

Fish Assemblages from the Upper Devonian of the South Urals (Russia)

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Abstract—Diverse and abundant fish remains are described from the Upper Devonian of 10 sections on the western slope of the South Urals. The distribution of the fish taxa was analyzed in these sections, and the fish assemblages have been established in all Frasnian and Famennian regional stages of that region. The assemblages include taxonomically diverse phoebodontiforms, jalodontiform, symmoriiforms, ctenacanthiforms, squatinactiform, and euselachians chondrichthyans. Ten fish taxa are reported in the Upper Devonian of the South Urals at first time. The occurrence of *Phoebodus latus* in the Lower–Middle *triangularis* Zone is the youngest in the world. This species survived the Kellwasser biotic crisis. The new data of occurrence of *Phoebodus* species in the studied sections confirms the boundaries of the phoebodontid zones.

Keywords: fishes, Upper Devonian, South Urals, Russia

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INTRODUCTION

Late Devonian vertebrates are well studied in several regions of European part of Russia, but they were unknown in the Urals until the 90s of the last century. The collection of numerous fish remains from the Upper Devonian of the South Urals was gained as a result of detailed stratigraphic research by a group of geologists from the Institute of Geology, subdivision of the Ufa Federal Research Centre of the Russian Academy of Sciences (Ufa), and included A.N. Abramova, O.B. Artyushkova, V.N. Baryshev, V.N. Pazukhin, and R.Ch. Tagarieva. The fish remains were collected in the sections or extracted from conodont residues obtained by the standard processing of samples. A first description of teeth from this collection was given in the revision of chondrichthyans of the family Phoebodontidae and five new species established (Ginter and Ivanov, 1992, 1995). Preliminary data on the distribution of fish taxa have been provided for the Upper Frasnian and Famennian of the South Urals (Ivanov, 1995). The phoebodontid zonation was proposed for the Givetian–Famennian interval based on the distribution of *Phoebodus* species in the sections of the South Urals and Holy Cross Mountains (Ginter and Ivanov, 1995, 2000). Recently the boundaries of some zones were updated as new data appeared on the occurrence of some zonal species outside their previously known stratigraphic intervals

(Ivanov, 2020). Besides phoebodontids, the diverse remains of other fish groups were not described, and data on the distribution of taxa in each sections was not provided.

This study includes a description of all fish remains recovered from the Upper Devonian of 10 sections on the western slope of the South Urals (Fig. 1) and an analysis of the taxa distribution in these sections and fish assemblages in most regional stages of Frasnian and Famennian of that region is presented. Most samples contain abundant conodont remains, the conodont zones of previous zonation (Ziegler and Sandberg, 1990) were well determined in the interval from the Middle Frasnian to the Uppermost Famennian (Fig. 2).

The collection includes the scarce macroremains of placoderms and sarcopterygian, and very abundant microremains such as teeth, scales and denticles of chondrichthyans; plate fragments of placoderms; scales and tesserae of acanthodians; teeth, tooth plates, scales and jaw fragments of sarcopterygians and actinopterygians. Most microremains are well preserved but some remains are abraded, with rounded, unornamented or broken cusps, and sometimes preserve bioerosion traces in the form of microborings. The fish microremains studied here were extracted from samples of carbonate-cemented rocks using standard processing by diluted acetic or formic acids

and heavy liquid separation. The fish microremains were microphotographed using the scanning electron microscopes JEOL JSM-T300, Hitachi S-3400N, and Tescan VEGA-II XMU in the Center for Geo-Environmental Research and Modelling “Geomodel” of the Research Park of St. Petersburg State University and in the Borissiak Paleontological Institute of the Russian Academy of Sciences.

The described specimens are housed in the Paleontological Museum of St. Petersburg State University (collection abbreviation PMSPU). Abbreviations of other museum collections: GSC—Geological Survey of Canada, Calgary, Canada; IGPUW—Institute of Geology, Warsaw University, Poland; MB.f—Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany; UTGD—the Geology Department of the University of Tasmania, Australia.

STRATIGRAPHY

The position of the Middle/Upper Devonian and hence the Givetian/Frasnian boundary on the East European Platform and western slope of the South Urals is a matter of debate. The shallow-water terrigenous sediments of the Upper Givetian and Lower Frasnian yield no conodonts, and thus direct correlation to the standard conodont zones is impossible (Artyushkova et al., 2022; Ivanov, 2023). For this reason, the Givetian–Frasnian boundary is not clearly defined there, and various authors have put forward different opinions on its position. The Kynian and Sargaevian regional stages correspond to the boundary interval in Devonian sections of the western slope of the South Urals. This boundary in the standard conodont zonal scale is accepted within the Early *falsiovalis* Zone, above the *Skeletognathus norrisi* Zone, and determined by a first appearance of *Ancyrodella* species (Becker et al., 2020). The findings of conodont species that determine this boundary are extremely rare in Russia, and it can be suggested from them that this boundary should be defined within the Kynian (Timanian) Regional Stage (Artyushkova et al., 2022). Thus, the Frasnian Stage on the western slope of the South Urals is represented by deposits of the upper part of the Kynian, Sargaevian, Domanikian, Mendymian, and Askynian regional stages; the Famennian Stage—deposits of the Barmian, Makarovian, Murzakaevian, Kushelgian, and Lytvian regional stages (Fig. 2).

The deposits of the **Kynian** Regional Stage rarely expose in the natural outcrops. They are represented by clotted clayey limestones, calcareous shales, marls and greenish-grey clays. The limestones contain bioclastic detritus, numerous small pyritic aggregates and ferrous hydroxide nodules. The fossils of these deposits includes brachiopods, bivalves, corals, ostracods, gastropods, scarce tentaculites, conodonts and fish remains. The thickness of the Kynian deposits in the best exposed Ryauzyak section is 4.65 m (Abramova, 1999).

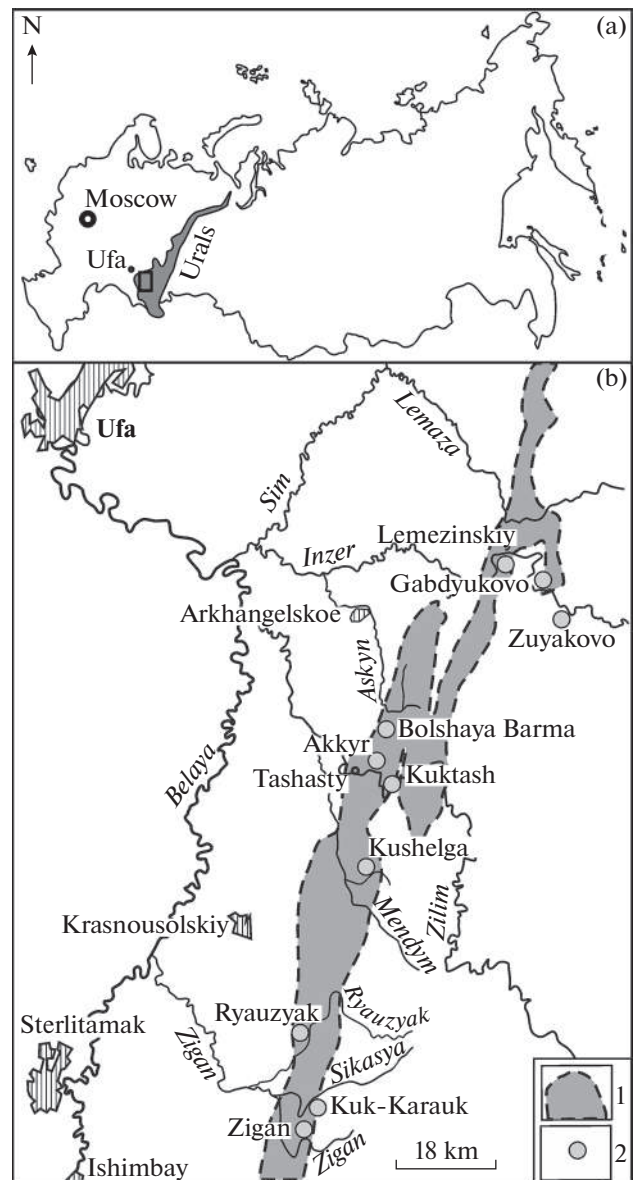


Fig. 1. Location of the studied area in Russia (a) and the sections (b). Legend: (1) boundary of the West Uralian Folded Zone; (2) studied sections.

The **Sargaevian** Regional Stage is probably correlated with the Upper *falsiovalis*–*transitans* conodont Zones (Artyushkova et al., 2011). The Sargaevian deposits are rather widespread within the West Uralian Folded Zone. They consist of grey and dark-grey clayey limestones, almost black bituminous in the upper part, with thin interbedding of black carbonaceous shales containing pyritic inclusions. The thickness of the Sargaevian deposits varies from 3.2 m (Ryauzyak section) to 9.75 m (Gabdyukovo section). Fossils are represented by brachiopods, goniatites, tentaculites, ostracods, conodonts and rare fish remains.

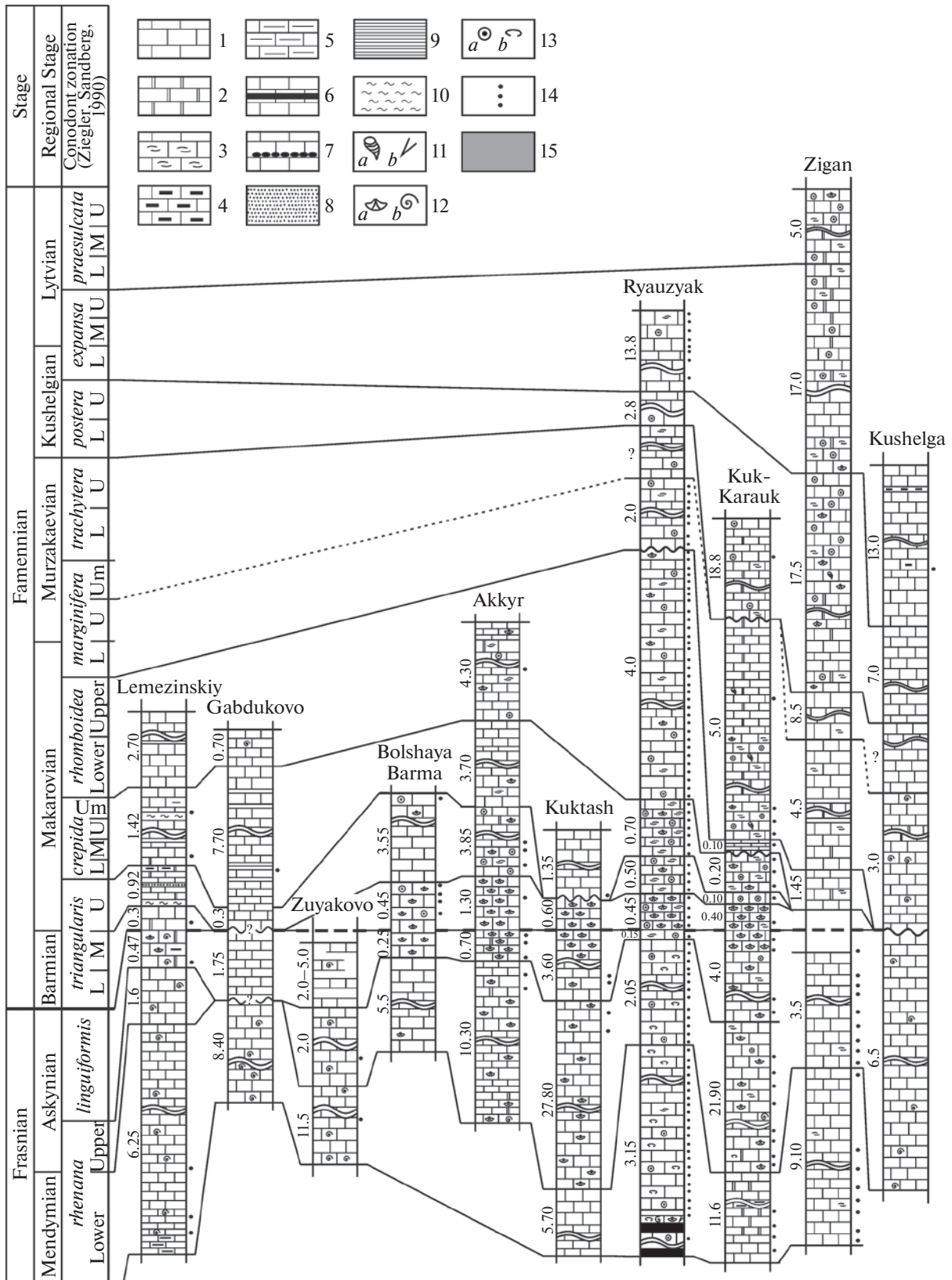


Fig. 2. Correlation of the Upper Devonian studied sections in the western slope of the Soth Urals (modified from Pazukhin, 1989; Abramova, 1999; Artyushkova et al., 2011). Legend: (1–6) limestones: (1) diversely layered limestones, (2) dolomitized limestones, (3) organogenic-polydetritic limestones, (4) bituminous limestones, (5) clayey limestones, (6) limestones with carbonaceous shales, (7) limestones with nodules, (8) sandstones, (9) clay shales, (10) siltstones; (11–13) fossils: (11a) rugose corals, (11b) tentaculites, (12a) brachiopods, (12b) goniatites, (13a) crinoids, (13b) ostracods; (14) samples with fish remains, (15) gap. Abbreviations: L—Lower, M—Middle, U—Upper, Um—Uppermost.

The **Domanikian** Regional Stage corresponds to the *punctata–jamieae* Zones (Artyushkova et al., 2011). The deposits consist of dark-grey and black clayey and calcareous bituminous shales interlayered with dark-grey bituminous limestones and black cherts. The thickness varies from 2 to 150 m in different sections. The Domanikian deposits on the Inzer River (Gabyukovo and Zuyakovo sections) are characterized by complex folding, and it is quite difficult to estimate their true thickness (Abramova, 1999). Fossils include tentaculites, ammonoids, bivalves, brachiopods, conodonts and fishes.

The **Mendymian** Regional Stage is correlated with the Lower *rhenana* Zone and named by Markovskiy as *Manticoceras* Beds. The Mendymian deposits contain light-grey compact thick-layered, often silicified limestones. Two types of the Mendymian deposits were established: the Askyn (brachiopod) type in the Akkyr, Kuk-Karauk and Zigan sections, and the Inzer (goniatite) type in the Gabyukovo, Lemezinskiy, Mendym, and Zuyakovo sections (Artyushkova et al., 2011). The Ryauzyak section belongs to the transitional type. The thickness of the deposits in different sections comprises 2.2 m in the Mendym section up to 9 m in the Zigan section (Abramova, 1999). Diverse fossils are goniatites, tentaculites, gastropods, pelecypods, brachiopods, ostracods, crinoids, conodonts and fishes. The boundary between the Mendymian and Askynian regional stages is not distinct in some sections (Abramova, 1999).

The **Askynian** Regional Stage corresponds to the Upper *rhenana–linguiformis* Zone (Artyushkova et al., 2011). The deposits often consist of light-grey massive or thick-layered organogenic limestones, sometimes dolomitized, with intercalation of brachiopod-crinoid coquinas in some sections. The other type of the Askynian deposits in the Lemezinskiy and Mendym sections is the Inzer type which is represented by light-grey and dark-grey, bedded bituminous limestones with numerous goniatite shells, and named as the *Crickites* Beds. The thickness of these deposits varies from 2.2 m in the Ryauzyak section to 26 m in the Kuk-Karauk section. Diverse fossils include corals, goniatites, ostracods, brachiopods, conodonts and fish remains.

The Famennian **Barmian** Regional Stage is correlated with the Lower–Middle *triangularis* Zones (Artyushkova et al., 2011). The deposits are represented by light-grey or brownish-grey, thick-bedded brachiopod coquinas or bioclastic limestones, sometimes dolomitized. The brachiopod coquinas occur at different stratigraphical levels and form lens-shaped accumulations of various thicknesses (Tagarieva, 2013). The thickness of the Barmian deposits varies from 0.45 m in the Ryauzyak section up to 1.75 m in the Bolshaya Barma section. Fossils include numerous brachiopods, crinoids, conodonts, and rare corals, bryozoans, bivalves, gastropods, and fishes.

The **Makarovian** Regional Stage corresponds to the Upper *triangularis*–Lower *marginifera* Zones, and is

named as the *Cheiloceras* Beds in some sections (Artyushkova et al., 2011). The deposits consist of light-grey and pinkish-grey, fine and medium-layered organogenic limestones, sometimes with crinoid-coral varieties. The deposits of the Makarovian Regional Stage on the western slope of the South Urals are not fully represented everywhere, including in the stratotype area. Breaks in the deposits are most often observed at the boundary of the Frasnian and Famennian stages, and equal to an interval from one to several conodont zones (Artyushkova et al., 2011; Tagarieva, 2013). The thickness of the Makarovian deposits in the most complete sections is 5.2 m in the Ryauzyak section to 11.9 m in the Akkyr section. Diverse fossils include corals, goniatites, ostracods, brachiopods, crinoids, conodonts and fishes.

The **Murzakaevian** Regional Stage is correlated with the Upper *marginifera*–Upper *trachytera* Zones (Artyushkova et al., 2011). Murzakaevian deposits in the Askyn type are represented by grey and light-grey, bedded, limestones, sometimes dolomitized and recrystallized. These deposits in the Inzer type include grey and brownish-grey, fine and medium-layered, dense limestones, with interlayers of siliceous shales, goniatite coquinas and lenses of chert. The Murzakaevian Regional Stage conformably overlies the Makarovian deposits. The conodont assemblage of this interval does not include the zonal species, and the division of zones is carried out conditionally. The thickness varies from 2 m in the Ryauzyak section up to 18 m in the Zigan section (Artyushkova et al., 2011). The fossils present are foraminifers, ammonoids, brachiopods, conodonts and rare fish remains.

The **Kushelgian** Regional Stage probably corresponds to the Lower *postera*–Lower *expansa* Zones (Artyushkova et al., 2011). The deposits include dark-grey and grey, bedded, dolomitized limestones with brachiopod coquinas at the base, and an ammonoid layer at the top. The Kushelgian deposits are connected with the Murzakaevian beds by a gradational transition. The thickness varies from 0.9 up to 22 m (Pazukhin, 1989). Fossils present are foraminifers, ammonoids, ostracods, brachiopods, conodonts and fishes.

The uppermost Famennian **Lytvian** Regional Stage belongs to the Middle *expansa–praesulcata* Zones and is subdivided into the Abiyuskan and Zigan beds (Artyushkova et al., 2011; Kulagina et al., 2019). The deposits of Abiyuskan Beds consist of grey and dark-grey, mainly finely clotted, with intercalations of crinoid and finely brecciated limestone, and with lenses of chert. The bed thickness varies from 5 up to 15 m. The Zigan Beds include light-grey and grey, crinoid-brachiopod, fine-layered, slightly dolomitized, bioclastic limestones, with siliceous and algal nodules. The range of thickness is 0.3–2.8 m. The fossils of the Lytvian Regional Stage are foraminifer, brachiopod, ostracod, conodont, fish and algae remains.

Fish remains have been found in the Upper Devonian of 10 sections on the western slope of the South

Urals (Republic of Bashkortostan, Russia): Akkyr, Bolshaya Barma, Gabdyukovo, Kuk-Karauk, Kuktash, Kushelga, Lemezinskiy, Ryauzyak, Zigan, Zuyakovo (Fig. 1). The **Akkyr** section is situated on the right bank of the Zilim River, 6 km upstream from the villages of Tashasty, in the mouth of the Bolshaya Kingerlya Creek. The section includes the Givetian–Frasnian massive limestones, the organogenous limestones of Frasnian Askynian, Famennian Barmian and Makarovian regional stages.

