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## FISH ASSEMBLAGES FROM THE MIDDLE–UPPER DEVONIAN OF THE MIDDLE URALS, RUSSIA

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### Abstract

New assemblages of diverse fishes from the Givetian–Famennian were described in six sections in the Middle Urals: Pokrovskoe, Baronskaya, Sulem, Pershino, Yokva, and Vilva. *Diademodus*, *Wellerodus*, and *Mimipiscis* genera were discovered in the Urals for the first time. Data on the occurrence of *Phoebodus* species in the Pokrovskoe section were used to specify the boundary between the *Phoebodus sophiae* and *Ph. latus* phoebodontid zones. Four phoebodontid zones can be recognized in the sections of the Middle Urals.

**Keywords:** fishes, Devonian, Middle Urals

### Introduction

In the Urals region, fish assemblages have been recorded earlier in the Late Devonian of the South Urals [1–3] and the Famennian of the Polar Urals [4], but fishes from the Middle and Late Devonian of the Middle Urals are still poorly known, with only one *Phoebodus* species recently described [5].

A new collection of diverse and abundant fishes from the Givetian–Famennian deposits of the Middle Urals is studied in this paper. The fish microremains were obtained from the processed conodont samples (coll. by A.Z. Bikbaev and M.P. Snigireva, Institute of Geology and Geochemistry, Ekaterinburg) and micrographed using Hitachi S-3400N, Cambridge CamScan-4, and Tescan VEGA-II XMU scanning electron microscopes. All specimens described here are housed at the Paleontological Museum of St. Petersburg State University (PMSPU).

### Geological Setting

The new assemblages of fishes under study come from six sections (localities) of the Middle Urals: Pokrovskoe, Baronskaya, Sulem, Pershino, Yokva, and Vilva. Five sections (Pokrovskoe, Baronskaya, Sulem, Pershino, and Yokva) are located in the Sverdlovsk Region, and one (Vilva) in the Perm Region.

The Pokrovskoe section is in the vicinity of the village of Pokrovskoe on the Bobrovka River (left tributary of the Irbit River), 10 km west of the town of Artemovskiy. The Givetian and Frasnian deposits of the Vysotinkian and Brodovkian regional stages (RS) are exposed on both banks of the river for over 2 km. The Givetian deposits of

the Vysotinkian RS include sandy limestones with clay interbeds, while the deposits of the Brodovkian RS, corresponding to the Lower Frasnian and possibly Upper Givetian, contain unbedded and massive reef limestones [6–8].

The Baronskaya section is situated on the right bank of the Mezhevaya Utka River (right tributary of the Chusovaya River), 6.5 km from the river mouth. The Upper Frasnian deposits of the Askynian RS and the Lower Famennian deposits of the Makarovian RS are represented by limestones, dolomitized limestones with intercalations of marls, mudstones, clayey and calcareous-siliceous shales [9, 10].

The Sulem section is on the left bank of the Sulem River, near the river mouth, 15 km south of the Baronskaya section. The Upper Frasnian deposits of the Askynian RS and the Lower Famennian deposits of the Makarovian RS are formed by micritic and dolomitized limestones with intercalations of marls and clayey limestones [11].

The Yokva section is on the right bank of the Chusovaya River, 3 km downstream of the village of Yokva. The section comprises the Upper Frasnian–Tournaisian deposits. The Upper Frasnian deposits of the Askynian RS and the Famennian deposits of the Makarovian–Lytvian RS of the section consist of limestones and dolomites with diverse fossils [12].

The Pershino section is located near the village of Pershino on the Rezh River, 10 km north of the town of Rezh. The massive limestones of the Upper Frasnian deposits of the Gubinskian RS and the detrital limestones and siltstones of the Lower Famennian deposits of the Shameyskian RS are exposed in the section [10, 13].

The Vilva (Krivoy Rog) section is located on the left bank of the Vilva River, 2 km southeast of the town of Gremyachinsk. The deposits of the section belong to the Frasnian Sargaevian, Domanikian, Mendymian, Askynian RS and Lower Famennian Makarovian RS. The Upper Frasnian and Lower Famennian deposits are composed of limestones, dolomites, and marls with various invertebrate fossils [14].

