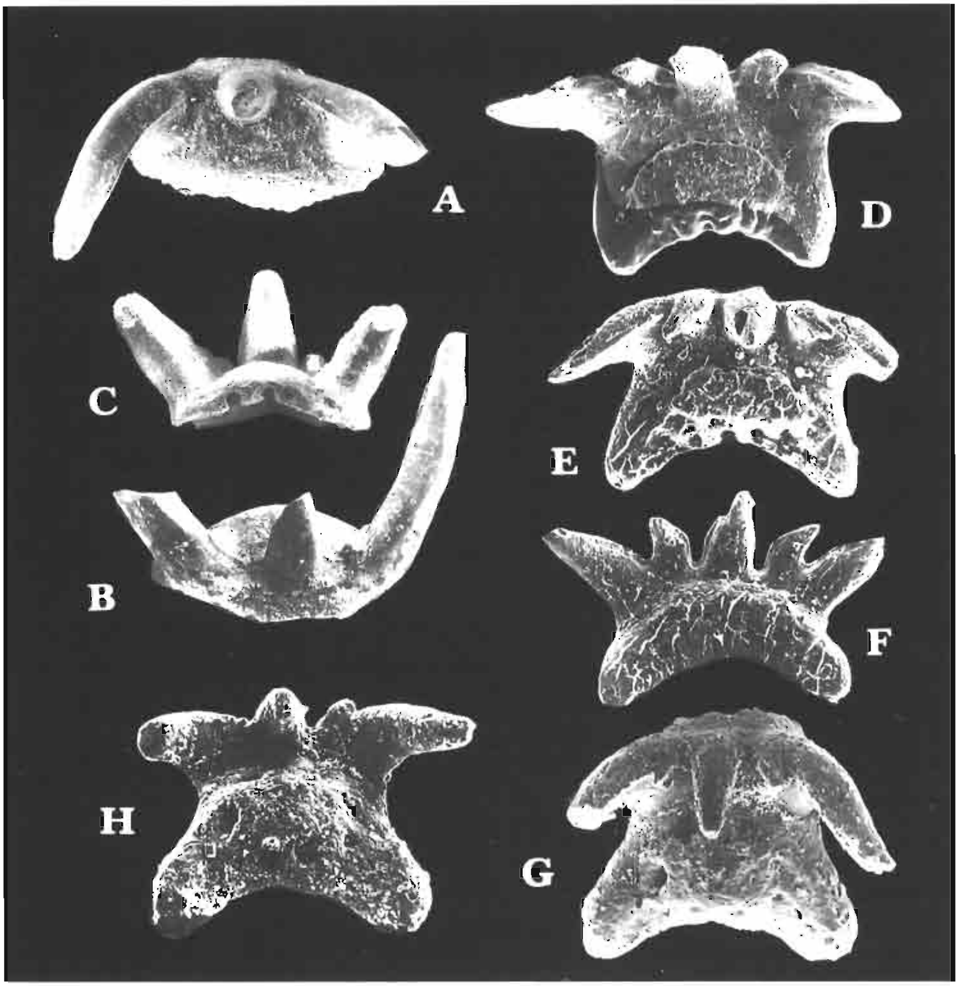

Fig. 5. ❑A-C. *Phoebodus* sp. C. Specimens LP 7-12 (A, B) in occlusal and labio-occlusal views, Ryauzyak, Mendym Substage, *P. gigas* Zone and IGPUW Ps/1/103 (C) in lingual view, Wietrznia, *P. gigas* Zone. ❑D-H. *Ph. bifurcatus* sp. n. D. Specimen LP 7-10 in occlusal view, Kuk-Karauk, Askyn Substage, *P. gigas* Zone. E-F. Juvenile tooth LP 7-9 in occlusal and lingual views, Zigan, Mendym or Askyn Substage, *P. gigas* Zone. G-H. Juvenile tooth LP 7-11 in occlusal and lingual views, Zigan, Mendym or Askyn Substage, *P. gigas* Zone. A-D × 30; E-H × 60.

additional, intermediate cusps are shorter and usually thinner. The base is regularly shaped, almost symmetrical; it extends linguad and forms a normal or acute angle with the crown; a button is present on the apical surface of the base. It must be emphasised here, however, that the number of intermediate cusplets may be different even in two teeth of the same species, and, probably, even of the same individual. It may vary from none (Fig. 8E) to four (Fig. 7A-B).

List of included species: see Tab. 1.

Tab. 1. List of species included in *Phoebodus*.