The **Bolshaya Barma** section is located on the right bank of the Bolshaya Barma River, 1.3 km upstream from its mouth. The deposits of the section consist of dense, organogenic-polydetritic limestones of Askynian Regional Stage, the Upper Askynian and Barmian brachiopod coquinas, and dense, thick-layered, dolomitized limestones of Makarovian Regional Stage.

The **Gabdyukovo** section on the right bank of the Inzer River, 4.5 km upstream from the villages of Gabdyukovo is in a railway cut of exposed Emsian–Famennian deposits. The Frasnian Sargaevian rocks overlie the underlying deposits with a sedimentation hiatus, and contain fine and medium-layered organogenous limestones. The Domanikian deposits include bituminous shales and limestones. The undivided Mendymian–Askynian deposits are represented by dense, thick-layered, dolomitized limestones. The overlying Famennian deposits overlie the Upper Frasnian rocks with a hiatus of the Lower–Middle *triangularis* conodont Zones (Artyushkova et al., 2011). The Makarovian deposits include fine-layered, silicified and clayey limestones, siltstones and chert.

The **Kuk-Karauk** section includes two outcrops (Kuk-Karauk I and II) and is located on the right bank of the Sikaza River, opposite the mouth of the Kuk-Karauk Creek. The deposits of the Lower and Middle Devonian, and Lower and Middle Frasnian are poorly exposed and were studied in trenches (Abramova, 1999). The well exposed Upper Devonian deposits are represented by Upper Frasnian Askynian, and Famennian Barmian, Makarovian and Murzakaevian regional stages (Fig. 13). The Askynian deposits include massive, bioclastic, dolomitized limestones with coquina intercalations. The Barmian rocks contain brachiopod coquinas. The Makarovian deposits combine interbedded dense limestones and crinoid-coral limestones. The deposits of Murzakaevian Regional Stage are represented by brecciform, dolomitized limestones.

The **Kuktash** section is situated on the right bank of the Zilim River, 2.4 km upstream from the mouth of Bolshaya Kingerlya Creek. The deposits of the section includes massive, thick-layered, probably Mendymian limestones; crinoid-brachiopod coquinas and interbedded dolomitized limestones of the Askynian and Barmian regional stages, and dense, dolomitized limestones of the Makarovian Regional Stage.

The **Kushelga** section is located 3 km south the village of Karan-Elga, in the mouth of the Bolshaya Kushelga Creek. The deposits of the undivided

Mendymian–Askynian include bituminous limestones. A large sedimentation hiatus between these and overlying deposits belongs to the interval of *linguiformis*–Lower *rhomboidea* conodont Zones. The overlying deposits are represented by dense, fine-layered limestones of the Murzakaevian Regional Stage; the limestones of Kushelgian Regional Stage; and medium-layered, clayey limestones with thin interlayers of marls and mudstones of the Lytvian Regional Stage.

The **Lemezinskiy** section on the left bank of the Inzer River, near the former village of Lemezinskiy belongs to the Inzer type of sections, and includes the Pashian sandstones and Kynian limestones at the base. The Sargaevian deposits include clayey shales and limestones. The Domanikian as well as the lower part of Mendymian rocks contain bituminous mudstones, clayey shales and limestones. The upper part of the Mendymian deposits include thick-layered limestones with ammonoid shells. The Askynian and Barmian deposits contain bedded and bituminous limestones. The deposits of the Makarovian Regional Stage are represented by the intercalation of fine-layered, pelitomorphous, dense limestones, fine grained sandstones, siltstones and ferruginous clays.

The most complete **Ryauzyak** section is located on the right bank of the Ryauzyak River, 5 km upstream from the village of Sargaevo and includes condensed thin deposits of the Givetian, Frasnian, Famennian and Tournaisian (Figs. 12a and 12b). The Upper Devonian deposits contain the Kynian fine-layered, clayey limestones, marls and clays, the Sargaevian bituminous limestones and coaly shale, the Domanikian bituminous mudstones and siliceous shales, the brachiopod and crinoid limestones of the Mendymian, Askynian and Barmian regional stages, the Makarovian and Murzakaevian fine- to medium-layered organogenic-polydetrital limestones with brachiopod coquinas, the Kushelgian bedded, bioclastic, dolomitized limestones, and the Lytvian clayey and dolomitized limestones.

The **Zigan** section on the right bank of the Zigan River, 9 km upstream from the village of Gumerovo contains Emsian–Tournaisian deposits. The Upper Devonian deposits are represented by the Kynian limestones, marls and clayey shales; the Sargaevian limestones with thin interbeds of marls and clayey shales; the Domanikian bituminous limestones and siliceous-clayey shales; the thick- to medium-layered crinoid limestones of Mendymian and Askynian regional stages; the Makarovian pelitomorphous, bioclastic limestones; the Murzakaevian and Kushelgian bedded, bioclastic limestones; and the Lytvian pelitomorphous, bioclastic and crinoid-brachiopod limestones. A closed interval of 1 m is in the Frasnian–Famennian boundary beds.

The **Zuyakovo** section on the right bank of the Inzer River, near the village of Zuyakovo includes the Sargaevian clays, bioclastic and sandy limestones, and clayey shales; the Domanikian fine-layered, bitumi-

nous and siliceous limestones, thin interbeds of coaly shale; the Mendymian thick-layered, dense, siliceous limestones; and the Askynian dense, silicified limestones and medium-layered, pelitomorphic limestones.

The distribution of fish remains in these sections is irregular. Rare fish remains in single samples occur in the Bolshaya Barma, Gabdyukovo, Kushelga, and Zuyakovo sections. Several samples with the remains from two to four regional stages were collected from the Akkyr, Kuktash, Lemezinskiy, and Zigan sections. The fish remains in the Kuk-Karauk section were discovered in 49 samples from the five regional stages. The most impressive collection comes from the Ruauzyak section where fish remains were recovered from 152 samples of 10 regional stages. Moreover, some samples include a large amount of microremains, for example, the sample 4242 from the Kuk-Karauk section contains 40 teeth of *Phoebodus bifurcatus*, as well as the sample K-K.1—193 scales of ctenacanthid type.

SYSTEMATIC PALAEONTOLOGY
CLASS CHONDRICHTHYES
SUBCLASS ELASMOBRANCHII

Order Phoebodontiformes

Family Phoebodontidae Williams in Zangerl, 1981

Genus *Phoebodus* St. John et Worthen, 1875

Phoebodus bifurcatus Ginter et Ivanov, 1992

Figs. 3q–3y, 11b

H o l o t y p e. PMSPU 7–8, tooth; South Urals, Republic of Bashkortostan, Zigan section; Devonian, Upper Frasnian, Mendymian Regional Stage, Lower *rhenana* Zone (Ginter and Ivanov, 1992, Figs. 4D–4F).

D e s c r i p t i o n. The teeth vary in the mesio-distal size of the base from 0.6 to 3.1 mm, some teeth are largest among other *Phoebodus* teeth in the collection. The teeth possess a crown with three to seven cusps and cusplets, but usually with five. The cusps are rounded in cross section, incurved sigmoidally, inclined lingually, acuminate in apex. The labial face of the cusps is smooth in the small (“juvenile”) teeth (Figs. 3q–3s, 3u) and ornamented with strong, subparallel cristae in the teeth of medium and large size (Figs. 3t, 3v–3y). The cristae on the lateral cusps are spirally curved. The lingual face of the cusps is smooth or covered by a few tiny short cristae. The lateral cusps are considerably higher and wider than the other cusps. The intermediate cusps are smaller than the central one. The inner intermediate cusps in the seven-cusped crown are slightly shorter than the central cusp, but the outer intermediate cusplets are smaller than other cusps (Figs. 3x, 3y). The lateral carina is well-developed on the cusps but missing between them.

The tooth base is thick and arched, typically bifurcated, with extended linguo-lateral ends and short median part. The apical button is prominent, from round in the small teeth and oval in the large teeth, often contacts with the median part of the lingual rim. The labio-basal projection is wide and prominent. The large foramina of the main vascular canals open at the lingual rim and sometimes form narrow notches (Figs. 3t, 3v, 3x). Small foramina perforate the occlusal and basal surfaces, surrounding the apical button and labio-basal projection.

R e m a r k s. The collection contains 171 teeth *Phoebodus bifurcatus* includes three pathological teeth. The teeth in the described collection vary considerably in size, number of cusps, their length, sizes of the linguo-lateral ends, shape and size of apical button, and cusp ornamentation.

O c c u r r e n c e. Upper Devonian, Upper Frasnian of the Middle and South Urals, South Timan, Central Devonian Field, Kuznetsk Basin, Gorniy Altay; China; Mauritania; Iran; Poland; Czech Republic; Belgium; Utah, USA, Australia.

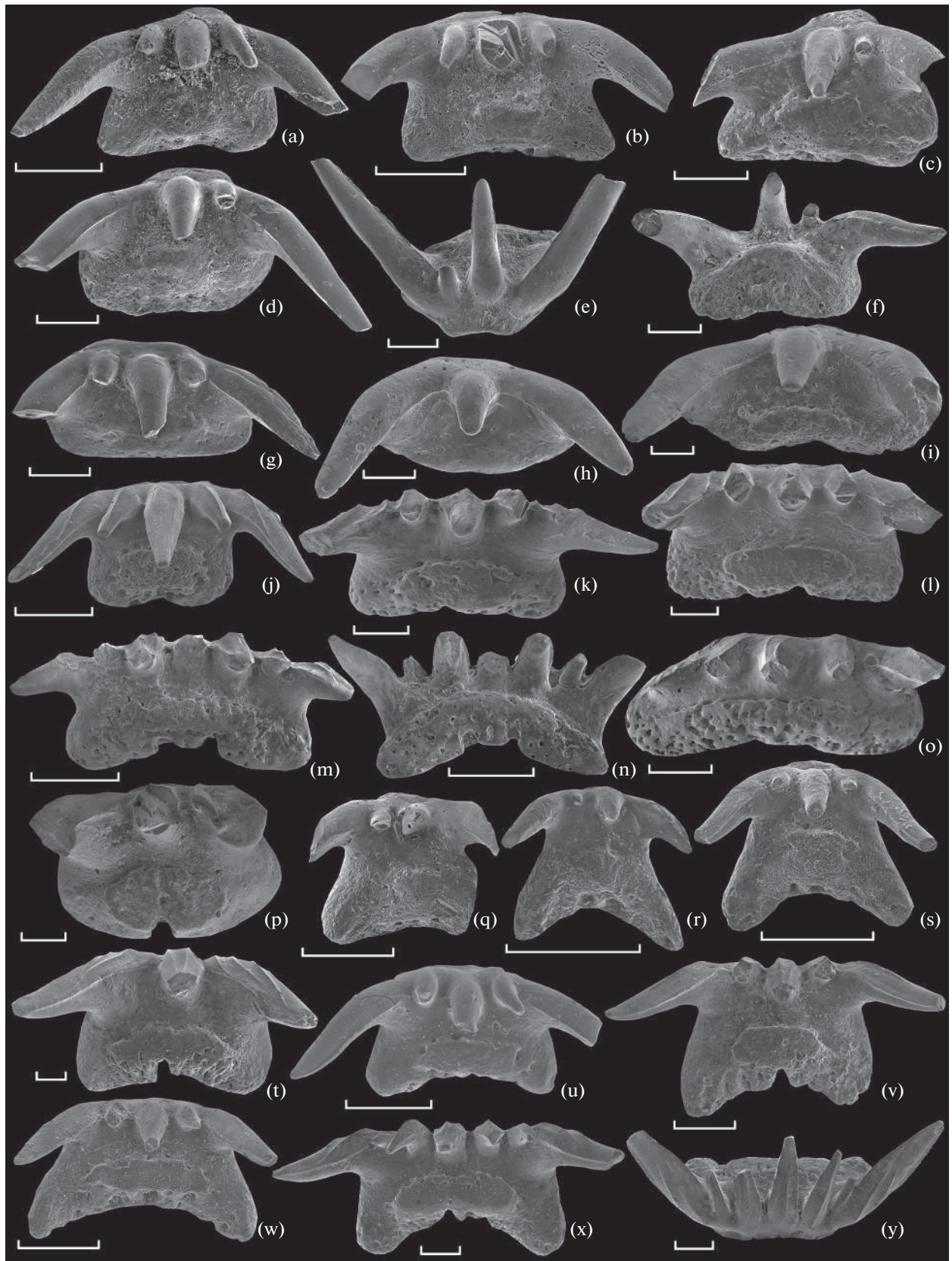
M a t e r i a l. One tooth from the Lower *rhenana* Zone, Mendymian Regional Stage, 65 teeth from the Upper *rhenana* Zone, and one tooth from the *linguiformis* Zone, Askynian Regional Stage of the Ruauzyak section; 56 teeth from the Lower *rhenana* Zone, Mendymian Regional Stage and nine teeth from the Upper *rhenana* Zone of the Kuk-Karauk section; one tooth from the Lower *rhenana* Zone, Mendymian Regional Stage and one tooth from the *linguiformis* Zone, Askynian Regional Stage of the Lemezinskiy section; two teeth from the Upper *rhenana* Zone, Askynian Regional Stage of the Kuktash section; three teeth from the Upper *rhenana* Zone, Askynian Regional Stage of the Akkyr section; 22 teeth from the Lower *rhenana* Zone, Mendymian Regional Stage and nine teeth from the Upper *rhenana* Zone, Askynian Regional Stage of Zigan section; one tooth from the *rhenana* Zone, Mendymian–Askynian Regional stages of Zuyakovo section.

Phoebodus curvatus, Ivanov, 2021

Figs. 3d–3i

H o l o t y p e. PMSPU 74-1, tooth; South Urals, Republic of Bashkortostan, Lemezinskiy section; Devonian, Frasnian, Mendymian Regional Stage, Lower *rhenana* Zone (Ivanov, 2021, pl. 12, Fig. 1).

D e s c r i p t i o n. The small teeth are with a width at base from 0.8 to 1.8 mm mesio-distally. The phoebodont crown contains three main cusps and two intermediate cusplets. The very long lateral cusps are considerably curved lingually, diverged mesially and distally from the central cusp forming an acute angle. The cusps are thin and smooth, slightly sigmoidally curved, round in cross section. The lateral carina is well-developed on the cusps and in the depression



between them. The small intermediate cusplets are displaced in the labial direction. They are completely absent in some teeth (Figs. 3h, 3i) or missing in one side of the tooth (Fig. 3d).

The tooth base is oval in shape, elongated mesio-distally, directed lingually, with a narrow labial part. The convex occlusal surface of the base bears a large apical button. The oval button is occupying most of the occlusal face and placed close to the lingual rim. The concave basal surface has a narrow labio-basal projection and thickened lingual edge. The large foramina of the vascular canals are situated at the lingual edge and in the center of basal face of the base

Remarks. The teeth vary in the number of intermediate cusplets, their height and the outline of tooth base. The teeth of *Phoebodus curvatus* were described recently from the Givetian–Frasnian of the Middle Urals (Ivanov, 2021) where teeth with three to five cusps and cusplets also were collected.

Occurrence. Middle Devonian, upper Givetian–Upper Devonian, Upper Frasnian of the Middle and South Urals, Kuznetsk Basin, Poland and Australia.

Material. Nine teeth from the Upper *rhenana* Zone, Askynian Regional Stage of the Ryauzyak section; one tooth from the Lower *rhenana* Zone, Mendymian Regional Stage of the Lemezinskiy section; one tooth from the Upper *rhenana* Zone, Askynian Regional Stage of the Akkyr section; one tooth from the Upper *rhenana* Zone, Askynian Regional Stage of the Kuktash section.

Phoebodus fastigatus Ginter et Ivanov, 1992

Figs. 3a–3c

Holotype. PMSPU 5-1, tooth; Kuznetsk Basin, Mazalovskiy Kitat River; Devonian, Upper Givetian, Mazalovskokitatian Regional Stage, Mazalovskiy Kitat Beds, *Icriodus brevis* Zone (Ginter and Ivanov, 1992, Figs. 3A, 3B). Z

Description and remarks. The small teeth (0.6 to 0.8 mm mesio-distally) have a phoebodont crown consisting of three main cusps and one or two gentle intermediate cusplets. The cusps and cusplets are smooth, rounded in cross-section, inclined lingually, slightly sigmoidally incurved. The main cusps are long and slender, bear delicate lateral carina missing between cusps. The small intermediate cusplet is absent on some tooth side (Fig. 3c). The tooth base is quite thin, trapezoid in shape, extended lingually, with a slightly concave lingual edge. The compact apical button is circular in shape, situated centrally, close to the lingual rim. The large foramina are surrounded the apical button.

The teeth from other regions include the tricuspid teeth (Ginter and Ivanov, 1992; Trinajstić and George, 2009) but the studied collection contains only a small tooth with four-cusped crown. The known teeth of *Phoebodus fastigatus* from different regions show the minimum of variation in the tooth morphology among other species of *Phoebodus*.

Occurrence. Middle Devonian, Givetian–Upper Devonian, Upper Frasnian of the Middle and South Urals, Kuznetsk Basin; Poland; Spain; Iowa, Indiana, New York and Utah of USA; Mauritania, Morocco, China, Australia.

Material. Two teeth from the Lower *rhenana* Zone, Mendymian Regional Stage and 15 teeth from the Upper *rhenana* Zone, Askynian Regional Stage of the Ryauzyak section; one tooth from the Lower *rhenana* Zone, Mendymian Regional Stage of Lemezinskiy section; one tooth from the *rhenana* Zone, Mendymian–Askynian Regional stages of Zuyakovo section.

Phoebodus gothicus Ginter, 1990

Figs. 5e–5i

Holotype. IGPUW/Ps/1/1, tooth; Poland, Ostrówka Quarry; Devonian, Upper Famennian,

Fig. 3. Teeth of *Phoebodus* from the Frasnian (a–h, k–y) and Lower Famennian (i, j) of the South Urals in occlusal (a–d, g–m, o–x), labial (e, y) and lingual (f, n) views. (a–c) *Phoebodus fastigatus* Ginter et Ivanov, 1992: (a) PMSPU 115-1, sample T12-121; (b) PMSPU 7-2, sample 6426; (c) PMSPU 115-2, sample T12-120; Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone. (d–i) *Phoebodus curvatus* Ivanov, 2021: (d–f) PMSPU 74-1, holotype, sample 7208, Lemezinskiy section, Mendymian Regional Stage, Lower *rhenana* Zone; (g) PMSPU 115-3, (h) PMSPU 115-4, sample T12-122, Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone; (i) PMSPU 115-5, sample 2008-A-5b, Akkyr section, Askynian Regional Stage, Upper *rhenana* Zone. (j–o) *Phoebodus latus* Ginter et Ivanov, 1995: (j) PMSPU 115-6, sample R-4, Ryauzyak section, Barmian Regional Stage, Lower–Middle *triangularis* Zones; (k) PMSPU 13-2, sample 6398, Ryauzyak section, Mendymian Regional Stage, Lower *rhenana* Zone; (l) PMSPU 115-7, sample 4702, Kuktash section, Askynian Regional Stage, Upper *rhenana* Zone; (m, n) PMSPU 7-13, sample 6393, Ryauzyak section, Mendymian Regional Stage, Lower *rhenana* Zone; (o) PMSPU 7-17, sample 6403, Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone. (p) *Phoebodus* cf. *sophiae* St. John et Worthen, 1875, PMSPU 115-8, sample 6401, Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zones. (q–y) *Phoebodus bifurcatus* Ginter et Ivanov, 1992: (q) PMSPU 19-1, sample 6428, Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone; (r) PMSPU 115-09, sample T12-112, Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone; (s) PMSPU 115-10, sample 7276, Kuk–Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone; (t) PMSPU 115-11, sample 4702, Kuktash section, Askynian Regional Stage, Upper *rhenana* Zone; (u) PMSPU 115-12, sample R-v/2, Ryauzyak section, Askynian Regional Stage, *linguiformis* Zone; (v) PMSPU 115-13, sample 7272, Kuk–Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone; (w) PMSPU 115-14, sample 5396, Zigan section, Mendymian Regional Stage, Lower *rhenana* Zone; (x, y) PMSPU 115-15, sample 5411, Zigan section, Mendymian Regional Stage, Lower *rhenana* Zone. Scale bars 300 µm.