Species of *Phoebodus*	Reference	Occurrence	Dating
Ph. australiensis LONG 1990	?Wang & Turner 1985	S. China	*S. praesulcata*
	Wang 1989	S. China	*S. praesulcata - S. sulcata*
	Long 1990	Thailand	*P. expansa*
	Ginter 1990	Poland	Early *P. trachytera*, Late *P. expansa - ? S. crenulata*
	Derycke *et al.* in press	France	*S. sulcata*
	this paper	Urals	*P. postera*
		Poland	*P. postera - P. praesulcata*
Ph. bifurcatus sp. nov.	Hladil *et al.* (in press)	Moravia	Late *P. gigas*
	this paper	Urals	Late *P. gigas - ?P. linguiformis*
		Timan	*P. gigas*
		Poland	*P. gigas - ?P. linguiformis*
Ph. fastigatus sp. nov.	Gross 1973	Indiana	Middle Devonian
	this paper	Kuzneck Basin	Late Givetian
Ph. aff. *fastigatus*	Ginter 1990	Poland	*A. triangularis - P. gigas*
	this paper	Urals	*P. gigas*
		Poland	*A. triangularis - P. gigas*
Ph. gothicus GINTER 1990	Gross 1973	Iowa	late Late Devonian
	Ginter 1990	Poland	Late *P. trachytera* - - Early *S. praesulcata*
	Kietzke & Lucas 1992	New Mexico	Famennian
	this paper	Urals	*P. postera - P. expansa*
		Poland	Early *P. marginifera* - - *S. praesulcata*
Ph. limpidus GINTER 1990	Ginter 1990	Poland	Late *P. expansa* - - Early *S. praesulcata*
	this paper	Poland	*P. trachytera - P. postera*
?Ph. macisaacsii St. JOHN & WORTHEN 1875	St. John & Worthen 1875	Iowa	Givetian
Ph. politus NEWBERRY 1889	Newberry 1889	Ohio	Late Famennian
	?Eastman 1899	Illinois	Late Famennian
Ph. sophiae St. JOHN & WORTHEN 1875	St. John & Worthen 1875	Iowa	Givetian
Ph. turnerae sp. nov.	this paper	Urals	*P. crepida* - - Early *P. marginifera*
		Poland	*P. rhomboidea - P. marginifera*

Phoebodus australiensis Long 1990
Fig. 8L-M.

cf. *Phoebodus politus* Newberry; Wang & Turner 1985: p. 225, Pl. 3: 2a-b.
cf. *Phoebodus politus* Newberry; Wang 1989: pp. 103-104, Pl. 27: 1a-b.
'Cladodus' spp.; Wang 1989: pp. 104-105, Pl. 28: 2a-b, 4a-b, 5a-b, non 3a-b; Pl. 29: 3a-b, non 1a-b, 4a-b, 5a-b, 6.
Phoebodus australiensis sp. n.; Long 1990: pp. 59-61: 2A-M, 3J-O, 4A-E.
Phoebodus australiensis Long; Ginter 1990: pp. 73-74, Pl. 1: 3-11.

Remarks.– Material includes both Morphotypes 1 and 2 *sensu* Ginter (1990). One specimen (Fig. 8L) possesses grooves on the upper side of the base going linguad from between the cusps.

Material and occurrence.– Four specimens from S. Urals, Popovskiy, *P. postera* or Lower *P. expansa* Zone; 27 specimens from the Holy Cross Mountains: 24 from Ostrówka, *P. postera* - *S. praesulcata* Zones, three from Jabłonna, *P. trachytera* Zone (see also Ginter 1990).

Phoebodus bifurcatus sp. n.
Figs 4A-F, 5D-H, 6A.

Holotype: Tooth LP 7-8, Fig. 4D-F.
Type locality: Zigan, South Urals, Bashkiria.
Type horizon: Late Frasnian, Mendym Substage, *P. gigas* Zone.
Derivation of the name: Latin *bifurcatus* - bifurcated, dichotomous.

Diagnosis.– The crown consists of five cusps. Three main cusps are strongly inclined linguad and form large angles between each other. The labial face of central and of two smaller intermediate cusps is covered by strong, subparallel ridges. The sculpture of the main lateral cusps is spirally curved. The base is thick, advanced far linguad; its linguo-lateral angles may be expanded linguad farther than its median part. The underside of the base forms an almost semicylindrical arch. A broad oval button occurs on the upper side.

Description.– The intermediate cusps are fused to the major ones by their lower parts. The button lies close to the lingual rim of the base and is surrounded by a chain of foramina, which makes the button more distinct (Fig. 5D). Two canals open in the median part of the lingual rim and continue close to the underside of the base. Parts of them are often seen as grooves (Fig. 4C, F), even if only a slight abrasion of the lower surface took place.

In juvenile stages, the labial part of the base is distinctly narrower than its lingual part. The button is vague and rounded. The cusps are relatively thinner and their sculpture is weaker than in the adult stage.

Dimensions of the holotype (see Fig. 6B): a = 2.80 mm, b = 1.40 mm, c = 1.10 mm, d = 1.25 mm.

Remarks.– *Ph. bifurcatus* sp. n. was also found in the Lesni Lom Quarry, Moravia in the Late *P. gigas* Zone (Hladil *et al.*, in press).

Material and occurrence.– 86 specimens from S. Urals: 48 from Ryauzyak, Mendym Substage, 12 from Kuk-Karauk, Askyn Substage, 17 from Zigan, Mendym - Askyn Substage, four from Kuktash, Askyn Substage, two from Lemeza, Mendym Substage, one from Askyn, Askyn Substage,

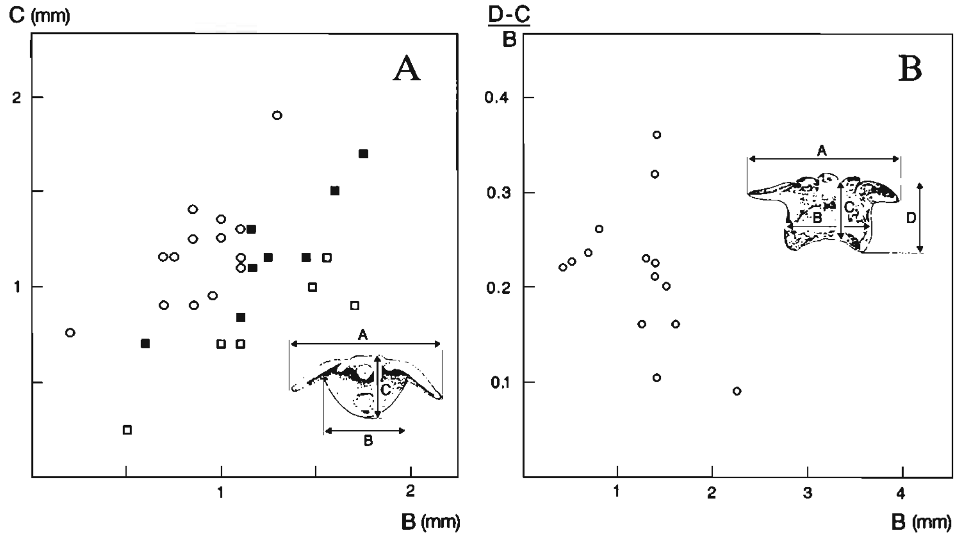

Fig. 6. Variation of tooth-base dimensions in some of *Phoebodus* species. ❑A. *Ph. gothicus* Ginter 1990 (circles), *Ph. turnerae* sp. n. (black squares) and *Ph.* sp. B (white squares). ❑B. *Ph. bifurcatus* sp. n.

all *P. gigas* Zone, three from Zuyakovo, Askyn Substage, *P. gigas* - ?*P. linguiformis* Zone; 11 from Timan, Vezha-Vozh, Lyaiol Substage, *P. gigas* Zone; 29 specimens from the Holy Cross Mountain: 19 from Karczówka, *P. gigas* or *P. linguiformis* Zone, two from Kostomłoty, *P. gigas* Zone, eight from Tudorów, late Frasnian.

Phoebodus fastigatus sp. n.
Fig. 3A-B, G.

Phoebodus floweri Wells; Gross 1973: Pl. 35: 7a-b, non 8a-b.

Holotype: Tooth LP 5-1, Fig. 3A, B.

Type locality: Kuznetsk basin, Mazalovskiy Kitat River.

Type horizon: Late Givetian Mazalovskiy Kitat Substage.

Derivation of the name: Latin *fastigatus* - sharp-ended.

Diagnosis.– The crown consists of three, almost equal, recurved cusps which are smooth, thin, and rounded in cross section. The trapezoidal base, narrow in the crown region, becomes wider lingually. The lingual part is straight and thin. The rounded oval button is situated in the center of the base.

Description.– The basal parts of the cusps are very close to each other, but separate. One end of the main canal opens on the lingual face of the button and the other into the center of the underside.

Dimensions of the holotype (see Fig. 6): a = 1.40 mm, b = 1.05 mm, c = 0.65 mm.

Remarks.– *Phoebodus fastigatus* sp. n. is similar in overall appearance to *Ph. bifurcatus* sp. n., particularly to its juvenile stage. However, the base of the latter species is characterized by a strong arch and far linguad expanded angles. The cusps of *Ph. fastigatus* lack the so characteristic