Lower *postera*—Lower *expansa* conodont Zones (Ginter, 1990, Pl. 2, Figs. 6a, 6b).

Description. The small teeth (0.6 to 1.3 mm mesio-distally) are characterised by aphoebodont crown with very long three main cusps and two gentle intermediate cusplets. The cusps are slender, strongly sigmoidally curved, circular in cross section, with well-developed lateral carina. The cusps and cusplets are ornamented with distinct, subparallel cristae on both sides which are spirally curved on the lateral cusps. The lingual ornamentation is more delicate than the labial one.

The tooth base is narrow, considerably elongated and pointed lingually. The shape of the base is elongated triangular (Figs. 5e–5h) or oval elongated linguo-labially with a triangular lingual end (Fig. 5j). The small apical button is compact, semispherical, circular or oval in shape, situated in the center of base occlusal surface. Numerous small foramina penetrate the occlusal surface. One large foramen of the main vascular canal opens between the apical button and lingual rim. Teeth from the described collection vary in the shape and size of base and apical button.

Occurrence. Upper Devonian, Lower–Uppermost Famennian of the South Urals; Poland, Germany, France, Armenia, Iran, Morocco, China; Iowa, Ohio and Utah in the USA.

Material. Three teeth from the Lower *expansa* Zone, Kushelgian Regional Stage and one tooth from the Middle–Upper *expansa* Zones, Lytvian Regional Stage of the Ryauzyak section; three teeth from the *postera* Zone, Kushelgian Regional Stage of the Kuk-Karauk section.

Phoebodus latus Ginter et Ivanov, 1995

Figs. 3j–3o

Holotype. PMSPU 7-16, tooth; South Urals, Republic of Bashkortostan, Ryauzyak section; Devonian, Upper Frasnian, Askynian Regional Stage, Upper *rhenana* Zone (Ginter and Ivanov, 1995, Fig. 1E).

Description. The small teeth vary from 0.5 to 1.8 mm in the mesiodistal size of the base. The teeth possess a phoebodont crown with five to seven cusps and cusplets. The cusps are round in cross section, incurved sigmoidally, inclined lingually, acuminate in apex. The small teeth (Fig. 3j) have a lateral and central cusps of almost the same size, and the lateral cusps are directed lingually. The lateral cusps of large teeth (Figs. 3k–3o) are longer than other cusps and inclined mesially and distally. The intermediate cusps in the five-cusped teeth are smaller than the central cusp. In the seven-cusped teeth they are occasionally higher than the central cusp. The outer intermediate cusplets in the multicuspoid crown are small (Figs. 3m, 3n) or tiny (Fig. 3o). The intermediate cusps are commonly displaced labially compared with

other cusps. The labial face of the cusps is ornamented with strong, subparallel cristae. The cristae of the lateral cusps are spirally curved. The lingual face of the cusps is smooth or covered by tiny short cristae. The lateral carina is developed on the cusps and between them in the large teeth.

The tooth base is thick, arched, rectangular in shape of different width, with rounded angles, and sometimes with concave lingual edge (Figs. 3m, 3o). The large and prominent apical button is oval in shape, contacts with median part of the lingual rim, and occupies most of the occlusal surface. The labio-basal projection is wide and low. The large foramina of main vascular canals open at the lingual rim, sometimes form narrow notches (Figs. 3l–3n). The occlusal and basal surfaces are penetrated by foramina of small vascular canals.

Remarks. The studied collection includes 193 teeth of *Phoebodus latus*. The teeth demonstrate a large variation in the width and shape of the tooth base, number and size of cusps and cusplets, shape and size of apical button. The tooth of this species from the Frasnian of Australia has a central cusp that is smaller than any cusps including the inner and outer intermediate ones (Trinajstić and George, 2009). The teeth described as *Phoebodus* cf. *latus* from the Lower Frasnian of Iran possess a crown consisting of ten cusps and cusplets where the lateral cusps are high (Hairapetian et al., 2008). This material indicates the dentition of this species was heterodont.

Occurrence. Middle Devonian, uppermost Givetian—Upper Devonian, Upper Frasnian of the Middle and South Urals, South Timan, Kuznetsk Basin, Gorniy Altay; Poland, Mauritania, Iran, Australia.

Material. One tooth from the *hassi* Zone, Domanikian Regional Stage, 62 teeth from the Lower *rhenana* Zone, Mendymian Regional Stage, 103 teeth from the Upper *rhenana* Zone, four teeth from the *linguiformis* Zone, Askynian Regional Stage, and two teeth from the Lower–Middle *triangularis* Zones, Barmian Regional Stage of the Ryauzyak section; four teeth from the Lower *rhenana* Zone, Mendymian Regional Stage, seven teeth from the Upper *rhenana* Zone and two teeth from the *linguiformis* Zone, Askynian Regional Stage of the Kuk-Karauk section; five teeth from the Lower *rhenana* Zone, Mendymian Regional Stage and one tooth from the *linguiformis* Zone, Askynian Regional Stage of the Lemezinskiy section; three teeth from the Upper *rhenana* Zone and one tooth from the *linguiformis* Zone, Askynian Regional Stage of the Kuktash section; two teeth from the Upper *rhenana* Zone, Askynian Regional Stage of the Akkyr section; two teeth from the Lower *rhenana* Zone, Mendymian Regional Stage of the Zigan section.

Phoebodus limpidus Ginter, 1990

Figs. 5a–5d

Holotype. IGPUW/Ps/1/39, tooth; Poland, Ostrówka Quarry; Devonian, Upper Famennian, Upper *expansa*–Lower *praesulcata* Zones (Ginter, 1990, Pl. 4, Figs. 5a, 5b).

Description. The small teeth (0.4–1.2 mm mesio-distally) possess a tricuspid or pentacuspoid phoebodont crown with long and slender three main cusps and two intermediate cusplets. The intermediate cusplets are different in length or absent in the crown. The cusps and cusplets are oval in cross section, smooth or covered with delicate cristae. The weakly developed lateral carina is present only on the cusps. The tooth base is thin, oval or semilunar in shape. The apical button is weakly developed, with vague margins. The labio-basal projection is wide and prominent. The several large foramina of vascular canals open at the lingual rim.

Occurrence. Upper Devonian, Upper Famennian of the South Urals, North Caucasus; Poland, Germany, France, Italy, Morocco, China; Nevada, Wyoming and Utah of the USA.

Material. Seven teeth from the Lower *expansa* Zone, Kushelgian Regional Stage of the Ryauzyak section.

Phoebodus rayi Ginter et Turner, 1999

Figs. 4m–4o

Holotype. GSC 115385, tooth, Arctic Canada, Melville Island; Devonian, Middle Famennian, Lower–Middle *crepida* Zones, Parry Islands Formation, Cape Fortune Member (Ginter and Turner, 1999, text–Figs. 3E–3G).

Description. The teeth are small in size measuring from 0.4 to 0.6 mm mesiodistally and possess a tricuspid phoebodont crown. The central cusp is considerably shorter than lateral cusps. The cusps are round in cross section, sigmoidally incurved, ornamented with straight cristae on both sides. A distinct lateral carina is developed on the cusps and between them. The tooth base is pentagonal with rounded corners, with large apical button and prominent labio-basal projection. The button is oval in shape, located at the lingual rim, and surrounded by large foramina of vascular canals.

Remarks. The first description of *Phoebodus rayi* includes the typical teeth with wide pentagonal base with oval or round apical button close located to the lingual rim (Ginter and Turner, 1999, Figs. 3E–3G). But other teeth possess a subrectangular base and the lateral cusps strongly directed mesially and distally, are similar to the teeth of *Phoebodus typicus* (Ginter and Turner, 1999, Fig. 4B, 4C, 4J, 4K). One tooth with a trapezoid shaped base resembles the teeth of *Phoebodus fastigatus* (Ginter and Turner, 1999, Fig. 4A). The unclear diagnosis and large variation of morphotypes

allow comparison only with the typical teeth from the type collection.

Occurrence. Upper Devonian, Lower–Middle Famennian of the South Urals, Kuznetsk Basin; Lithuania, Iran, Arctic Canada.

Material. Three teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section.

Phoebodus turnerae Ginter et Ivanov, 1992

Figs. 4g–4l

Holotype. PMSPU 7-21, tooth; South Urals, Republic of Bashkortostan, Ryauzyak section; Devonian, Middle Frasnian, Makarovian Regional Stage, Lower *rhomboidea* Zone (Ginter and Ivanov, 1992, Fig. 8A, 8B).

Description and remarks. The small teeth vary from 0.3 to 1.2 mm in the mesiodistal size of the base. The teeth possess a phoebodont crown with two long lateral and moderate-sized central cusps, sometime with small intermediate cusplets of different sizes. The lateral cusps are strongly inclined mesially and distally. The cusps are circular in cross section, sigmoidally incurved, smooth or ornamented with subparallel delicate cristae. A distinct lateral carina is traced also between cusps. The shape of tooth base is almost oval extended linguo-labially or narrow pentagonal with rounded corners. The apical button is prominent and round in shape, occupies most of the occlusal surface of the base. The button is located close to the lingual rim (Figs. 4g, 4j) or more centrally (Figs. 4i, 4k). The prominent labio-basal projection is narrow. Two or three large foramina of vascular canals open at the lingual rim. The described teeth vary in the base shape, number of intermediate cusplets, and size and position of apical button.

Occurrence. Upper Devonian, Lower–Upper Famennian of the South Urals, North Timan; Belarus, Poland, Belgium, Armenia, Iran, Algeria, Morocco, Alaska of the USA.

Material. One tooth from the Upper *triangularis* Zone, two teeth from the *crepida* Zone, 21 teeth from the Lower *rhomboidea* Zone, and one tooth from the Lower *marginifera* Zone, Makarovian Regional Stage, one tooth from the Lower *expansa* Zone, Kushelgian Regional Stage of the Ryauzyak section; one tooth from the Middle–Upper *expansa* Zones, Lytvian Regional Stage of the Kushelga section.

Phoebodus typicus Ginter et Ivanov, 1995

Figs. 4a–4f

Holotype. PMSPU 7-19, tooth; South Urals, Republic of Bashkortostan, Ryauzyak section; Devonian, Middle Famennian, Makarovian Regional Stage, Lower *rhomboidea* Zone (Ginter and Ivanov, 1995, Fig. 2C).

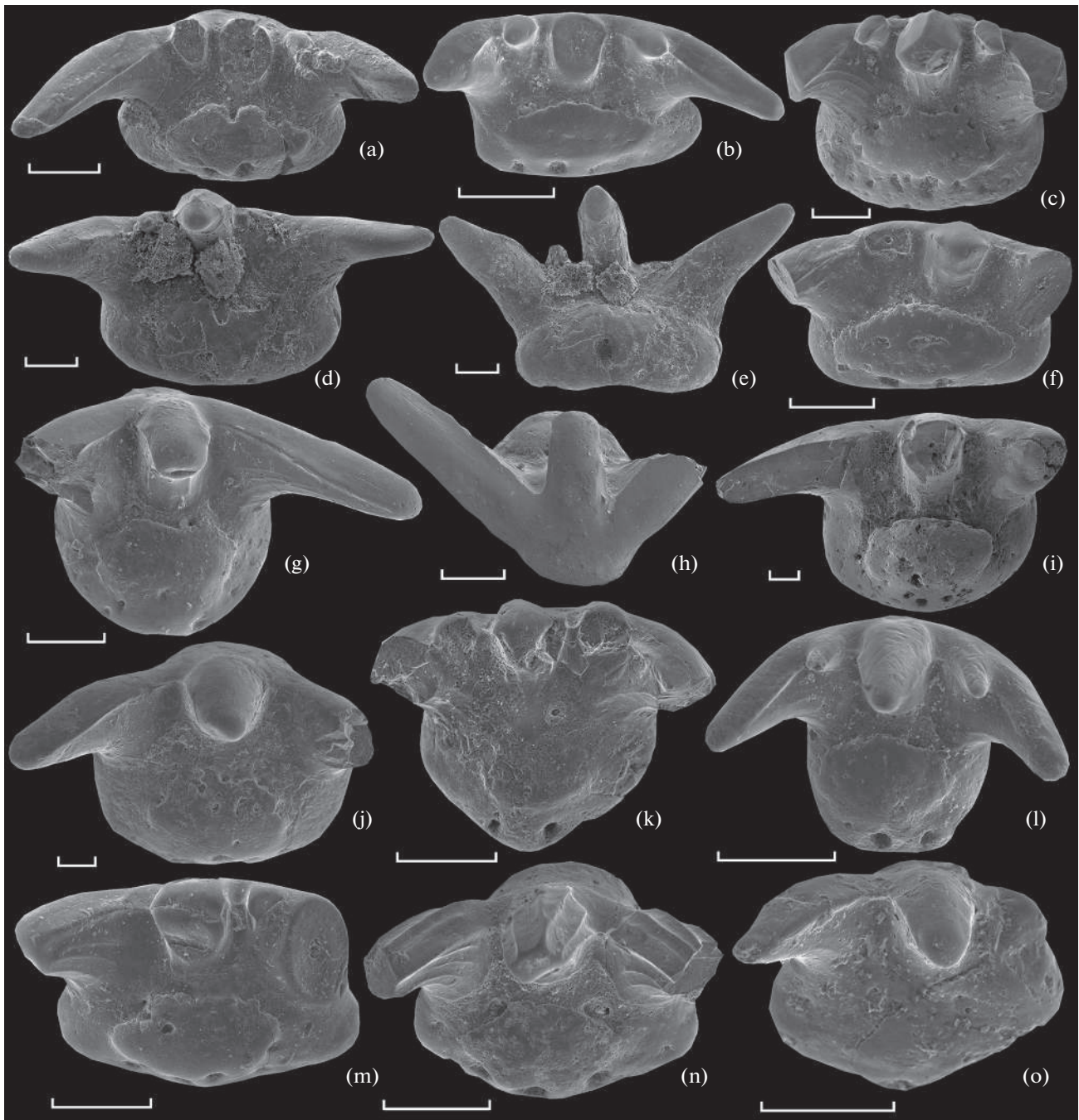


Fig. 4. Teeth of *Phoebodus* from the Famennian of the South Urals in occlusal (a–d, f, g, i–o), lingual (e) and labial (h) views. (a–f) *Phoebodus typicus* Ginter et Ivanov, 1995: (a) PMSPU 115-16, sample T12-143; (b) PMSPU 115-17, sample 6478; (c) PMSPU 13-5, sample 6479; (d, e) PMSPU 14-3, sample 6474; (f) PMSPU 115-18, sample 6479; Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (g–l) *Phoebodus turnerae* Ginter et Ivanov, 1992: (g, h) PMSPU 115-19, sample 6479; (i) PMSPU 115-20, sample 6484; (j) PMSPU 115-21, sample 6469; (k) PMSPU 115-22, sample T12-154; (l) PMSPU 115-23, sample T12-143; Ryauzyak section, (g, h, j–l) Makarovian Regional Stage, Lower *rhomboidea* Zone; (i) Makarovian Regional Stage, Lower *marginifera* Zone. (m–o) *Phoebodus rayi* Ginter et Turner, 1999: (m) PMSPU 115-24, sample 6479; (n) PMSPU 115-25, sample T12-143; (o) PMSPU 115-26, sample 6471; Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. Scale bars 200 μ m.

Description and remarks. The small teeth (0.5 to 0.9 mm mesio-distally) possess a phoebodont crown consists of three long main cusps and one or two intermediate cusplets. The central cusp is

slightly smaller than the lateral ones. The intermediate cusplets are gentle, vary in size or missing on one tooth side. The lateral cusps are considerably inclined mesially or distally. The cusps are smooth or covered by

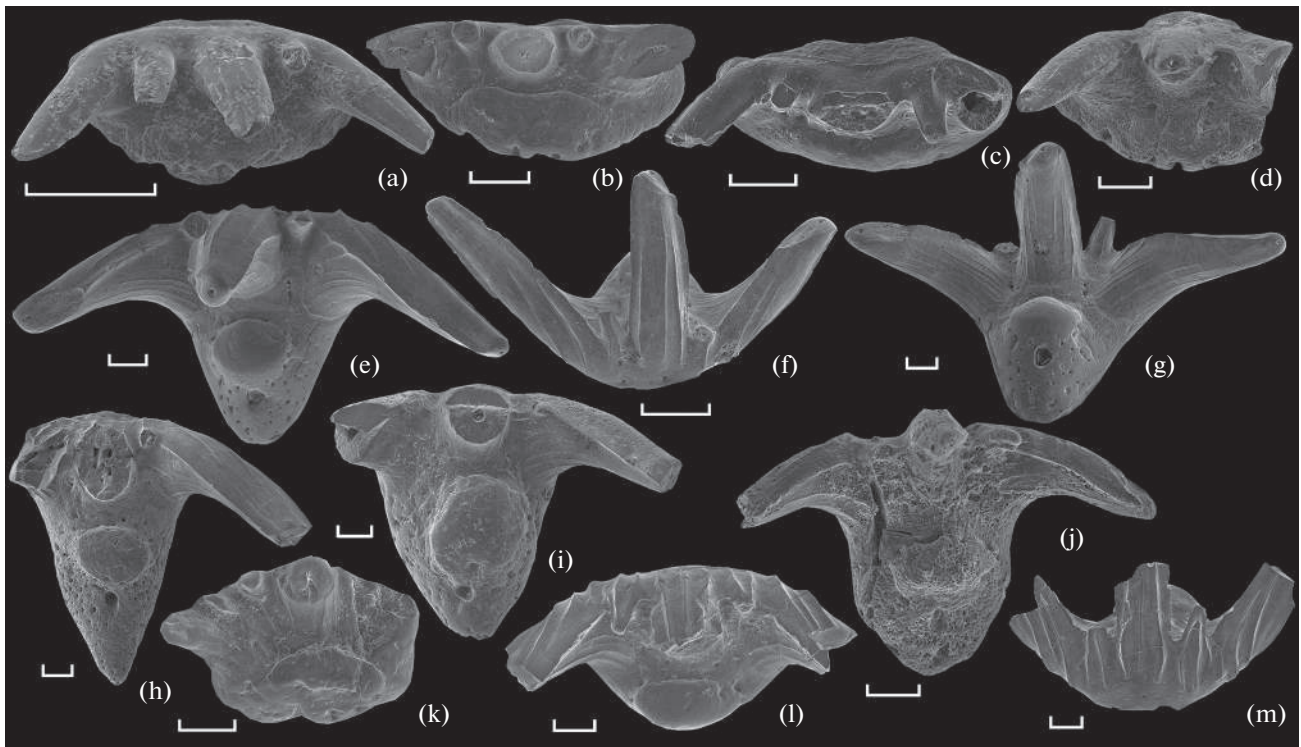


Fig. 5. Teeth of *Phoeboodus* from the Famennian of the South Urals in occlusal (a–e, h–l), labial (f) and lingual (g) views. (a–d) *Phoeboodus limpidus* Ginter, 1990: (a) PMSPU 115-27, sample 0157; (b) PMSPU 115-28, (c) PMSPU 115-29, sample 0168; (d) PMSPU 115-30, sample 0155; Ryauzyak section, Kushelgian Regional Stage, Lower *expansa* Zone. (e–j) *Phoeboodus gothicus* Ginter, 1990: (e–g) PMSPU 7-31, sample 5152, (h) PMSPU 115-32, (i) PMSPU 115-33, sample 5144, Kuk-Karauk II section, Kushelgian Regional Stage, *postera* Zone; (j) PMSPU 115-34, sample 0152, Ryauzyak section, Kushelgian Regional Stage, Lower *expansa* Zone. (k) *Phoeboodus* sp. 1, PMSPU 115-35, sample 6475, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (l, m) *Phoeboodus* sp. 2, PMSPU 115-36, sample K-I-J, Kuk-Karauk section, Makarovian Regional Stage, Lower *marginifera* Zone. Scale bars 200 μ m.

delicate, straight striae on both preserved sides, bear the weakly developed lateral carina only on the cusps. The tooth base is oval or subrectangular with strongly rounded angles, elongated mesio-distally, rather thick. The apical button is large, prominent, with oval outlines, occupying almost all the occlusal face, placed centrally or close to lingual rim, and surrounded by numerous foramina of large vascular canals. The labio-basal projection is quite narrow, slightly prominent.