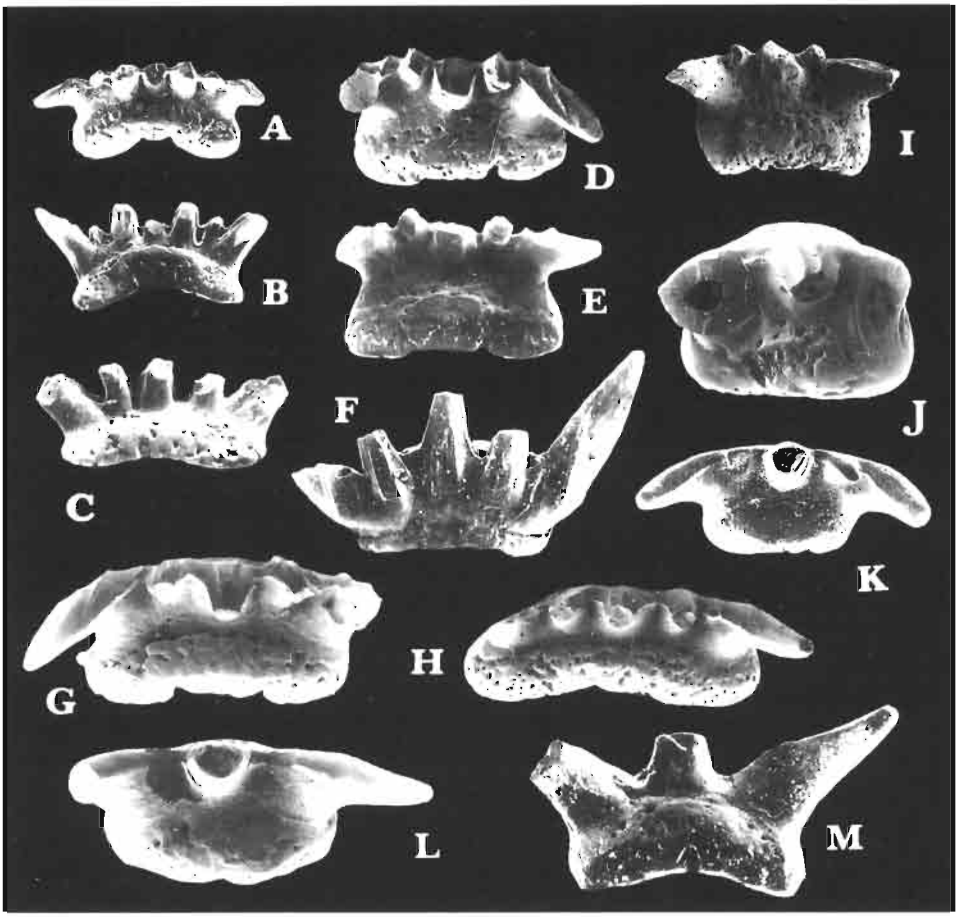

Fig. 7. ❑A-I. *Phoebodus* sp. A. A, B. Tooth with seven cusps LP 7-17 in occlusal and lingual views, Ryauzyak, A. *P. triangularis* Zone. C-H. Specimens LP 7-14, 15, 16, 17 in lingual (C, E), occlusal (D, G, H), and labial (F) views, Ryauzyak, *P. gigas* Zone. I. Specimen IGPUW Ps/1/89 in occlusal view, Kadzielnia, *P. gigas* Zone. ❑J-M. *Ph.* sp. B, Specimens LP 7-18, 19, 20 in occlusal (J, K, L) and lingual (M) views, Ryauzyak, *P. rhomboidea* Zone. A, B, D, E, H-J × 20; C × 27; F, G × 30; K × 40.

ornament of *Ph. bifurcatus*. Gross (1973: Pl. 35: 7a-b) illustrated a specimen very similar to the new described species as *Ph. floweri*. The first description of *Ph. floweri* given by Wells (1944: p. 139-140, Text-fig. 8b-d, Pl. 3: 22-23) was based on undefinable fragments, which is why the tooth published by Gross (1973) is included here as *Ph. fastigatus*.

Material and occurrence.– Four specimens from the Late Givetian of Kuznetsk Basin, one from Mazalovskiy Kitat River, Mazalovskiy Kitat Substage, three specimens from Lebedyanka Quarry, Alchedat Substage.

Ph. aff. *fastigatus* sp. n.

Fig. 3C-F.

Phoebodus limpidus sp. n.; Ginter 1990: Pl. 4: 6a-b, non 2-5.

Remarks.– This tooth form differs from *Ph. fastigatus* sp. n. by possessing a five-cusped crown and a larger angle between the main lateral cusps. The base is thicker and slightly bifurcated, which makes this form resemble a little the juvenile stage of *Ph. bifurcatus* sp. n. The specimen from Wietrznia was referred by Ginter (1990: Pl. 4: 6a-b) to *Ph. limpidus* because of the smooth surface of the cusps. The base outline, however, is in this tooth form completely different from that in the type of *Ph. limpidus*.

Material and occurrence.– Four specimens from the S. Urals, Ryauzyak, Mendym and Askyn Substage, *P. gigas* Zone; one specimen from the Holy Cross Mountains, Wietrznia, *A. triangularis* or *P. gigas* Zone.

Phoebodus gothicus Ginter 1990

Fig. 8I-K.

Phoebodus politus Newberry; Gross 1973: pp. 132-133, Text-figs 29C-G, 30A, 31A, and Pl. 34: 12-22.

Phoebodus gothicus sp. n.; Ginter 1990: pp. 74-75, Pl. 2: 1-6, Pl. 3: 5-7.

Phoebodus politus Newberry; Kietzke & Lucas 1992: p. 17: 2A-C.