The teeth in the observed collection slightly vary in the base shape, in the number and length of intermediate cusps.

Occurrence. Upper Devonian, Lower–Middle Famennian of the Middle and South Urals, North Timan, Kuznetsk Basin; Iran, Morocco, Australia.

Material. Two teeth from the *crepida* Zone and 19 teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section.

Phoeboodus cf. *sophiae* St. John et Worthen, 1875

Fig. 3p

Description and remarks. The small teeth are from 0.9 to 1.5 mm in mesiodistal size.

The teeth possess a phoeboodont tricuspid or pentacuspoid crown and thick base. The cusps are thick, round in cross section, ornamented with distinct, incurved cristae on the labial face, and bear delicate lateral carina. The small intermediate cusplets when presented in the crown are placed labially. The tooth base is broad, oval in shape, elongated mesio-distally, rather directed lingually, with a wide labial part. The large, oval, prominent apical button occupies the large part of the occlusal surface of the base, and is surrounded by numerous small foramina. The button is closely placed to the lingual rim. The labio-basal projection is wide and tick. The large foramen of the main vascular canal opens at the lingual rim forming a narrow notch.

The known teeth of *Phoeboodus sophiae* differ from the described teeth in the central position of apical button on the occlusal surface of the tooth base so there remains a wide band before the lingual rim (Ginter et al., 2010).

Material. One tooth from the Lower *rhenana* Zone, Mendymian Regional Stage and two teeth from the Upper *rhenana* Zone, Askynian Regional Stage of the Ryauzyak section.

Phoebodus sp. 1

Fig. 5k

Description and remarks. The teeth are small with 0.7–0.9 mm mesiodistal size, possess a phoebodont crown with five to seven cusps. The cusps are rounded in cross section, ornamented with coarse cristae. The wide tooth base is pentagonal or trapezoidal in shape, with rounded corners. The apical button is oval, elongated mesiodistally, situated in the centre of occlusal surface.

The teeth are similar to the teeth of *Phoebodus rayi*, *Ph. turnerae*, *Ph. typicus* but differ in the large intermediate cusps and in the narrow, elongated apical button.

Material. One tooth from the Lower *rhenana* Zone, Mendymian Regional Stage, four teeth the Upper *rhenana* Zone, Askynian Regional Stage, and one tooth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section.

Phoebodus sp. 2

Figs. 5l, 5m

Description and remarks. The teeth are small with 0.9–1.1 mm mesiodistal size, possess a phoebodont crown with five cusps and very small base. The cusps bear well-developed lateral carina, and are ornamented with very coarse, subparallel cristae on both sides which are spirally curved on the lateral cusps. The tooth base has a short lingual part, is semi-oval in shape. The compact, oval apical button is located at the lingual rim.

These teeth are strongly distinguished from the teeth of all known species in the rough ornamentation of the cusps and the shape of small base.

Material. One tooth from the Lower *rhenana* Zone, Mendymian Regional Stage and five teeth the Upper *rhenana* Zone, Askynian Regional Stage of the Ryauzyak section; one tooth from the *crepida* Zone and one tooth from the Lower *marginifera* Zone, Makarovian Regional Stage of the Kuk-Karauk section.

Genus *Diademodus* Harris, 1951*Diademodus* sp.

Figs. 6a–6c

Description. The teeth are small in size, vary from 1.2 to 1.6 mm mesiodistally and possess a multicuspoid phoebodont crown. The main cusps are from three to five. The number of cusps and cusplets varies from 5 to 11. The central cusp is equal or slightly smaller than lateral ones. The intermediate cusps are narrower than the lateral and central cusps. Some teeth bear lateral cusplets in the mesial and distal angles of the crown (Figs. 6b, 6c). The cusps and cusplets are inclined lingually, rounded in cross section, and have a weakly developed lateral carina. Their labial faces are ornamented with straight, coarse cristae, the lingual faces are smooth.

The tooth base is considerably wide, with short lingual part, rectangular in outline with rounded angles. The occlusal surface is lacking the apical button but the short shelf is present on the labio-basal edge. The tooth labial face bears a very shallow and wide depression. The numerous foramina of vascular canals open at the lingual rim and along the crown/base junction.

Remarks. The described teeth differ from the teeth of *Diademodus hydei* Harris 1951 and *D. utahensis* Ginter, 2008 (Ginter et al., 2010) in the ornamented cusps with coarse cristae and flat tooth base. The wide tooth morphotype of *Phoebodus latus* with wide tooth base are similar to the described teeth of *Diademodus* sp., but differ in the lingually extended tooth base, a well developed apical button and labio-basal projection.

Material. Three teeth from the Upper *rhenana* Zone, Askynian Regional Stage of the Ryauzyak section; one tooth from the the Upper *rhenana* Zone, Askynian Regional Stage of the Kuk-Karauk section.

Genus *Thrinacodus* St. John et Worthen, 1875*Thrinacodus ferox* (Turner, 1982)

Figs. 6g–6k

Syntypes. UQG F72974-F72993, teeth; Australia, Queensland, Broken River; Carboniferous, Upper Tournaisian—lower Viséan (Turner, 1982).

Description. The small teeth vary in the mesiodistal size of the base from 0.1 to 0.5 mm. The asymmetrical teeth are characterised by a tricuspoid crown with large distal and small lateral mesial cusps. The central cusps are wider and longer than the mesial cusp, but smaller than distal ones. The distal and mesial cusps in some teeth are strongly directed mesially and distally accordingly. The cusps are round in cross section, acuminate in the apex, sigmoidally curved, inclined lingually. They are smooth or ornamented with subparallel distinct cristae. Lateral carina are preserved on the cusps and between them.

The tooth base is with an elongated lingual part of different length. The base is rather narrow, considerably twisted, with an oblique lingual edge. The foramen of the main vascular canal opens in the centre of the occlusal face, sometimes displaced mesially (Fig. 6k) or at the lingual rim (Figs. 6i, 6j).

Remarks. The tooth with short tooth base (Figs. 6i, 6j) resembles the teeth of *Thrinacodus* cf. *incurvus* (Newberry and Worthen, 1866) described from New Mexico, USA (Ivanov and Lucas, 2011) but the later differ in massive tooth base and thick cusps.

Occurrence. Upper Devonian, Upper Famennian—Carboniferous, Mississippian, Viséan of the Middle and South Urals; England, Ireland, France, Germany, Poland, Armenia, Iran, China, Australia; Utah, New Mexico in the USA.

Material. Three teeth from the Lower *expansa* Zone, Kushelgian Regional Stage and one tooth from the Middle—Upper *expansa* Zones, Lytvian Regional Stage of the Ryauzyak section.

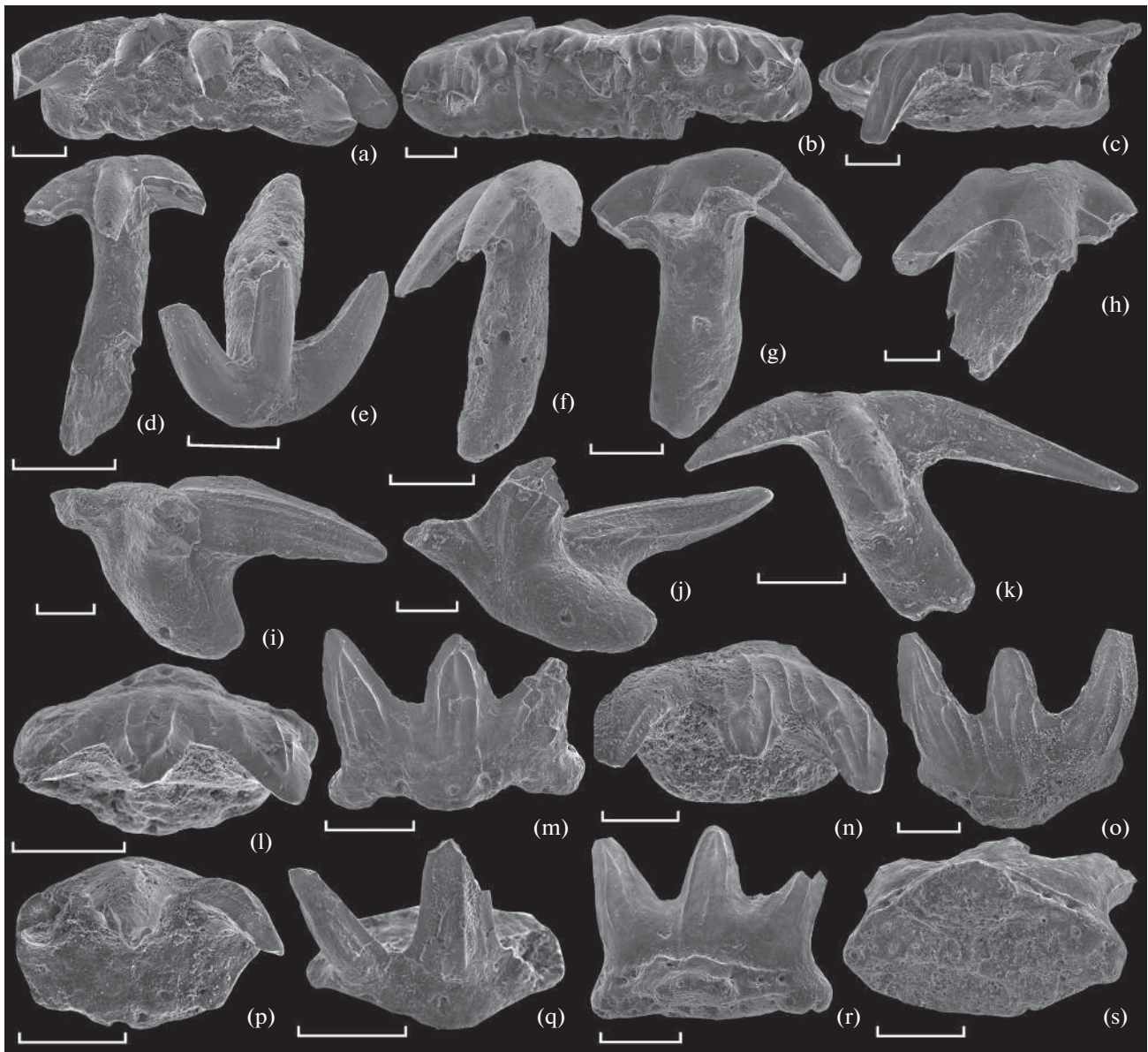


Fig. 6. Teeth of phoedodontiforms (a–k) and jalodontiform (l–s) from the Famennian of the South Urals in occlusal (a–d, h, i, k, l, n, p), oblique occlusal (f, g), labial (e, m, o, q, r), lingual (j) and basal (s) views. (a–c) *Diademodus* sp.: (a) PMSPU 115-37, (b) PMSPU 115-38, sample 20P, (c) PMSPU 115-39, sample 6422; Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone. (d–f) *Thrinacodus tranquilus* Ginter, 2000: (d) PMSPU 115-40, sample 0113, Ryauzyak section, Lytvian Regional Stage, Middle-Upper *expansa* Zones; (e, f) PMSPU 115-41, sample 4292, Ryauzyak section, Kushelgian Regional Stage, Lower *expansa* Zone. (g–k) *Thrinacodus ferox* (Turner, 1982): (g) PMSPU 115-42, sample 0152, Ryauzyak section, Kushelgian Regional Stage, Lower *expansa* Zone; (h) PMSPU 115-43, sample 0183, Ryauzyak section, Lytvian Regional Stage, Middle-Upper *expansa* Zones; (i, j) PMSPU 115-44, sample 0168; (k) PMSPU 115-45, sample 0152, Ryauzyak section, Kushelgian Regional Stage, Lower *expansa* Zone. (l–s) *Jalodus australiensis* (Long, 1990): (l, m) PMSPU 85-2, (n, o) PMSPU 115-46, (p, q) PMSPU 115-47, (r, s) PMSPU 85-3, sample 7162, Lemezinskiy section, Makarovian Regional Stage, *crepida* Zone. Scale bars 200 μ m.

Thrinacodus tranquilus Ginter, 2000

Figs. 6d–6f

Holotype. IGPUW/Ps/1/47, tooth; Poland, Ostrówka Quarry; Devonian, Upper Famennian, Upper *trachytera* Zone (Ginter, 2000, text-Figs. 2A–2C).

Description. The small teeth are with 0.1–0.3 mm mesiodistal base size, have a tricuspid phoedodont crown. The crown is symmetrical or almost

symmetrical with a more incurved distal cusp. The central cusp is slightly shorter than the lateral cusps. The cusps are subequal, thin, smooth, round in cross section, considerably sigmoidally incurved and inclined lingually. They bear the delicate lateral carina on the cusps and between them. The tooth base is narrow, strongly elongated lingually, twisted, with asymmetrical lingual depression. The large foramen of the

main vascular canal opens in the middle of the base occlusal surface.

Occurrence. Upper Devonian, Middle–Upper Famennian of the Middle and South Urals; France, Germany, Poland, Morocco, Iran, China.

Material. Two teeth from the Lower *expansa* Zone, Kushelgian Regional Stage and one tooth teeth from the Middle–Upper *expansa* Zones, Lytvian Regional Stage of the Ryauzyak section

Order Jalodontiformes

Family Jalodontidae Ginter, Hairapetian et Klug, 2002

Genus *Jalodus* Ginter, 1999

Jalodus australiensis (Long, 1990)

Figs. 6l–6s

Holotype. UTGD 123877, tooth, Thailand, road cutting near Mae Sam Lap; Devonian, upper Famennian (Long, 1990, Figs. 2A, 2B).

Description. The teeth are small, with a width at the base from 0.45 to 0.62 mm mesiodistally, possess a crown of phoebodont morphology with three cusps. The cusps are either subequal or the central cusp is shorter. The cusps are triangular, straight or slightly recurved, inclined lingually, labio-lingually compressed, and closely packed. The lateral cusps are slightly inclined mesially and distally. The labial surface of the cusps is ornamented with lanceolate and subparallel cristae. The lanceolate ornamentation includes one or two cristae. The lingual face is either smooth or bears a few straight cristae. A delicate lateral carina connects the cusps to each other. The narrow groove marks the crown/base junction on the labial face.

The tooth base is rounded, oval in outline, sometimes with narrowed mesial and distal parts (Fig. 6s). The convex occlusal face is missing the apical button. The concave basal faces bear alabio-basal tubercle. The tubercle is prominent, horseshoe-shaped. The central cusp of one tooth is wider the lateral one, and the notches between the cusps are deeper than in other teeth (Figs. 6p, 6q).

Remarks. The two tooth morphotypes were distinguished for the teeth of Ginter (1999) and Ginter et al. (2010). The teeth from the studied collection belong to the second morphotype and are characterized by straight cusps slightly inclined lingually, less number of lanceolate cristae, and wide central cusp.

Occurrence. Middle Famennian–Carboniferous, Mississippian, Lower Tournaisian of the Polar and South Urals, Timan–Pechora Province, Poland, Germany, France, Italy, Morocco, China, Thailand.

Material. Four teeth from the *crepida* Zone, Makarovian Regional Stage of the Lemezinskiy section.

Superorder Cladodontomorphi

Order Symmoriiformes

Family Symmoriidae Dean, 1909

Genus *Stethacanthus* Newberry, 1889

Stethacanthus sp.

Figs. 7i–7m

Description. The teeth are from 1.2 to 1.6 mm in mesiodistal size. They possess a typical cladodont crown with a large and prominent central cusp flanked by small intermediate and moderate lateral cusps. The cusps are round in cross section, curved and inclined lingually, with ornamentation with straight cristae on the labial and lingual faces, and with delicate lateral carina. The lingually extended tooth base is oval in shape, elongated mesiodistally. The elongated mesiodistally, oval button occupies most of the occlusal surface. The prominent labio-basal projection is wider than the base of the central cusp.

The tooth file contains four tricuspid crowns gradually arranged on the fused base (Figs. 7k, 7l). The smaller crown is slightly twisted mesially or distally.

Material. Four teeth and tooth file from the Lower *rhomboidea* Zone and two teeth from the *crepida* Zone, Makarovian Regional Stage of the Ryauzyak section; one tooth from the *linguiformis* Zone, Askynian Regional Stage and one tooth from the Upper *triangularis* Zone, Makarovian Regional Stage of the Kuk-Karauk section; one tooth from the *crepida* Zone, Makarovian Regional Stage of the Lemezinskiy section.

Family Falcatidae Zangerl, 1990

Genus *Denaea* Pruvost, 1922

Denaea sp.

Figs. 7n–7r

Description. The small teeth are from 0.5 to 1.1 mm in mesiodistal size, have a five- to seven-cusped cladodont crown. The cusps are delicate, acuminate at the top, round in cross section, incurved, inclined lingually, and separated from each other by deep notches. The lateral cusps diverge mesially and distally from the central cusp. The intermediate cusplets are considerably smaller than the main cusps. Some teeth have lateral cusplets (Fig. 7n). The straight delicate cristae cover both the labial and lingual faces of the cusps.

The tooth base is triangular in shape, moderately extended lingually with a prominent central part of the lingual rim. The occlusal face is convex in the central part, restricted mesially and distally by shallow depressions. The apical button is rounded, without distinct margins, placed closely to the lingual rim. The basal surface is slightly concave, with narrow, prominent labio-basal tubercles under the central cusp. The tiny foramina of vascular canals open at the lingual rim and on the labial face of the labio-basal tubercle.