Material and occurrence.– Four specimens from S. Urals, Ryauzyak, Kushelga Substage, *P. postera* - *P. expansa* Zones, one specimen from Kuk - Karauk, Kushelga Substage, *P. postera* Zone; 59 new specimens from the Holy Cross Mountains: 53 from Ostrówka, *P. trachytera* - Middle *P. praesulcata* Zones, six from Łagów, Early and Late *P. marginifera* Zone (see also Ginter 1990).

Phoebodus turnerae sp. n.

Figs 6B-C, 8A-H.

Holotype: Tooth LP 7-21, Fig. 8A-B.

Type locality: Ryauzyak, South Urals, Bashkiria.

Type horizon: Famennian Makarovo Substage, *P. rhomboidea* Zone.

Derivation of the name: In honour of Dr. Susan Turner, Queensland Museum, Brisbane, Australia.

Diagnosis.– Three to (seldom) five cusps, central is somewhat smaller than lateral ones, which may be slightly sigmoidal, with a low blade separating their labial and lingual faces; the cusps are only slightly inclined linguad. Sculpture of the cusps consists of many subparallel, thin ribs. The base ends lingually in an obtuse angle, its length and width are almost equal; the base outline may be clearly polygonal and rather narrow or wider and rounded. The hemispherical button lies close to the lingual rim of the base, with a large canal opening on its linguo-basal face.

Dimensions of the holotype (Fig 6A): a = 2.7 mm, b = 1.1 mm, c = 1.2 mm.

Remarks.– *Phoebodus turnerae* sp. n. resembles *Ph. gothicus* in the shape and distinctness of the button and in the sculpture of the cusps. They differ, however, in the outline of the base - in the latter species it is longer, with an acute angle at the lingual end in typical specimens (Fig. 8K), and the button lies closer to the crown. The cusps of *Ph. turnerae* are less sigmoidal and recurved than in *Ph. gothicus*.

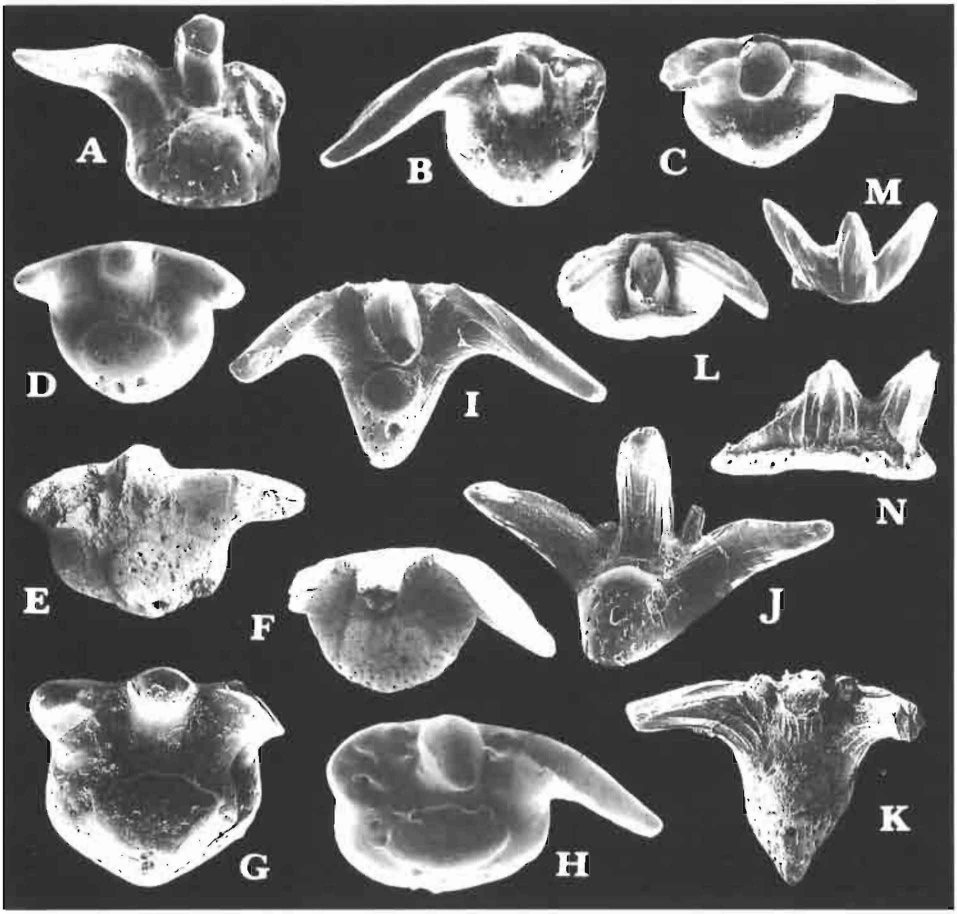

Fig. 8. ❑A-H. *Phoebodus turnerae* sp. n. A, B. Holotype LP 7-21 in lingual and occlusal views, Ryauzyak, Early *P. marginifera* Zone. C, D, G. Specimens LP 7-22, 23, 24 in occlusal views, Ryauzyak, *P. rhomboidea* Zone. E. Specimen IGPUW Ps/1/102 in occlusal view, Miedzianka, *P. rhomboidea* or *P. marginifera* Zone. F. Specimen ZPAL P.IV/10, transitional to *Ph. gothicus*, in occlusal view, Łagów, Early *P. marginifera* Zone. H. Specimen LP 7-25, transitional to *Ph.* sp. B, in occlusal view, Ryauzyak, Early *P. marginifera* Zone. ❑I-K. *Ph. gothicus* Ginter 1990 I-J. Specimen LP 7-26 in occlusal and oblique lingual views. Kuk-Karauk, *P. postera* Zone. K. Specimen LP 7-27 in occlusal view, Ryauzyak, *P. postera* or *P. expansa* Zone. ❑L-N. *Ph. australiensis* Long 1990, Popovskiy, *P postera* or Early *P. expansa* Zone. L. Specimen LP 7-28 with grooves between cusps in occlusal view. M. Specimen LP 7-29 in labial view. N. Specimen LP 7-30, Morphotype 2?, labial view. C × 10; A, B, D-F, I, J × 20; G, K, M, N × 27; H, L, × 40.

There are gradations between *Ph. turnerae* sp. n. and the *Ph.* sp. B group, from which *Ph. turnerae* was separated. The Australian specimens, designated as *Phoebodus* cf. *P. politus* by Turner (1982: Fig. 6A-B), and referred by Long (1990: Fig. 3F-G) to *Ph. australiensis*, are similar to some teeth included here in *Ph.* sp. B (Fig. 7J) but also resemble, in some extent, those of *Ph. turnerae* (Fig. 8H). The specimens mentioned above have an almost rectangular outline of the base (see Turner 1982; Fig. 6B), which is typical of *Ph.* sp. B, but the button is very distinct and is situated close to the lingual rim, which is one of the diagnostic features of *Ph. turnerae.* However, the first specimen figured by Turner (1982: Fig. 6A) displays very coarse striation on the labial face of the cusps. This can hardly be found in the specimens of *Ph. turnerae.*

Material and occurrence.– 18 specimens from Urals, Ryauzyak, Makarovo Substage, Late *P. crepida* - Early *P. marginifera* Zone; two specimens from the Famennian of the Holy Cross Mountains: one from Łagów, Early *P. marginifera* Zone, and one from Miedzianka, *P. rhomboidea* or *P. marginifera* Zone.

Phoebodus sp. A

Fig. 7A-I.

Description.– Five to seven cusps in the tooth crown, central main cusp a little lower than the lateral ones. Labial face of the cusps is covered with strong ridges. Sculpture of main lateral cusps is spirally curved.

The base is short and very wide, showing high variability of outline. The laterally elongated button lies close to the lingual rim. In some of the specimens (Fig. 7H), it occupies the whole lingual part of the base. The underside of the base varies from slightly concave to planar.

Remarks.– The crown of *Phoebodus* sp. A is almost identical to that of *Ph. bifurcatus* sp. n., but the base of the former is much wider and shorter, lacks the typical arch and bifurcated outline. The button of *Ph. bifurcatus* is more distinct. We include in *Ph.* sp. A a group of teeth with variable features, connected both with crown (e.g. forms with seven cusps; Fig. 7A-B) and base. This variability does not substantiate, however, distinguishing of more separate species. It may be the result of various positions of the teeth on the jaw.

Material and occurrence.– 53 specimens from the S. Urals, 44 from Ryauzyak, Domanik - Mendym Substage, *A. triangularis* - *P. gigas* Zone, seven from Lemeza, Askyn Substage, *P. gigas* Zone, two from Kuktash, Askyn Substage, *P. gigas* Zone; two specimens from the Holy Cross Mountains, Kadzielnia, *P. gigas* Zone.

Phoebodus sp. B

Fig. 7J-M.

Description.– Three to five cusps in the crown. Central cusp is lower than the main lateral ones, which form a large angle between each other. The base is almost rectangular, slightly elongated laterally. A button lies close to the lingual rim or in the center of the base.

Remarks.– *Ph.* sp. B consists of a group of forms characterized by a stable outline of the base, but varying ornamentation of the cusps. As in the case of *Ph.* sp. A, the differences between specimens are not clear enough to establish more than one separate new species. *Ph.* sp. B is similar in overall appearance to *Phoebodus* cf. *P. politus* figured by Turner (1982: Fig. 6A-B), but the latter has much more prominent and rounded apical button (see *Ph. turnerae* sp. n. here above).