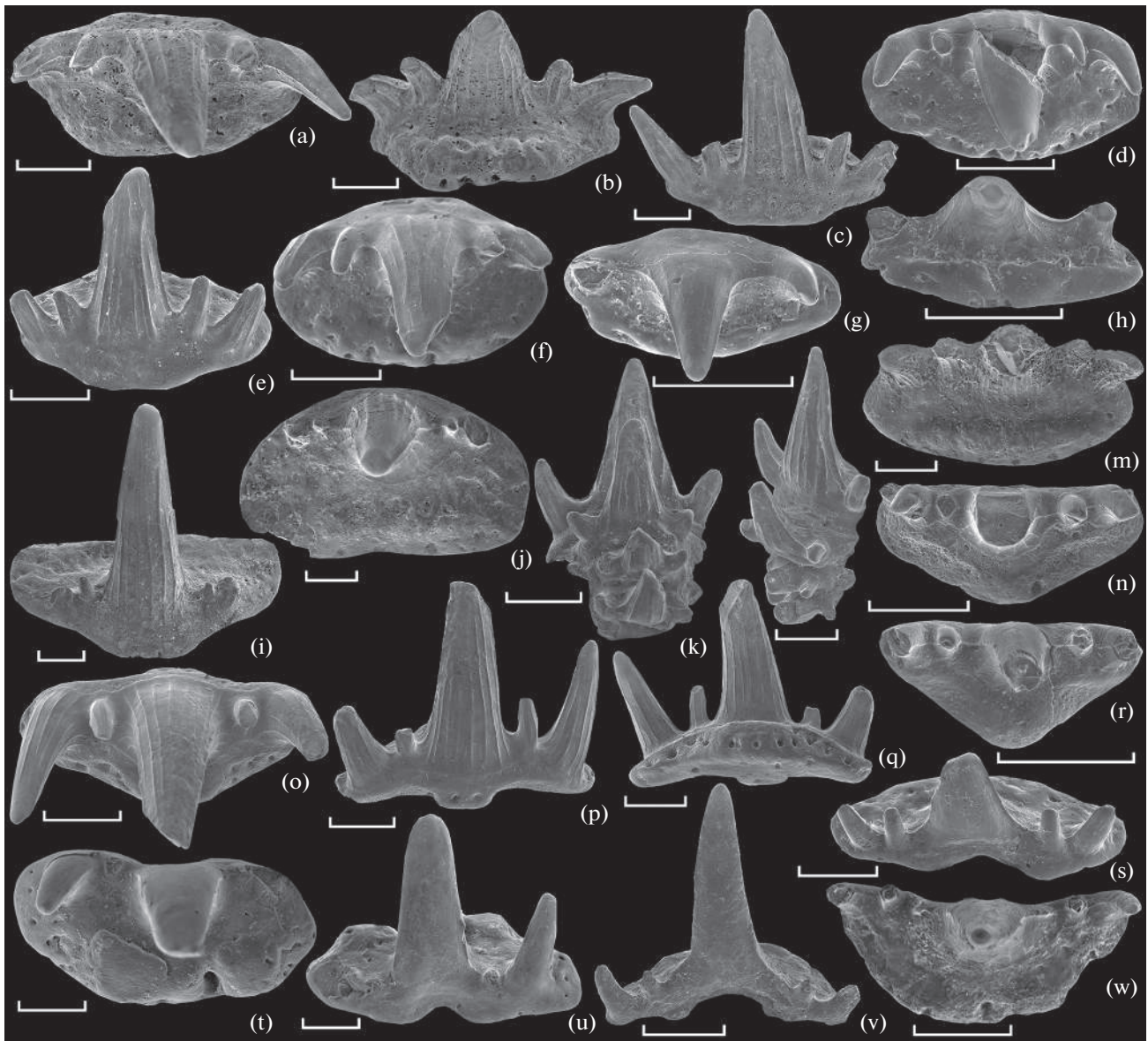


Fig. 7. Teeth and tooth file (k, l) of cladodontomorphs from the Upper Devonian of the South Urals in occlusal (a, d, f, g, j, m–o, r, t, w), lingual (b, h, q), labial (c, e, i, k, p, s, u, v) and oblique lateral (l) views. (a–f) *Cladodoidea* cf. *wildungensis* (Jaekel, 1921): (a–c) PMSPU 115-48, sample 6428, Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone; (d) PMSPU 115-49, sample T12-154, (e, f) PMSPU 115-50, sample 6483, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (g, h) *Cladodoidea* sp., PMSPU 115-51, sample 6478, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (i–m) *Stethacanthus* sp.: (i, j) PMSPU 115-52, sample 6478, (k, l) PMSPU 115-53, sample T12-152, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone; (m) PMSPU 115-54, sample 7191, Lemezinskiy section, Makarovian Regional Stage, *crepida* Zone. (n–r) *Danaea* sp.: (n) PMSPU 115-55, sample 0183, Ryauzyak section, Lytvian Regional Stage, Middle-Upper *expansa* Zone; (o–q) PMSPU 115-56, sample T12-29, Kuk-Karauk section, Murzakaevian Regional Stage, Upper *marginifera* Zone; (r) PMSPU 115-57, sample 0168, Ryauzyak section, Kushelgian Regional Stage, Lower *expansa* Zone. (s–w) *Squatina* sp.: (s) PMSPU 115-58, sample T12-146, (t, u) PMSPU 13-14, sample 6475, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone; (v, w) PMSPU 115-59, sample 6850, Akkyr section, Makarovian Regional Stage, Lower *rhomboidea* Zone. Scale bars 300 μ m.

Remarks. The teeth of *Danaea* cf. *fournieri* Pruvost, 1922 (Ginter et al., 2010) are similar to the described teeth but differ in more extended lingual part of the tooth base, larger apical button and labio-basal tubercle. The teeth of *Danaea saltsmani* Ginter et Hansen, 2010 are different from the teeth described

here in wider and longer tooth base, and in the sigmoidally incurved, delicate cusps (Ginter and Hansen, 2010).

Material. One tooth from the Lower *expansa* Zone, Kushelgian Regional Stage and two teeth from the Middle-Upper *expansa* Zones, Lytvian Regional

Stage of the Ryauzyak section; one tooth from the Upper *marginifera* Zone, Murzakaevian Regional Stage of the Kuk-Karauk section.

Order Ctenacanthiformes

Family Incertae Sedis

Genus *Cladodoides* Maisey, 2001

Cladodoides cf. *wildungensis* (Jaekel, 1921)

Figs. 7a–7f

Description. The teeth are of small sizes (width mesiodistal size from 0.8 to 1.1 mm). The teeth possess a five-cuspid cladodont crown with large central, moderate lateral, and short intermediate cusps. The cusps are oval in cross-section, flattened labiolingually, inclined lingually, slightly incurved, with weakly developed lateral carina. The central cusp is almost twice higher than the lateral cusps. The lateral cusps are divergent mesially or distally from the central cusp. The bases of all cusps are placed on a slightly curved line. The cusps are ornamented with straight, coarse cristae on the labial and lingual faces. The cusp apexes are smooth, lacking the cristae.

The tooth base is oval in shape, elongated mesiodistally, extended lingually, with convex occlusal and concave basal surfaces. The apical button is prominent, oval in shape, occupies most of the occlusal face and reaches of the lingual rim. A very wide and short prominent labio-basal projection is located at the labial edge of the basal surface. Numerous foramina of the large vascular canals open around the button.

Remarks. *Cladodoides wildungensis* (Jaekel, 1921) was described from the Upper Frasnian of Bad Wildungen, Germany (Gross, 1937, 1938). The preservation of teeth in the type specimen of *C. wildungensis* does not permit a detailed description of tooth morphology and complicates the comparison with the isolated teeth. Most isolate teeth found in different regions of the world have been mainly determined as *Cladodoides* cf. *wildungensis* (Ivanov, 2018). The genus *Cladodoides* was referred to the Order Ctenacanthiformes (Ginter et al. 2010) but this needs further clarification

Material. Three teeth from the Upper *rhenana* Zone, Askynian Regional Stage and nine teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section.

Cladodoides sp.

Figs. 7g, 7h

Description and remarks. The teeth have a cladodont crown with three to five cusps. The cusps are smooth or ornamented with tiny cristae. The tooth base is oval in shape, with a short lingual part. The wide apical button is located closely to the lingual rim and occupies most of the occlusal surface of the tooth base. The lateral carina is distinct on the cusps

and between them connect the cusps in the crown. These teeth are distinguished from the teeth of *Cladodoides* cf. *wildungensis* by the shorter lingual part of the tooth base, and developed lateral carina between the cusps.

Material. Four teeth from the Upper *rhenana* Zone, Askynian Regional Stage, nine teeth from the Upper *triangularis* Zone, one tooth from the *crepida* Zone, 12 teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section; two teeth from the Lower- Middle *triangularis* Zones, Barmian Regional Stage, five teeth from the Upper *triangularis* Zone and two from the *crepida* Zone, Makarovian Regional Stage of the Kuk-Karauk section; one tooth from the Upper *triangularis* Zone, Makarovian Regional Stage of the Akkyr section; two teeth from the *crepida* Zone, Makarovian Regional Stage of the Gabdyukovo section.

Order Squatinactiformes

Family Squatinactidae Cappetta, Duffin et Zidek, 1993

Genus *Squatinactis* Lund et Zangerl, 1974

Squatinactis sp.

Figs. 7s–7w

Description and remarks. The small teeth (measuring from 0.9 to 1.5 mm mesiodistally) are slightly abraded. They have a cladodont crown consisting of three main cusps and two intermediate cusplets. The central cusp is considerably higher and wider than the lateral cusps, placed lingually with respect to the other cusps and cusplets. The intermediate cusplets vary from small (Figs. 7v, 7w) to moderate (Fig. 7s) size. The main cusps are compressed labiolingually, oval in cross section, slightly inclined lingually, smooth, with distinct lateral carina. The cusplets are rounded in cross section.

The tooth base is extended lingually, wide mesiodistally, semi-circular in shape. The occlusal surface of the tooth base bears two wide, rounded apical buttons. A shallow and wide median depression is located on the labial side and below the central cusp. This depression is flanked by two small labio-basal projections. Large foramina of vascular canals surround the button and are arranged in rows. The large foramen of the main vascular canal opens near the lingual rim, between the apical buttons.

The teeth from the studied collection vary in the proportion of main cusps, the depth of median depression, the size of buttons. Probably these teeth belong to the different species but their preservation does not allow accurate determination. They are similar to the teeth of *Squatinactis glabrum* Ginter, 1999 but the later differs in thinner cusps considerably incurved lingually, smaller apical buttons and narrower labio-basal projections.

Material. Four teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the

Ryauzyak section; one tooth from the *rhomboidea* Zone, Makarovian Regional Stage of the Akkyr section; one tooth from the Middle–Upper *expansa* Zones, Lytvian Regional Stage of the Kushelga section.

Cohort Euselachii Hay, 1902

Order Incertae Sedis

Superfamily Protacrodontoidea Zangerl, 1981

Family Protacrodontidae, Cappetta, Duffin et Zidek, 1993

Genus *Protacrodus* Jaekel, 1925

Protacrodus aequalis Ivanov, 1996

Figs. 8a, 8b

H o l o t y p e. PMSPU 11-18, tooth; South Urals, Republic of Bashkortostan, Sikaza section; Carboniferous, Lower Tournaisian, *sulcata* conodont Zone (Ivanov, 1996, Figs. 6a, 6b).

D e s c r i p t i o n a n d r e m a r k s. The teeth are of small size, with a width at the base 0.6–0.7 mm mesio-distally. The tooth crown consists of three conical cusps. The cusps are round in cross section, separate, and basally fused. The central cusp is slightly wider and higher than the other lateral ones. The labial and lingual faces are covered by ornamentation consisting of distinct, coarse ridges. The ridges diverge basally from the cusp apex. The tooth base is oval in shape, elongated mesiodistally, slightly extended lingually, with convex occlusal and concave basal surfaces. The occlusal surface is slightly convex, the basal surface is almost flat.

The teeth of *P. aequalis* include two morphotypes: one with a symmetrical crown and equal cusps, and second with asymmetrical, inclined crown and higher central cusp (Turner, 1982; Ivanov, 1996; Ivanov and Lucas, 2011). The teeth described herein belong to a second morphotype.

O c c u r r e n c e. Upper Devonian, Middle Famennian–Carboniferous, Mississippian, Lower Tournaisian of the South Urals, Timan–Pechora Province, Kuznetsk Basin; Belarus, Australia, Canada.

M a t e r i a l. Two teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section.

Protacrodus vetustus Jaekel, 1925

Figs. 8c–8f

L e c t o t y p e. MB.f.201, Germany, Hesse, Bad Wildungen; Devonian, upper Frasnian, *Manticoceras* Beds, Upper Adorfer Limestones (Gross, 1938, Taf. 2, Figs. 1–11).

D e s c r i p t i o n. The teeth are small, with the mesiodistal size of the base from 1.3 to 1.9 mm. The protacrodont crown is pyramidal, includes five to seven cusps gradually arranged in their height. The cusps are conical, round in cross section or slightly flattened labio-lingually, fused basally, and separated

by narrow notches. The outer intermediate cusps are sometimes wider than the neighboring cusps. The dominant central cusp is straight, the other cusps are occasionally inclined mesially or distally. The cusps are ornamented with coarse, incurved or straight ridges diverging from the cusp apex. The short ridges are placed sometimes between the long ridges. The tooth base is quite thin, lingually extended, slightly arched, and strongly perforated with foramina of vascular canals in the occlusal and basal surface, also forming a row along the crown/base junction on the labial face. The teeth vary in the degree of labio-lingual compression, number of ornamentation ridges, and height of inner intermediate cusps.

O c c u r r e n c e. Upper Devonian, Upper Frasnian–Upper Famennian of the South Urals; Poland, Germany, Morocco.

M a t e r i a l. One tooth from the Lower *rhenana* Zone, Mendymian Regional Stage, one tooth from the Upper *rhenana* Zone, Askynian Regional Stage, two teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section; two teeth from the Lower *rhenana* Zone, Mendymian Regional Stage, one tooth from the Upper *rhenana* Zone, Askynian Regional Stage, one tooth from the *linguiformis* Zone, Askynian Regional Stage, and one tooth from the *postera* Zone, Kushelgian Regional Stage of the Kuk-Karauk section; one tooth from the Lower *rhenana* Zone, Mendymian Regional Stage of the Lemezinskiy section; one tooth from the Upper *rhenana* Zone and one tooth from the *linguiformis* Zone, Askynian Regional Stage of the Akkyr section; two teeth from Upper *rhenana* Zone, Askynian Regional Stage of the Zigan section.

Protacrodus serra Ginter, Hairapetian et Klug, 2002

Figs. 8k, 8l

H o l o t y p e. IGPUW/Ps/5/23, tooth; Morocco, Tizi Nersas; Devonian, upper Famennian, Late *expansa* conodont Zone (Ginter et al., 2002, text-Figs. 11H–11J)

D e s c r i p t i o n. The small teeth (with base size 0.9–1.1 mm mesio-distally) possess a slightly asymmetrical, pyramidal protacrodont crown. The cusps are triangular, oval in cross section, labio-lingually compressed, slightly recurved and inclined distally, connected by the occlusal blade. The crown includes five cusps, basally fused and separated by deep and quite wide notches. The cusps are gradually arranged in their height, ornamented with straight or slightly recurved, coarse ridges. The central cusp is much larger than the other cusps. The tooth base is extended lingually, penetrated by numerous foramina of vascular canals on the occlusal, labial and basal faces.

R e m a r k s. The teeth described here are distinguished from known teeth of this species (Ginter et al., 2002, 2010) in the deeper notches between cusps, nar-

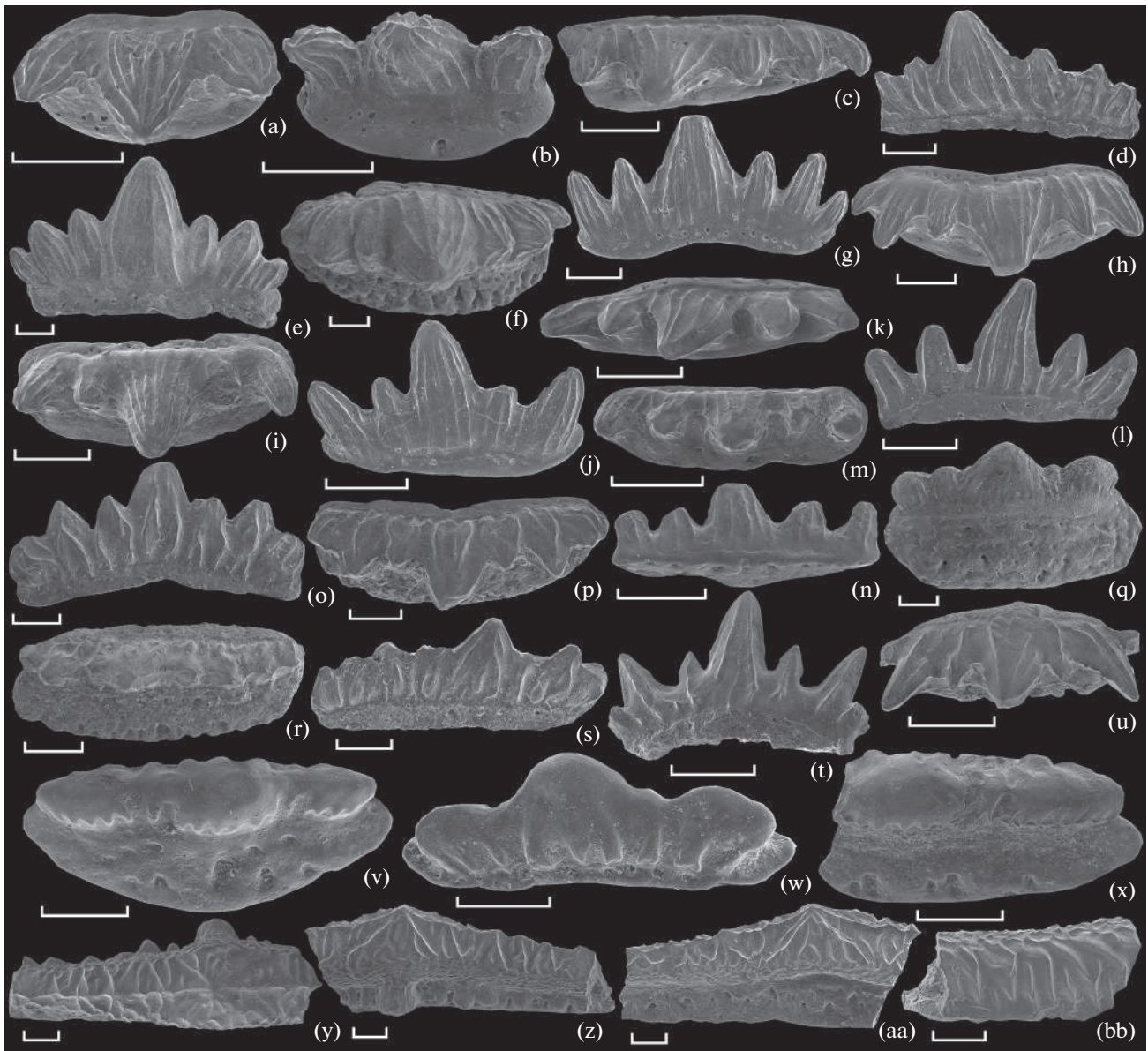


Fig. 8. Teeth of euselachians (a–x) and orodontiform (y–bb) from the Upper Devonian of the South Urals in occlusal (a, c, f, h, i, k, m, p, r, u, v, x, y), lingual (b, q, aa) and labial (d, e, g, j, l, n, o, s, t, w, z, bb) views. (a, b) *Protacrodus aequalis* Ivanov, 1996, PMSPU 115-60, sample 6478, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (c–f) *Protacrodus vetustus* Jaekel, 1925: (c) PMSPU 13-15, sample 6423, Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone; (d) PMSPU 115-61, sample 7279, Kuk-Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone; (e, f) PMSPU 115-62, sample 5882, Kuktash section, Askynian Regional Stage, Upper *rhenana* Zone. (g–j) *Protacrodus* sp.: (g, h) PMSPU 115-63, sample T12-146, (i, j) PMSPU 115-64, sample 6477, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (k, l) *Protacrodus serra* Ginter, Hairapetian and Klug, 2002, PMSPU 115-65, sample 6478, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (m, n) *Dalmehodus* sp., PMSPU 115-66, sample T12-143, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (o–q) Protacrodontidae indet.: (o, p) PMSPU 115-67, sample 5231, Kuk-Karauk section, Makarovian Regional Stage, Upper *triangularis* Zone.; (q) PMSPU 115-68, sample 6478, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (r, s) Euselachii ind. 1, PMSPU 115-69, sample 5413, Zigan section, Askynian Regional Stage, Upper *rhenana* Zone. (t, u) Euselachii ind. 2, PMSPU 115-70, sample 7276, Kuk-Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone. (v–x) *Deihim* sp., (v, w) PMSPU 115-71, sample 6478, (x) PMSPU 115-72, sample 6474, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (y–bb) Hybodontiformes indet.: (y–aa) PMSPU 115-73, sample 0169, (bb) PMSPU 115-74, sample 0171, Ryauzyak section, Lytvian Regional Stage, Middle-Upper *expansa* Zones. Scale bars 300 μ m.

row central cusp, and weakly developed occlusal blade.

O c c u r r e n c e. Upper Devonian, Upper Famennian of the South Urals; Poland, France, Iran, Morocco.

M a t e r i a l. Three teeth from the the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section.

Protacrodus sp.

Figs. 8g–8i

D e s c r i p t i o n a n d r e m a r k s. The teeth are small, with the base width from 0.9 to 1.2 mm. The protacrodont crown is pyramidal, flattened labio-lingually, includes five to seven cusps. The cusps are conical, straight, and oval in cross section, rather fused basally, and separated by quite wide notches. The intermediate cusps in a five-cusped crown or outer intermediate cusps in a crown with six or seven cusps are shorter and narrower than the lateral and inner intermediate cusps. This size of intermediate cusps displaces the gradual arrangement of the cusps in the crown as in the teeth of *Protacrodus vetustus*. The number of intermediate cusps can be different in the mesial and distal part, forming an asymmetrical crown. The cusps are ornamented with straight or slightly recurved, coarse ridges. The tooth base is slightly extended lingually and arched, penetrated by numerous foramina of vascular canals, sometimes with a very shallow labial depression (Fig. 8h).

The teeth described herein slightly resemble some teeth of *Junggarensis* (Roelofs et al., 2021). But, the later includes the teeth of several morphotypes: some teeth are similar to the *Protacrodus* teeth, other teeth—to *Dalmehodus*. One *Junggarensis* morphotype possesses a large central crown with considerably fused inner intermediate cusps (Roelofs et al., 2021, Fig. 4c, 4d).

M a t e r i a l. Seven teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage and one tooth from the Lower *expansa* Zone, Kushelgian Regional Stage of the Ryauzyak section; one tooth from the *linguiformis* Zone, Askynian Regional Stage of the Kuk-Karauk section; one tooth from the Lower *rhenana* Zone, Mendymian Regional Stage and one tooth from the Upper *rhenana* Zone, Askynian Regional Stage of the Zigan section.

Genus *Dalmehodus* Long et Hairapetian, 2000

Dalmehodus sp.

Figs. 8m, 8n

D e s c r i p t i o n a n d r e m a r k s. The small teeth with a width at base 0.8–0.9 mm mesio-distally. The tooth crown consists of five cusps. The central cusp is slightly higher than the other equal four ones. The cusps are round in cross section, separated by

deep notches each from other. The labial and lingual faces of the cusps are ornamented with a few straight ridges. The tooth base is with a short lingual part.

The authors of the first description of *Dalmehodus turnerae* Long et Hairapetian, 2000 did not provide a formal diagnosis, and described three teeth of two different protacrodontids (Long and Hairapetian, 2000). However, one tooth differs from the *Protacrodus* teeth, and other authors (Ginter et al., 2010) proposed to retain the name *Dalmehodus turnerae*. This species needs to be redescribed.

M a t e r i a l. Two teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section.

Genus *Deihim* Ginter, Hairapetian et Klug, 2002

Deihim sp.

Figs. 8v–8x

D e s c r i p t i o n a n d r e m a r k s. The teeth are slightly abraded, with the mesiodistal size of the base up to 1.3 mm. The crown is monolithic pyramidal, compressed labio-lingually, with prominent central and low lateral cusps. The labial face of the crown bears the distinct row of numerous accessory cusplets of different width. The lingual face is ornamented with coarse, straight ridges. The tooth base is typical euselachian type, lingually extended, subtriangular in outline, and perforated with numerous large foramina of vascular canals on the lingual surface and in the depression on the basal side.

These teeth resemble the teeth of *Deihim mansureae* Ginter, Hairapetian et Klug, 2002. But the later differs in the strongly prominent labial accessory cusplets and rougher lingual ornamentation (Ginter et al., 2002, 2010). The first description of *Deihim mansureae* includes four tooth morphotypes (Ginter et al., 2002). There are a larger number of tooth morphotypes (Ginter et al., 2010, Roelofs et al., 2015, 2016). Such a large variation in tooth structure cannot be explained by heterodonty of the dentition. Probably, the genus includes more than one species (Ivanov and Lucas 2011).

M a t e r i a l. Two teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section.

Protacrodontidae indet.

Figs. 8o–8q

D e s c r i p t i o n a n d r e m a r k s. The teeth possess a pyramidal protacrodont crown with cusps considerably fused basally. The conical cusps are separated by shallow notches. Some teeth (Figs. 8o, 8p) have a crown flattened labio-lingually with outer intermediate higher than inner intermediate and lateral cusps, and a tooth base with slightly extended lingual part. The cusps are covered with coarse incurved

ridges bifurcated to the crown/base junction. These teeth are similar to some teeth determined as *Protacrodus* spp. from the Famennian of Iran (Hairapetian and Ginter, 2009).

One tooth (Fig. 8q) possesses five thick, low cusps. The crown is inclined labially and forms an obtuse angle with base. The cusps are rounded in cross section, ornamented with straight cristae. The lateral cusps are larger than intermediate ones. The tooth base is strongly extended linguallly and bears numerous foramina of vascular canals.

M a t e r i a l. Two teeth from the Lower *rhomboidea* Zone, Makarovian Regional Stage of the Ryauzyak section; one tooth from the Upper *triangularis* Zone and one tooth from the *crepida* Zone, Makarovian Regional Stage of the Kuk-Karauk section.

Hybodontiformes indet.

Figs. 8y–8bb

Description. The small incomplete teeth (proximately 3 mm in mesio-distal size) have a monolithic, rather low, pyramidal crown elongated mesio-distally. The crown bears a distinct occlusal crest. The central cusp is low conical, without distinct boundaries; other cusps are barely visible. The crown ornamentation consists of anastomosing, curved, coarse long cristae. The long cristae diverge from the cusp apex and branch towards the base. The short cristae run from the occlusal crest between the cusps. The cristae are connected in the lower part of the crown and form a reticulated ornamentation resembling honeycomb cells. Such ornamentation reaches to the crown/base junction. This reticulated ornamentation is well developed on the labial face, but the lingual part bears just a narrow strip of this ornamentation. The crown/base junction is marked by a deep groove on the labial and lingual part.

The tooth base is smaller than the crown, with very short lingual and labial parts, and a flat basal face. The labial part bears a prominent, rounded median peg. The lingual and labial parts are perforated by numerous foramina of vascular canals of different diameters. The large foramina open at the labial rim forming a projection-like wavy edge.

R e m a r k s. These teeth are similar to the tooth named as *Protacrodontidae?* gen. et sp. indet. from the Lower Carboniferous of China (Ginter and Sun, 2007, Fig. 4E) but the later possesses distinct conical cusps. A similar reticulated ornamentation occurs in some teeth of the Devonian protacrodontids (Long and Hairapetian, 2000; Ginter et al., 2002; Hairapetian and Ginter, 2009), and frequently occurs in the teeth of the Mesozoic synchodontids (e.g. Klug, 2009). The labial peg is known in the crown of lonchidiid and acrodontid teeth (Ginter et al., 2010; Cappetta, 2012) but the labial peg developed in the tooth base is reported the first time for the hybodontiforms.

M a t e r i a l. Two teeth from the Lytvian Regional Stage, Middle-Upper *expansa* Zones of the Ryauzyak section.

Euselachii ind. 1

Figs. 8r, 8s

Description and remarks. The small tooth (1.5 mm in mesio-distal size) has a monolithic, pyramidal, flattened labio-lingually, rather low crown with slightly prominent central and outer intermediate cusps. The cusps are strongly fused basally and separated by very small notches. The crown is covered by incurved, bifurcated, coarse ridges extended basally. The tooth base has an extended lingual part and concave basal surface, bears numerous foramina of vascular canals forming longitudinal rows. The tooth slightly resembles the teeth of some protacrodontids from the Famennian of Iran (Hairapetian and Ginter, 2009).

M a t e r i a l. One tooth from the Upper *rhenana* Zone, Askynian Regional Stage of the Zigan section.

Euselachii ind. 2

Figs. 8t, 8u

Description and remarks. The teeth are small, with the base width from 0.7 to 0.8 mm. The crown possesses prominent cusps slightly fused basally, separated by deep notches, and connected with distinct lateral carina. The high central cusp is flanked by small inner intermediate cusps. The outer intermediate cusps are slightly smaller than the central one, but considerably large than the inner intermediate and lateral cusplets. The cusps are round in cross section, acuminate, and covered by slightly curved and serrated cristae of different length. The tooth base is thin, with a very short lingual part.

The teeth described herein are a little similar to some peculiar teeth of *Arduodens flammeus* Hairapetian et Ginter, 2009 from the Famennian of Iran (Hairapetian and Ginter, 2009).

M a t e r i a l. Two teeth from the Lower *rhenana* Zone, Mendymian Regional Stage of the Kuk-Karauk section.

Other Chondrichthyan Remains

Besides the numerous teeth of diverse elasmobranchs the studied collection includes chondrichthyan denticles and various scales. Rare chondrichthyan denticles occur in the Famennian Makarovian Regional Stage (Lower *rhomboidea* Zone) and in the Tournaisian Gumerovian Regional Stage of the Ryauzyak section. They possess a single-rowed crown including acuminate, recurved cusps (Fig. 9a). The cusps consecutively overlap each other and increase in length posteriorly. These denticles are of *Stemmatias*

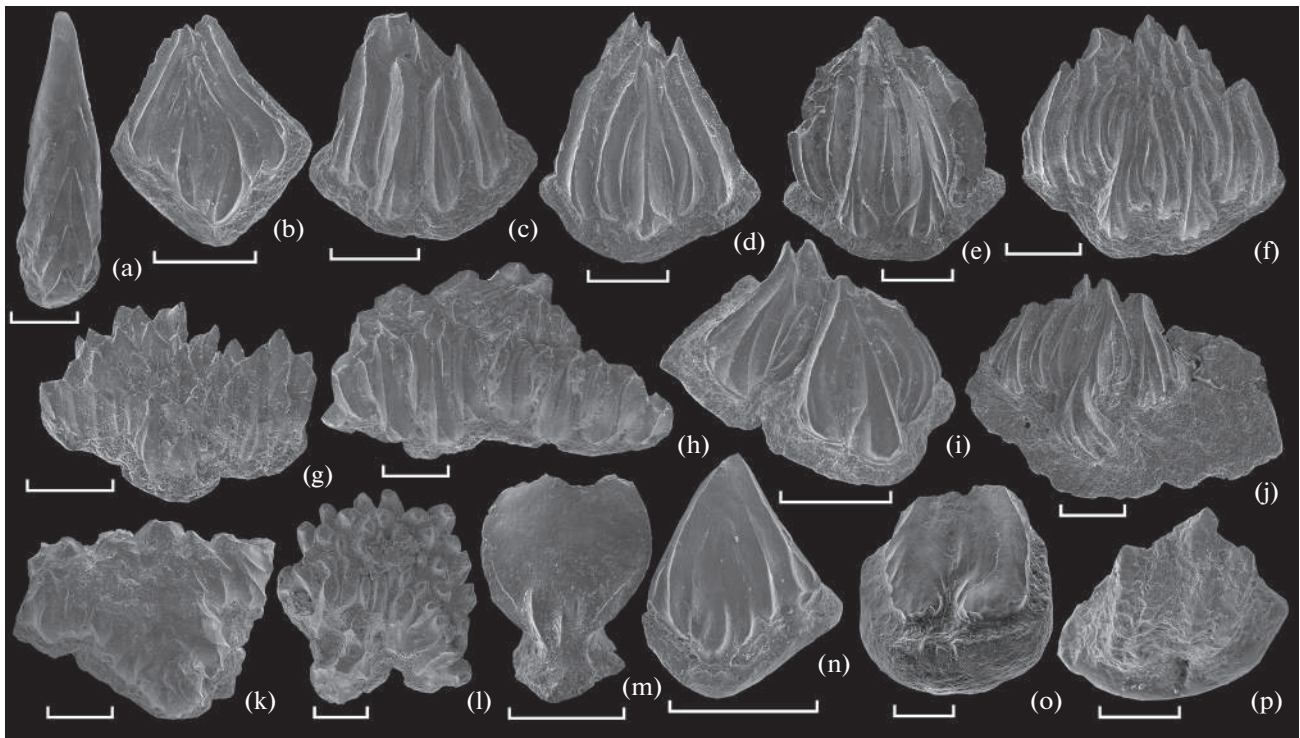


Fig. 9. Denticle (a) and scales (b–p) of chondrichthyans from the Upper Devonian and Lower Carboniferous of the South Urals in anterior (a, m) and crown (b–l, n–p) views. (a) Symmoriiform buccopharyngeal denticle, PMSPU 115-75, sample T13-24, Ryauzyak section, Makarovian Regional Stage, *rhomboidea* Zone. (b–j) Ctenacanthid type: (b) PMSPU 115-76, sample 7272, (c) PMSPU 115-77, (d) PMSPU 115-78, sample 7276, (e) PMSPU 115-79, sample 7272, (f) PMSPU 115-80, sample 7276, Kuk-Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone; (g) PMSPU 115-81, sample T12-112, Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone; (h) PMSPU 115-82, (i) PMSPU 115-83, (j) PMSPU 115-84, sample KK1, Kuk-Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone. (k) Tessera-like type, PMSPU 115-85, sample KK1, Kuk-Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone. (l) *Ohiolepis* type, PMSPU 115-86, sample 7276, Kuk-Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone. (m) Euselachian type, PMSPU 115-87, sample 6471, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (n, o) Protacrodontid type: (n) PMSPU 115-88, sample 6413, Ryauzyak section, Askynian Regional Stage, Upper *rhenana* Zone; (o) PMSPU 115-89, sample 0118, Ryauzyak section, Gumerovian Regional Stage. (p) Hybodontid type, PMSPU 115-90, sample 6448, Ryauzyak section, Makarovian Regional Stage, Upper *triangularis* Zone. Scale bars 300 μ m.

type and belong to buccopharyngeal denticles of symmoriiforms such as *Cobelodus*, *Stethacanthus*, *Stethacanthulus*, and *Symmorium* (Zangerl and Case, 1976; Williams, 1985).

The chondrichthyan scales are attributed to ctenacanthid, protacrodontid, hybodontid, euselachian, *Ohiolepis*, and tessera-like types. Abundant scales of ctenacanthid type (Figs. 9b–9j) have been found in the Mendymian, Askynian and Makarovian regional stages of the Ryauzyak, Kuk-Karauk and Zigan sections. They have a polyodontode complex crown, a weakly developed neck and a low base. The crown is rhomboid in shape, inclined and backwardly curved. The crown includes one or two anterior triangular odontodes placed centrally and narrow and elongate lateral odontodes which are closely spaced in a subparallel arrangement, separated by narrow grooves. The extended anterior part of odontodes is ornamented with curved cristae. The scale base is rhomboid or rough outline, with a concave or flat basal surface. The

scales may be strongly asymmetrical with an irregular arrangement of odontodes (Fig. 9h) or with a pathological enlarged lateral part (Fig. 9j). Two scales in the described collection were fused at the lateral edges (Fig. 9i). Such scales are attributed usually to the ctenacanthid type (e.g., Turner, 1993) but similar scales were described for the xenacanthiform (Dick, 1981) and the euselachian (Dick, 1998).

The rare scales of tessera-like type (Fig. 9k) occur in the Mendymian and Makarovian regional stages of the Ryauzyak and Kuk-Karauk sections. These scales possess a low crown consisting of odontodes-tubercles of different shapes. The odontodes are compactly placed each to others, and bear the ridges diverging from the apex. The scale base is slightly convex.

The single scales of *Ohiolepis* type (Fig. 9l) are recorded from the Mendymian Regional Stage of the Kuk-Karauk section. They are characterised by polyodontodia with numerous narrow, incurved odontodes compactly placed in the crown and slightly

diverging from the center. The scale base is with a rough edge and flat basal surface.

Scarce scales belonging to the euselachian type (Fig. 9m) have been found in the Makarovian Regional Stage (Lower *rhomboidea* Zone) of the Ryauzyak section. The scales possess a monolithic crown, a well developed, narrow neck and a small base. The crown is oval or rhomboid, inclined posteriorly, almost smooth with rare short cristae. Several large foramina of vascular canals open in the scale neck.

Scales of protacrodontid type (Figs. 9n, 9o) were collected in the Frasnian Askynian and Tournaisian Gumerovian regional stages of the Ryauzyak section. These subrhomboid scales have a low, flat, monolithic crown, weakly developed neck and a convex, large base. The crown possesses a compact odontocomplex consisting of a central odontode surrounded by elongate, narrow lateral odontodes (Fig. 9n) or a central odontode is missing (Fig. 9o). The odontodes are fused partly or completely, without distinct boundaries. Such scales were attributed to the protacrodontids (Gross, 1938; Ørvig, 1967) or to the orodontids (Ivanov and Nilov, 2017).

Rare scales of hybodontid type (Fig. 9p) occur in the Famennian Makarovian and Kushelgian regional stages of the Ryauzyak section. These scales have a cone-shaped crown apically elongated, a short neck and rhomboid base. The crown bears long ridges separated by longitudinal grooves. The base is wider than the crown, with a convex basal side.

Placoderm Remains

Rare placoderm macro- and microremains are represented by ptyctodontid remains, such as the tooth plates of *Rhynchodus* sp. (Fig. 11a) and an undetermined taxon (Fig. 10a) from the Frasnian Sargaevian and Mendymian regional stages of the Ryauzyak section, the Mendymian Regional Stage of the Kuk-Karauk section, and the Askynian Regional Stage of the Kuktash section; an incomplete median ventral plate (Fig. 10b) from Famennian Makarovian Regional Stage of the Ryauzyak section; vertebral elements (Fig. 10c) from the Makarovian Regional Stage of the Ryauzyak section. Placoderm tesseræ (Fig. 10d) have been found in the Frasnian Mendymian Regional Stage of the Kuk-Karauk section, the Askynian Regional Stage of the Ryauzyak and Akkyr sections. The tesseræ bear stellate tubercles of different sizes. Such tesseræ can belong to rhenanid or acanthothoracid placoderms (e.g., Burrow and Turner, 1999).

Acanthodian Remains

The acanthodian microremains are unique in the studied collection and include several acanthodiform scales (Fig. 10f) from the Domanikian and Barmian

regional stages of the Ryauzyak section, head tessera (Fig. 10e) from the Murzakaevian Regional Stage of the Kuk-Karauk section, and an acanthodian jaw fragment from the Kushelgian Regional Stage of the Ryauzyak section.