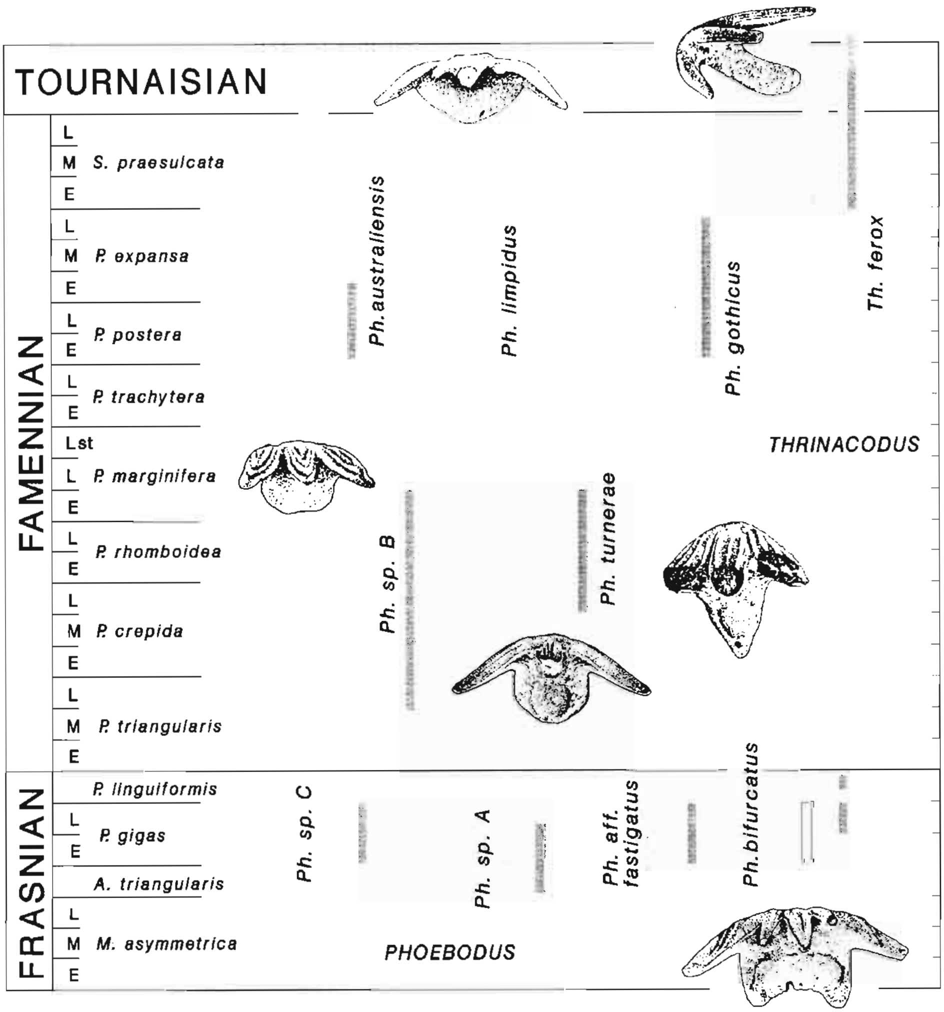

Fig. 9. Stratigraphic ranges of phoebodont species in the Late Devonian of the East European Platform margin. Grey - Holy Cross Mts, black - South Urals, white - Timan, hachured - Moravia.

Material and occurrence.– 12 specimens from South Urals, Ryauzyak, Makarovo Substage, Late *P. triangularis* - Early *P. marginifera* Zones.

Phoebodus sp. C

Fig. 5A-B.

Description.– The tooth crown consists of three or five cusps; the three main cusps are smooth, long and strongly inclined linguad, grow separately already from the base, their labial and lingual faces are separated by a well defined ridge. The base is oval, short, a little convex, with a high but not clear button.

Material and occurrence.– Four specimens from South Urals, two from Ryauzyak, two from Lemeza, all Mendym Substage, *P. gigas* Zone; two specimens from the Holy Cross Mountains, Wietrznia, *P. gigas* Zone.

Stratigraphical distribution and conclusions

The oldest known phoebodont teeth were found in the Givetian of North America (St. John & Worthen 1875; Wells 1944; Gross 1973; see Tab. 1), Poland (Racki 1985; Liszkowski & Racki in press) and Australia (S. Turner, personal communication). The specimens of *Omalodus bryanti* and *Phoebodus fastigatus* sp. n. described herein come from the late Givetian of the Kuznetsk Basin, Western Siberia. The stratigraphic position of the Paul Frank Quarry bone-beds, Indiana, from which Gross (1973: Pl. 35: 7a-b) figured a tooth referred here to *Ph. fastigatus*, is not certain, but it is probably also Givetian.

Early Frasnian phoebodonts are thus far unknown (Fig. 9). Starting from the *A. triangularis* Zone, a group of teeth, designated here as *Ph.* sp. A, appears abundantly in the East European regions. Soon after, in the Early *P. gigas* Zone, begins the first period of great diversification of the genus *Phoebodus*. Four forms were distinguished in the *P. gigas* Zone: *Ph. bifurcatus*, *Ph.* aff. *fastigatus*, *Ph.* sp. A and *Ph.* sp. C. All of them seem to be extinct close to the Frasnian/Famennian boundary.