Osteichthyan Remains

The osteichthyans are represented by sacropterigyan and actinopterygian remains. The sacropterigyan remains include numerous onychodontiform teeth (Figs. 10g, 10h) from the Kynian, Sargaevian, Mendymian, Askynian, Barmian, Makarovian regional stages of the Ryauzyak section, the Askynian, Makarovian and Kushelgian regional stages of the Kuk-Karauk section, the Mendymian and Barmian regional stages of the Lemezinskiy section, the Makarovian Regional Stage of Akkyr section, the Domanikian and Mendymian regional stages of the Zuyakovo section, the Mendymian and Askynian regional stages of the Zigan section, the Askynian and Makarovian regional stages of the Kuktash section; rare fragments of porolepiform scales (Fig. 10i) from the Sargaevian and Barmian regional stages of the Ryauzyak section; tooth plates of Dipteroidea (Figs. 11c, 11d) from the Makarovian Regional Stage of the Akkyr section; fragments of a sarcopterygian jaw (Fig. 10j) from the Makarovian Regional Stage of the Ryauzyak section, and teeth of undetermined sarcopterygians from almost all regional stages of most sections from which the fish remains were collected.

The actinopterygian remains include various flank scales of *Moythomasia* sp. (Figs. 10k–11m) from the Sargaevian, Askynian, Makarovian regional stages of the Ryauzyak section, the Askynian Regional Stage of the Kuk-Karauk section; the flank scales (Fig. 10n) and an incomplete bone (Fig. 10o) of *Mimipiscis* sp. from the Makarovian Regional Stage of the Ryauzyak section, the Mendymian and Askynian regional stages of the Kuk-Karauk section; jaw fragments (Figs. 10p, 10q), a tooth plate (Fig. 10r), and numerous teeth of undetermined actinopterygians from almost all regional stages of most sections from which the fish remains were collected.

FISH ASSEMBLAGES

The fish assemblages were established for the Kynian–Lytvian interval of the Ryauzyak section, the Mendymian–Kushelgian interval of the Kuk-Karauk sections, the Mendymian–Makarovian interval of the Lemezinskiy section, the Askynian–Makarovian interval of the Akkyr and Zigan sections, Mendymian–Askynian interval of the Zigan section, the Domanikian–Askynian interval of the Zuyakovo section, the Barmian Regional Stage of the Bolshaya Barma section, the Makarovian Regional Stage of the Gabdyukovo section and the Lytvian Regional Stage of the Kushelga section. The distribution of fish taxa was

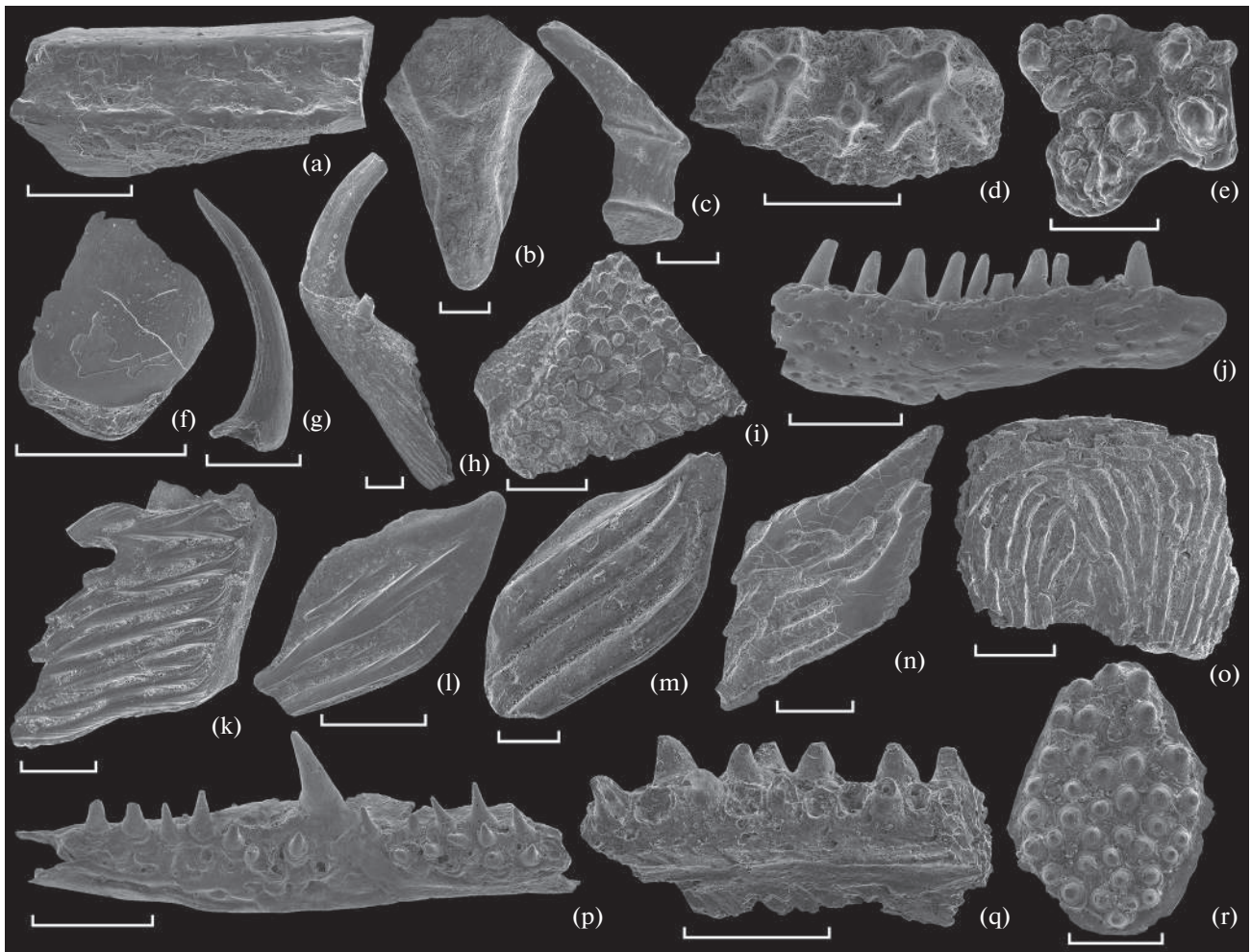


Fig. 10. Microremains of placoderms (a–d), acanthodians (e, f), sarcopterygians (g–j) and actinopterygians (k–r) from the Upper Devonian of the South Urals. (a–c) Ptectodontid remains: (a) PMSPU 115-91, tooth plate, occlusal view, sample T12-93, Ryauzyak section, Mendymian Regional Stage, Lower *rhenana* Zone; (b) PMSPU 115-92, incomplete median ventral plate, ventral view, sample 6474, (c) PMSPU 115-93, neural vertebral element, visceral view, sample T13-24, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (d) Placoderm tessera, external view, PMSPU 115-94, sample 126R, Akkyr section, Askynian Regional Stage, Upper *rhenana* Zone. (e, f) Acanthodian remains: (e) PMSPU 115-95, head tessera, dorsal view, sample T12-29, Kuk-Karauk section, Murzakaeian Regional Stage, Upper *marginifera* Zone; (f) PMSPU 115-96, acanthodiiform scale, oblique crown view, sample 6440, Ryauzyak section, Barmian Regional Stage, Lower–Middle *triangularis* Zones. (g, h) Onychodontiform teeth, lateral views: (g) PMSPU 115-97, sample 5602, Zuyakovo section, Domanikian Regional Stage, *hassi* Zone; (h) PMSPU 115-98, sample 5955, Kuktash section, Makarovian Regional Stage, *crepida* Zone. (i) Fragment of porolepiform scale, PMSPU 115-99, sample 02338, Ryauzyak section, Sargaevian Regional Stage, *transitans* Zone. (j) Sarcopterygian jaw, labial view, PMSPU 115-100, sample T12-135, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. (k–m) Flank scales of *Moythomasia* sp., external view, Ryauzyak section, (k) PMSPU 115-101, sample 02338, Sargaevian Regional Stage, *transitans* Zone, (l) PMSPU 115-102, sample 6404, Askynian Regional Stage, Upper *rhenana* Zone, (m) PMSPU 115-103, sample 6465, Makarovian Regional Stage, *rhomboidea* Zone. (n, o) *Mimipiscis* sp.: (n) flank scale, external view, PMSPU 115-104, sample 02331, Ryauzyak section, Kynian Regional Stage, *?falsiovalis* Zone; (o) incomplete bone, external view, PMSPU 115-105, sample 7272, Kuk-Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone. (p, q) Actinopterygian jaws, lingual views, Zigan section: (p) PMSPU 115-106, sample 5423, Askynian Regional Stage, Upper *rhenana* Zone; (q) PMSPU 115-107, sample 5416, Mendymian Regional Stage, Lower *rhenana* Zone. (r) Actinopterygian tooth plate, lingual view, PMSPU 115-108, sample T12-135, Ryauzyak section, Makarovian Regional Stage, Lower *rhomboidea* Zone. Scale bars 500 µm.

illustrated herein for two sections, Ryauzyak (Fig. 12) and Kuk-Karauk I (Fig. 13), where the microremains occurred in numerous samples.

Lists of fish remains found in the studied sections are shown in Tables 1–3.

Thus, the Frasnian fish assemblages include: of the **Sargaevian** Regional Stage—placoderm Ptectodon-

tida indet., sarcopterygians Struniiformes indet. and Porolepiformes indet., actinopterygian *Moythomasia* sp.; the **Domanikian** Regional Stage—chondrichthyan *Phoebodus latus*, Acanthodiformes indet., sarcopterygians Struniiformes indet. and Sarcopterygii indet.; the **Mendymian** Regional Stage—chondrichthyans *Phoebodus bifurcatus*, *Ph. fastigatus*, *Ph. latus*, *Ph. sp. 1*

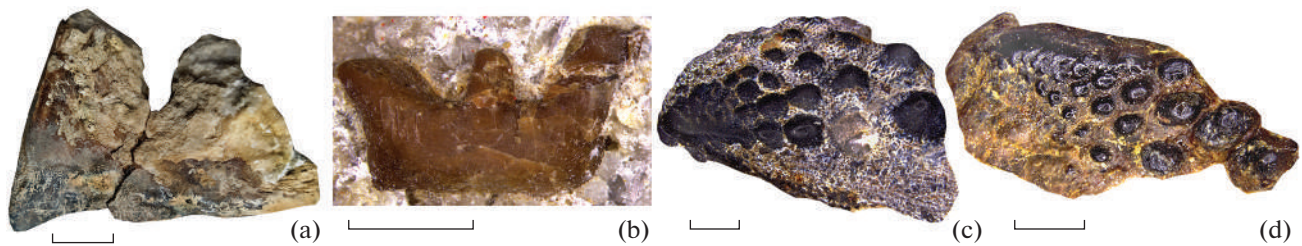


Fig. 11. Macroremains of placoderm (a), chondrichthyan (b) and sarcopterygians (c, d) from the Upper Devonian of the South Urals. (a) Tooth plate of ptyctodontid *Rhynchodus* sp., labial view, PMSPU 115-109, sample 7290, Kuk-Karauk section, Mendymian Regional Stage, Lower *rhenana* Zone. (b) Tooth of *Phoebodus bifurcatus*, labial view, PMSPU 115-110, sample 5903, Kuktash section, Askynian Regional Stage, Upper *rhenana* Zone. (c, d) Tooth plates of Dipteroide indet., occlusal views, Akkyr section, Makarovian Regional Stage, Upper *triangularis* Zone: (c) PMSPU 115-111, sample 7105, (d) PMSPU 115-112, sample 7096. Scale bars: (a) 1 cm, (b–d) 2 mm.

and 2, *Protacrodus vetustus*, *P. sp.*, Euselachii ind. 2, placoderms *Rhynchodus* sp., Ptyctodontida indet. and Placodermi indet., sarcopterygians Struniiformes indet. and Sarcopterygii indet., actinopterygians *Mimipiscis* sp. and Actinopterygii indet.; the **Askynian** Regional Stage—chondrichthyans *Phoebodus bifurcatus*, *Ph. curvatus*, *Ph. fastigatus*, *Ph. latus*, *Ph. cf. sophiae*, *Ph. sp. 1* and 2, *Ph. sp.*, *Diademodus* sp., *Stethacanthus* sp., *Cladodoides cf. wildungensis*, *C. sp.*, Cladodontomorphi indet., *Protacrodus vetustus*, Euselachii ind. 1, Placodermi indet., sarcopterygians Struniiformes indet. and Sarcopterygii indet., actinopterygians *Mimipiscis* sp., *Moythomasia* sp. and Actinopterygii indet.

The Famennian fish assemblages contain: the **Barmian** Regional Stage—chondrichthyans *Phoebodus latus*, *Cladodoides* sp., Cladodontomorphi indet., *Protacrodus* sp., sarcopterygians Struniiformes indet., Porolepiformes indet. and Sarcopterygii indet., Actinopterygii indet.; **Makarovian** Regional Stage—chondrichthyans *Phoebodus rayi*, *Ph. turnerae*, *Ph. typicus*, *Ph. sp. 1*, *Ph. sp. 2*, *Ph. sp.*, *Jalodus australiensis*, *Stethacanthus* sp., Stethacanthidae indet., Symmoriiformes indet., *Cladodoides cf. wildungensis*, *C. sp.*, *Squatina* sp., Cladodontomorphi indet., *Protacrodus aequalis*, *P. serra*, *P. vetustus*, *P. sp.*, *Dalmehodus* sp., *Deihim* sp., Protacrodontidae indet., placoderms Ptyctodontida indet. and Placodermi indet., sarcopterygians Struniiformes indet. and Sarcopterygii indet., actinopterygians *Mimipiscis* sp., *Moythomasia* sp. and Actinopterygii indet.; the **Murzakaevian** Regional Stage—chondrichthyans *Denaea* sp., Acanthodii indet., Sarcopterygii indet., Actinopterygii indet.; the **Kushelgian** Regional Stage—chondrichthyans *Phoebodus gothicus*, *Ph. limpidus*, *Ph. turnerae*, *Ph. sp.*, *Thrinacodus ferox*, *T. tranquilus*, *Denaea* sp., *Protacrodus vetustus*, *P. sp.*, Acanthodii indet., sarcopterygian Struniiformes indet., Actinopterygii indet.; the **Lytvian** Regional Stage—chondrichthyans *Phoebodus gothicus*, *Ph. turnerae*, *Thrinacodus ferox*, *T. tranquilus*, *Denaea* sp., Cladodontomorphi indet., Hybodontiformes indet., Actinopterygii indet.

The fishes from the Tournaisian Gumerovian Regional Stagen are represented by chondrichthyans *Thrinacodus ferox*, Symmoriiformes indet., “*Lissodus*” sp., Actinopterygii indet.

CONCLUSIONS

The fish assemblages from the Upper Devonian of the South Urals contain the teeth of phoebodontiform, jalodontiform, symmoriiform, ctenacanthiform, squatinactiform, euselachian chondrichthyans, various chondrichthyan scales, plate fragments of placoderms; scales and tesserae of acanthodians; teeth, tooth plates, scales and jaw fragments of sarcopterygians and actinopterygians. The chondrichthyan remains predominate among the remains of other fish groups. The onychodontiform teeth are very abundant in the Frasnian and Lower Famennian. The actinopterygian teeth occurs in almost all regional stages of most sections from which the fish remains were collected.

The assemblages include taxonomically diverse chondrichthyans such as phoebodontiforms, jalodontiforms, symmoriiforms, ctenacanthiforms, squatinactiforms, and euselachians. The sections of the South Urals are most diverse by phoebodontid taxa in the world and yielded a large number of their teeth. Some chondrichthyan taxa such as *Phoebodus rayi*, *Ph. cf. sophiae*, *Thrinacodus tranquilus*, *Denaea* sp., *Cladodoides cf. wildungensis*, *Squatina* sp., *Protacrodus serra*, *Dalmehodus* sp., *Deihim* sp., *Mimipiscis* sp. are reported in the Upper Devonian of the South Urals at first time.

The fish assemblages from the Upper Devonian of the South Urals include taxa widespread in many regions of the world. Most species of phoebodontiforms, symmoriiforms, jalodontiform and euselachians are distributed in the sections of the South Urals in the same stratigraphical ranges as worldwide. *Phoebodus sophiae* was early known from the Givetian–Lower Frasnian (Ginter et al., 2010; Ivanov, 2021). The finding of *Phoebodus cf. sophiae* in the

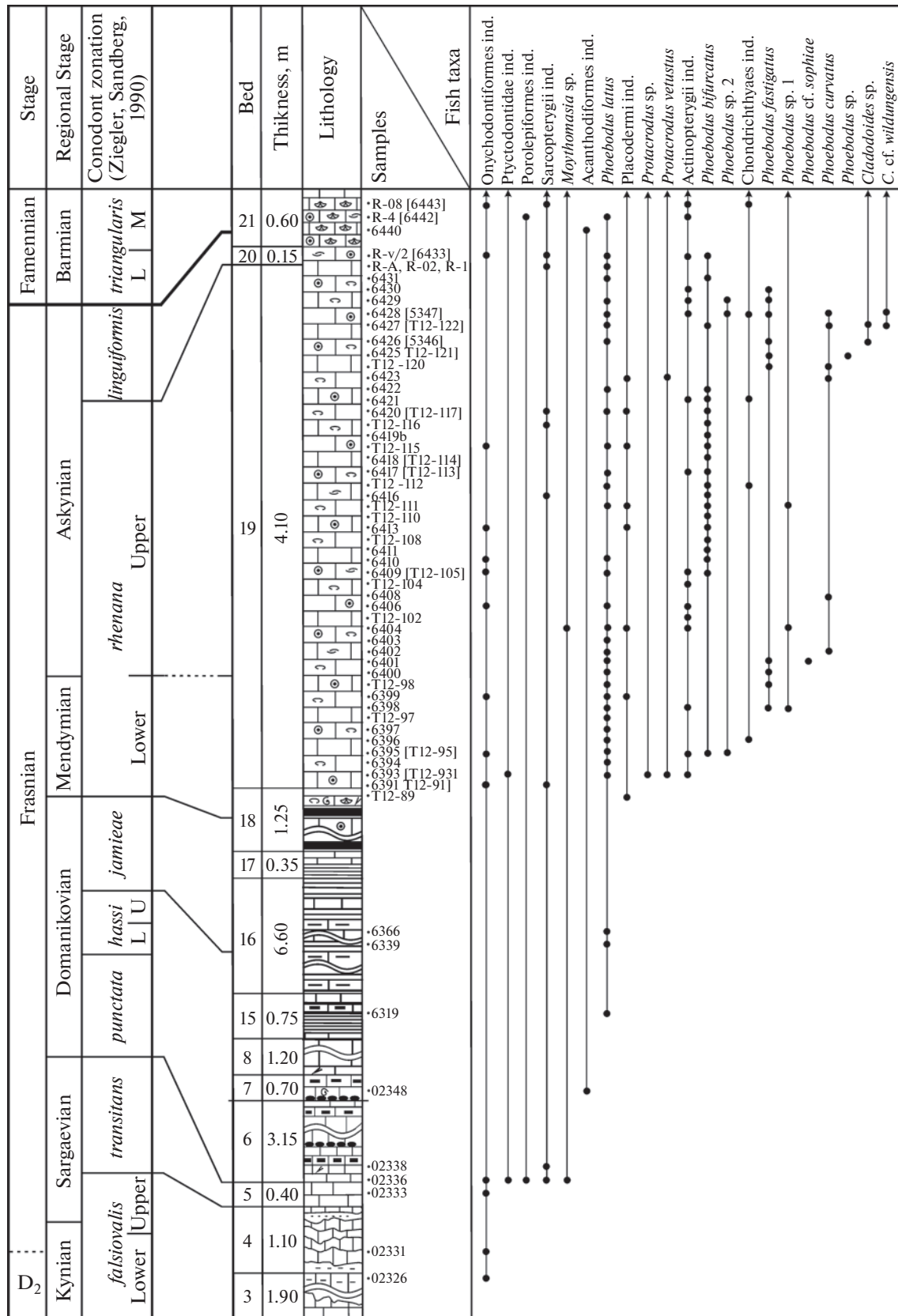


Fig. 12. Distribution of fish taxa in the Upper Devonian of the Ryauzyak section. Abbreviations: L—Lower, M—Middle, U—Upper, Um—Uppermost. Legend as for Fig. 2.

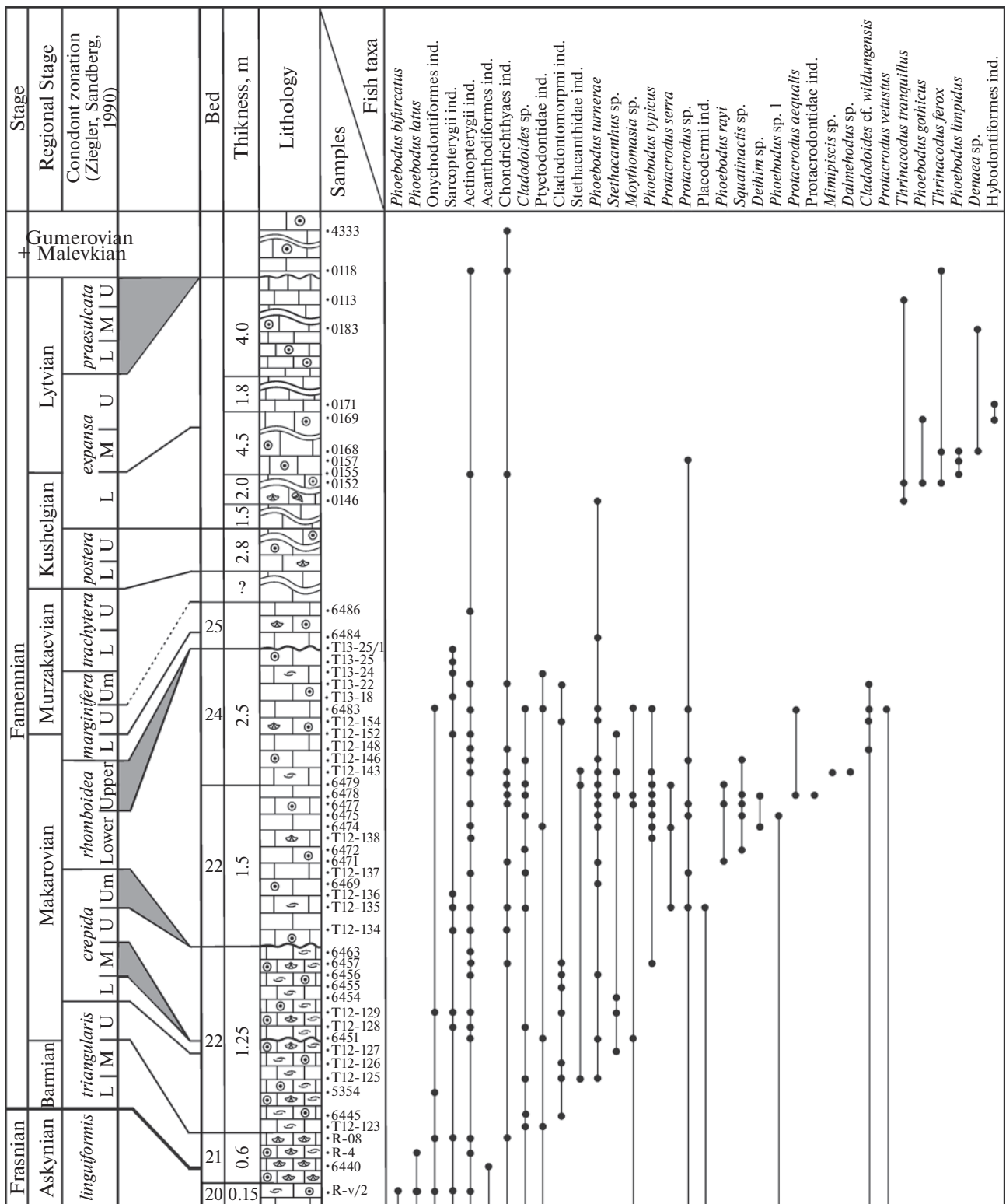


Fig. 12. (Contd.)

Upper Frasnian is first time. The occurrence of *Phoebodus latus* in Lower-Middle *triangularis* Zone, Barmian Regional Stage is youngest in the world. Most

Frasnian species of *Phoebodus* had disappeared at the Frasnian/Famennian boundary. But *Phoebodus latus* survived the Kellwasser biotic crisis.

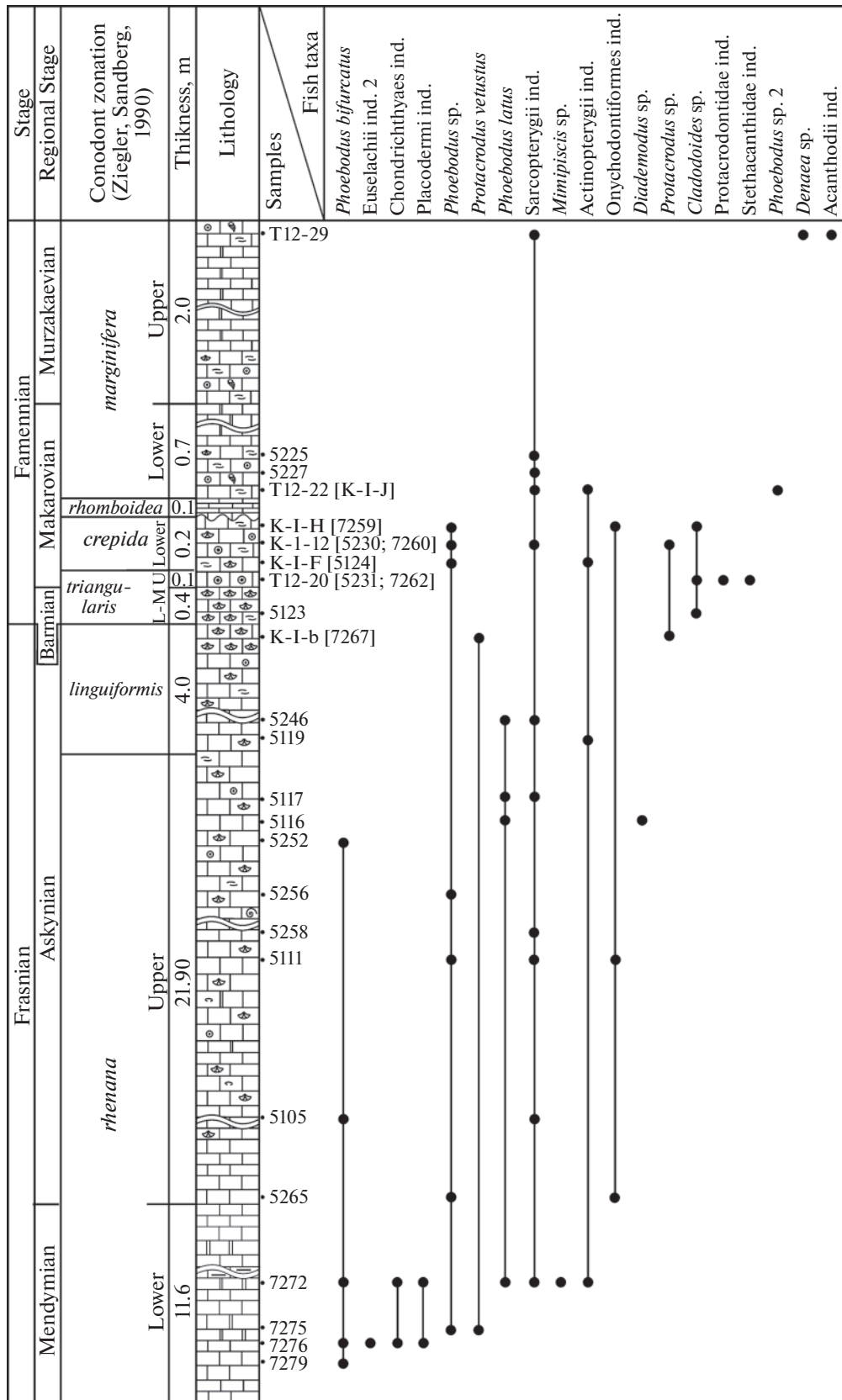


Fig. 13. Distribution of fish taxa in the Upper Devonian of the Kuk-Karauk section. Abbreviations: L—Lower, M—Middle, U—Upper. Legend as for Fig. 2.

Table 1. The fish remains occurring in the Ryauzyak section

Regional Stage	Conodont Zone	Fish remains
Kynian	<i>?falsiovalis</i>	Onychodontiform teeth
Sargaevian	<i>falsiovalis–transitans</i>	Ptyctodontid tooth plate, onychodontiform teeth and scale fragments, fragments of porolepiform scales, scales of <i>Moythomasia</i> sp.
Domanikian	<i>punctata–jamieae</i>	Teeth of <i>Phoebodus latus</i> , acanthodiform scales, sarcopterygian jaw fragments
Mendymian	Lower <i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. fastigatus</i> , <i>Ph. latus</i> , <i>Ph. sp. 1</i> and <i>2</i> , <i>Protacrodus vetustus</i> , <i>P. sp.</i> ; chondrichthyan scales of ctenacanthid and tessera-like types; ptyctodontid tooth plates, fragments of placoderm plates; onychodontiform and unidentified sarcopterygian teeth; actinopterygian teeth
Askynian	Upper <i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. curvatus</i> , <i>Ph. fastigatus</i> , <i>Ph. latus</i> , <i>Ph. cf. sophiae</i> , <i>Ph. sp. 1</i> and <i>2</i> , <i>Ph. sp.</i> , <i>Cladodoides cf. wildungensis</i> , <i>C. sp.</i> , <i>Protacrodus vetustus</i> ; chondrichthyan scales of ctenacanthid and protacrodontid types; placoderm tesserae and plate fragments; onychodontiform teeth; actinopterygian teeth, tooth plate and jaw fragments
	<i>Linguiformis</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. latus</i> ; teeth of onychodontiform and unidentified sarcopterygian; scales of <i>Moythomasia</i> sp., actinopterygian teeth
Barmian	Lower–Middle <i>triangularis</i>	Teeth of <i>Phoebodus latus</i> ; chondrichthyan scales of ctenacanthid type; acanthodiform scales; fragments of porolepiform scales, onychodontiform jaw and scales; actinopterygian teeth and tooth plate
Makarovian	Upper <i>triangularis</i>	Teeth of <i>Phoebodus turnerae</i> , <i>Cladodoides</i> sp., stethacanthid and cladodontomorph; fragments of ptyctodontid plates; onychodontiform teeth
	<i>Crepida</i>	Teeth of <i>Phoebodus turnerae</i> , <i>Ph. typicus</i> , <i>Stethacanthus</i> sp., <i>Cladodoides</i> sp. and cladodontomorph; chondrichthyan scales of ctenacanthid and hybodontid types; fragments of ptyctodontid plates; onychodontiform teeth; teeth and jaw fragments of unidentified sarcopterygian; scales of <i>Moythomasia</i> sp., actinopterygian teeth, tooth plate, jaw fragments and scales
	Lower <i>rhomboidea</i>	Teeth of <i>Phoebodus rayi</i> , <i>Ph. turnerae</i> , <i>Ph. typicus</i> , <i>Ph. sp. 1</i> , <i>Ph. sp.</i> , <i>Stethacanthus</i> sp., stethacanthid, <i>Cladodoides cf. wildungensis</i> , <i>C. sp.</i> , cladodontomorph, <i>Squatina</i> sp., <i>Protacrodus aequalis</i> , <i>P. serra</i> , <i>P. vetustus</i> , <i>P. sp.</i> , protacrodontid, <i>Dalmehodus</i> sp., <i>Deihim</i> sp.; symmoriiform denticles; chondrichthyan scales of ctenacanthid, euselachian, hybodontid and tessera-like types; ptyctodontid median ventral plate and postcranial elements, fragments of placoderm plates; onychodontiform teeth, sarcopterygian jaw fragments; scales of <i>Mimipiscis</i> sp. and <i>Moythomasia</i> sp., actinopterygian teeth, tooth plate and jaw fragments
	Lower <i>marginifera</i>	Teeth of <i>Phoebodus turnerae</i> ; sarcopterygian teeth.
Murzakaevian	Upper <i>marginifera</i>	Actinopterygian teeth
Kushelgian	Lower <i>expansa</i>	Teeth of <i>Phoebodus gothicus</i> , <i>Ph. limpidus</i> , <i>Ph. turnerae</i> , <i>Ph. sp.</i> , <i>Thrinacodus ferox</i> , <i>T. tranquillus</i> , <i>Denaeva</i> sp., <i>Protacrodus</i> sp.; chondrichthyan scales of hybodontid types; acanthodian jaw fragment; actinopterygian teeth and tooth plates
Lytvian	Middle–Upper <i>expansa</i>	Teeth of <i>Phoebodus gothicus</i> , <i>Thrinacodus ferox</i> , <i>T. tranquillus</i> , <i>Denaeva</i> sp., Hybodontiformes indet.

Table 2. The fish remains occurring in the Kuk-Karauk I and II sections

Regional Stage	Conodont Zone	Fish remains
Mendymian	Lower <i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. latus</i> , <i>Ph. sp.</i> , <i>Protacrodus vetustus</i> , <i>Euselachii</i> ind. 2; chondrichthyan scales of <i>Ohiolepis</i> , ctenacanthid and tessera-like types; tooth plates of ptyctodontid <i>Rhynchodus</i> sp., placoderm tesserae and plate fragments; sarcopterygian teeth; scale and bone fragment of <i>Mimipiscis</i> sp., actinopterygian teeth and bone fragments
Askynian	Upper <i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. latus</i> , <i>Ph. sp.</i> , <i>Diademodus</i> sp.; chondrichthyan scales of ctenacanthid type; onychodontiform and unidentified sarcopterygian teeth; bone fragment of <i>Mimipiscis</i> sp.
	<i>linguiformis</i>	Teeth of <i>Phoebodus latus</i> , <i>Stethacanthus</i> sp., <i>Protacrodus vetustus</i> , <i>P. sp.</i> ; sarcopterygian teeth; scales of <i>Moythomasia</i> sp., actinopterygian bone fragments
Barmian	Lower–Middle <i>triangularis</i>	Teeth of <i>Cladodoides</i> sp.
Makarovian	Upper <i>triangularis</i>	Teeth of <i>Phoebodus</i> sp. <i>Stethacanthus</i> sp., <i>Cladodoides</i> sp., stethacanthid and protacrodontid
	<i>crepida</i>	Teeth of <i>Phoebodus</i> sp., <i>Cladodoides</i> sp., <i>Protacrodus</i> sp.; onychodontiform and unidentified sarcopterygian teeth; actinopterygian teeth
	Lower <i>marginifera</i>	Teeth of <i>Phoebodus</i> sp.2 and cladodontomorph; chondrichthyan scales of ctenacanthid type; sarcopterygian and actinopterygian teeth
Murzakaevian	Upper <i>marginifera</i>	Tooth of <i>Denaea</i> sp.; acanthodian head tessera; sarcopterygian teeth
Kushelgian	<i>postera</i>	Teeth of <i>Phoebodus gothicus</i> and <i>Protacrodus vetustus</i> ; onychodontiform teeth

The phoebodontid zonation was proposed for the Givetian–Famennian interval based on the distribution of *Phoebodus* species including the sections of the South Urals (Ivanov, 2020). The new data of occurrence of *Phoebodus* species in the studied sections confirms the earlier known taxa ranges and boundaries of phoebodontid zones. The *latus* phoebodontid Zone corresponds to the Lower *falsiovalis*–*jamieae* conodont Zones, the *bifurcatus* Zone—the *rhenana* Zone, the *typicus* Zone—the Lower–Upper *triangularis* Zones, the *gothicus* Zone—the Lower *crepida*–Upper *marginifera* Zones, and the *limpidus* Zone—the Uppermost *marginifera*–Middle *praesulcata* Zones.

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Table 3. The fish remains occurring in the other studied sections

Section	Regional Stage	Conodont Zone	Fish remains
Akkyr	Askynian	Upper <i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. curvatus</i> , <i>Ph. latus</i> , <i>P. sp.</i> , cladodontomorph, <i>Protacrodus vetustus</i> ; placoderm tessera; sarcopterygian teeth
		<i>linguiformis</i>	Tooth of <i>Protacrodus vetustus</i> ; actinopterygian teeth and tooth plates
	Makarovian	Upper <i>triangularis</i>	<i>Cladodoidea</i> sp. and cladodontomorph, onychodontiform teeth
		<i>rhomboidea</i>	Tooth of <i>Squatinactis</i> sp. and sarcopterygian teeth
Lemezinskiy	Mendymian	Lower <i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. curvatus</i> , <i>Ph. cf. fastigatus</i> , <i>Ph. latus</i> , onychodontiform teeth
	Askynian	<i>linguiformis</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. latus</i>
	Barmian	Lower–Middle <i>triangularis</i>	Teeth of cladodontomorph and <i>Protacrodus</i> sp.; onychodontiform teeth
	Makarovian	<i>crepida</i>	Teeth of <i>Stethacanthus</i> sp., <i>Cladodoidea</i> sp. and <i>Jalodus australiensis</i>
Kuktash	Askynian	Upper <i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. curvatus</i> , <i>Ph. latus</i> , <i>Protacrodus vetustus</i> ; onychodontiform teeth
		<i>linguiformis</i>	Teeth of <i>Phoebodus latus</i> , <i>Ph. sp.</i> , tooth plate of ptyctodontid <i>Rhynchodus</i> sp., placoderm plate fragments; onychodontiform teeth
	Makarovian	<i>crepida</i>	Onychodontiform teeth
Zigan	Mendymian	Lower <i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. latus</i> , <i>Ph. sp.</i> , <i>Protacrodus</i> sp.; chondrichthyan scales of ctenacanthid type; onychodontiform teeth, sarcopterygian teeth; actinopterygian teeth and jaw fragments
	Askynian	Upper <i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Protacrodus vetustus</i> , <i>P. sp.</i> , Euselachii ind. 1; chondrichthyan scales of ctenacanthid type; onychodontiform teeth, sarcopterygian teeth; actinopterygian teeth and jaw fragments
Zuyakovo	Domanikian	<i>hassi</i>	Onychodontiform teeth
	Mendymian–Askynian	<i>rhenana</i>	Teeth of <i>Phoebodus bifurcatus</i> , <i>Ph. cf. fastigatus</i> , <i>Ph. sp.</i> , onychodontiform and actinopterygian teeth
Bolshaya Barma	Barmian	Lower–Middle <i>triangularis</i>	Teeth of cladodontomorph and <i>Protacrodus</i> sp.; chondrichthyan scale; sarcopterygian teeth
Gabdyukovo	Makarovian	<i>crepida</i>	Teeth of <i>Cladodoidea</i> sp.
Kushelga	Lytvian	Middle–Upper <i>expansa</i>	Teeth of <i>Phoebodus turnerae</i> and cladodontomorph, actinopterygian teeth

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interests.

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