No evidence of phoebodonts has been found in the early parts of the *P. triangularis* Zone. The first Famennian form, *Ph.* sp. B, appears in the Late *P. triangularis* Zone in the South Urals. The crisis in species diversity at the end of the Frasnian and in the earliest Famennian (Kellwasser event) in the East European regions has been already observed in some groups of invertebrates, such as corals and stromatoporoids in Moravia, or brachiopods and reef-building organisms in the South Urals and the Holy Cross Mountains (McGhee 1989; Racki *et al.* 1989). This is associated with global decimation of many groups of organisms (conodonts, calcareous foraminifers, rugose corals, fishes; Sandberg *et al.* 1988; McGhee 1989, Ivanov in press). Absence of phoebodonts in samples collected from the interval *P. linguiformis* through Middle *P. triangularis* Zone on the East European Platform margin and in Moravia (Hladil *et al.* in press) might be the result of the same factors, that caused the drop in species diversity of the organisms mentioned above. This event among the sharks has not yet been documented in the other places in the world.

In the Late *P. crepida Ph. turnerae* sp. n. appears. The second and last radiation of Late Devonian phoebodonts began in the *P. marginifera* Zone (Fig. 9). The first occurrences of *Thrinacodus* were found at the end of that or in the beginning of the next, *P. trachytera* Zone in the Holy Cross Mountains. *Th. ferox* is common in the late Famennian of Poland and South Urals (Fig. 9; Ginter 1990), Morocco (Derycke 1989), Thailand (Long

1990), South China (Wang & Turner 1985; Wang 1989), Australia (Turner 1982) and probably in New Mexico (Kietzke & Lucas 1992).

Most late Famennian phoebodont species disappear by the Middle *P. praesulcata* Zone. Only *Th. ferox* and *Ph. australiensis* (see Wang 1989; Ginter 1990; Derycke *et al.* in press), persisted across the Early Carboniferous boundary.

Since the sharks could actively swim and resist currents (only fishes and ammonites were able to do it in those times), they could reach environments inaccessible to other organisms, such as conodonts used as zone fossils. Phoebodonts appear to preferably inhabit the same facies as palmatolepids, but they can be also found in transitional facies, where icriodontidids or polygnathids predominate, and in facies where no conodonts are found. In such situations, phoebodont teeth acquire an independent biostratigraphic role. Most phoebodont species show a wide distribution and rather short ranges. They are thus recommended as useful stratigraphic tools, especially for Late Devonian deposits.

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Streszczenie

Wśród ichtiolitów, występujących w facjach pelagicznych górnego dewonu obrzeżenia Platformy Wschodnioeuropejskiej (w Górach Świętokrzyskich, na Południowym Uralu i w prowincji timańsko-peczorskiej; Fig. 1), do najczęściej spotykanych należą zęby rekinów typu phoebodontowego. Zostały one znalezione także w górnym żywecie Basenu Kuźnieckiego (zachodnia Syberia).

Korona tych zębów składa się z trzech głównych, smukłych wierzchołków prawie równej długości. Pomiędzy wierzchołkami głównymi mogą występować drobniejsze wierzchołki pośrednie. W zależności od kształtu i nachylenia podstawy zęba względem płaszczyzny korony wyróżnia się trzy rodzaje phoebodontidów: *Omalodus* gen. n., o podstawie skierowanej w stronę wargową; *Phoebodus* St. John & Worthen, o symetrycznej podstawie skierowanej w stronę językową; oraz *Thrinacodus* St. John & Worthen, charakteryzujący się podstawą wygiętą także w stronę językową, ale o niesymetrycznym zarysie i skręconą dodatkowo w osi prostopadłej do korony. Poszczególne gatunki z rodzaju *Phoebodus* rozróżnia się na podstawie drobnych cech morfologicznych podstawy i korony zęba, a w szczególności: zarysu podstawy, położenia i wielkości guzka zawiasowego oraz ornamentacji wierzchołków. Zęby rekinów z rodzaju *Phoebodus* były ułożone w szczęce i funkcjonowały prawdopodobnie w sposób zbliżony do aparatu szczękowego dzisiejszego rekina *Chlamydoselachus anguineus* Garman (patrz Gudger 1937). Różnicę stanowi wzmocnienie połączenia między kolejnymi, nakładającymi się na siebie zębami w spirali zębowej *Phoebodus* za pomocą guzków zawiasowych i wgłębień w podstawach (Fig. 2).

Z górnego żywetu Basenu Kuźnieckiego opisano nowy rodzaj *Omalodus* gen. n. (Fig. 3H-M) oraz nowy gatunek *Phoebodus fastigatus* sp. n. (Fig. 3A, B, G). W górnym dewonie obrzeżenia Platformy Wschodnioeuropejskiej znaleziono sześć gatunków phoebodontidów, w tym dwa nowe: frański *Ph. bifurcatus* sp. n. (Figs 4A-F, 5D-H) i fameński *Ph. turnerae* sp. n. (Fig. 8A-H). Istnieje znacząca luka w zapisie paleontologicznym phoebodontidów w poziomach *P. linguiformis* - *P. triangularis* (Fig. 9).