### Fish Assemblages

**Pokrovskoe section.** The diverse and abundant fish remains (Fig. 1) of the Pokrovskoe section were found at four levels: in the interval of the Givetian of the Upper *Polygnathus varcus*, Upper *Klapperina disparilis*, *Skeletognathus norrisi*, and Frasnian of the Upper *Mesotaxis falsovalis* conodont zones (CZ). The fish assemblage of the Upper *Po. varcus* CZ is made up of the teeth of the chondrichthyans *Phoebodus fastigatus* and *Ph. sophiae*, as well as ptyctodontid plates (Fig. 1.25), acanthodiform scales, teeth of struniiform sarcopterygians, and actinopterygian scales. The fish remains from the Upper *K. disparilis* CZ are as follows: teeth of *Phoebodus curvatus*, *Ph. fastigatus*, *Ph. Sophiae* (Fig. 1.2–8), and *Ph. sp.*; chondrichthyan scales of “*Ohiolepis*”, protacrodontid, ctenacanthid, and hybodontid types (Fig. 1.14, 16, 20, 21); uncompleted plates of ptyctodontids (Fig. 1.24) and undetermined placoderms; acanthodiform scales (Fig. 1.23); jaw fragments of osteolepiforms; teeth and jaw fragments of struniiforms; teeth, jaw fragments (Fig. 1.30), and scales of actinopterygians, including *Moythomasia* sp. The assemblage of the *S. norrisi* CZ includes: the teeth of *Phoebodus curvatus*, *Ph. fastigatus*, *Ph. latus* (Fig. 1.9, 10, 12, 13), and *Ph. sp.*; chondrichthyan scales of “*Ohiolepis*”, protacrodontid, ctenacanthid, and hybodontid types (Fig. 1.15, 19, 22); plate fragments of undetermined placoderms; osteolepiform scales; struniiform teeth, fragments of jaws, and scales (Fig. 1.26, 28, 29); teeth, jaw fragments, and scales of actinopterygians,

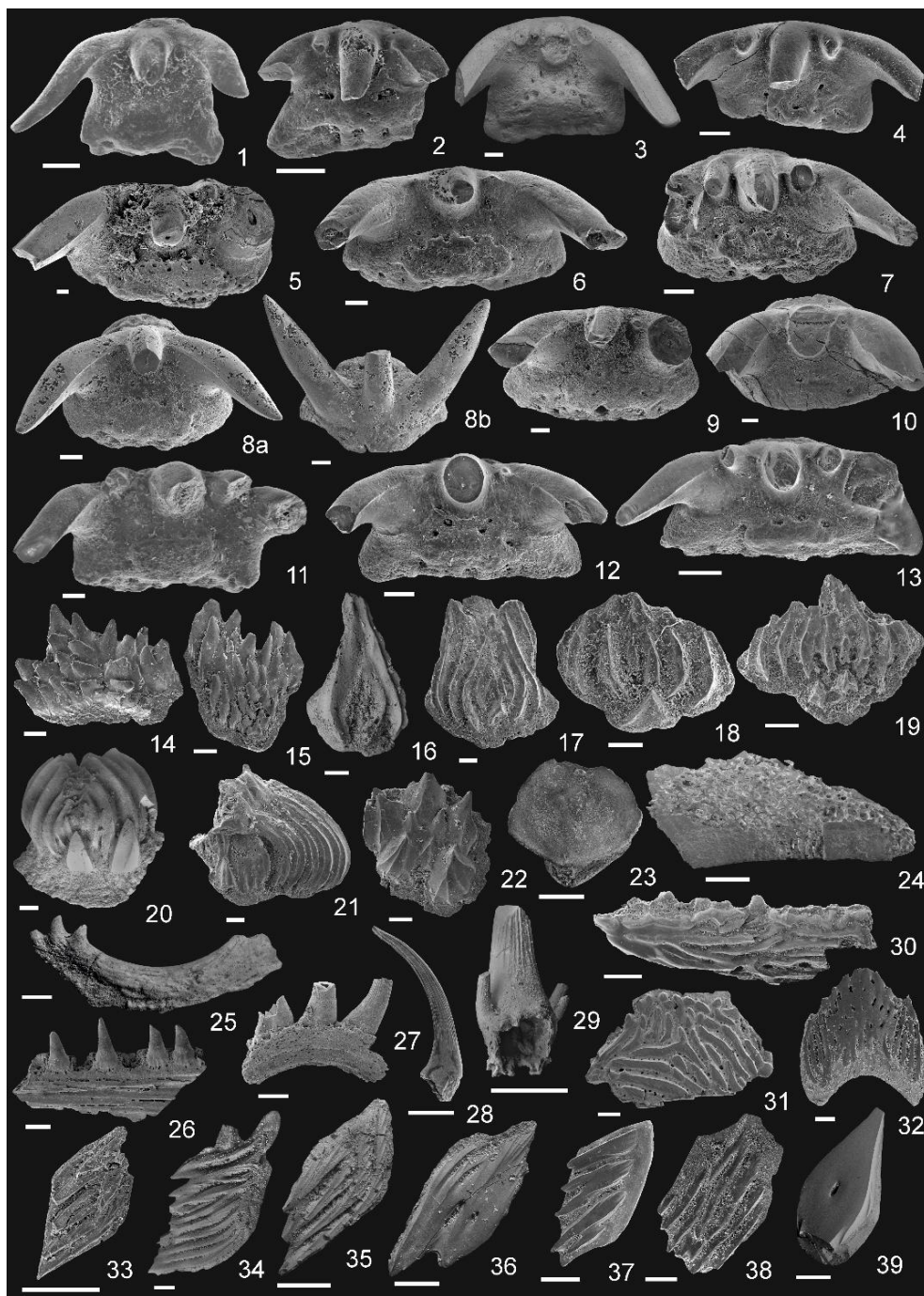


Fig. 1. Fish remains from the Givetian–Frasnian of the Pokrovskoe section. 1, 11, 17, 18, 27, 33 – Upper *M. falsiovalis* CZ; 2–8, 14, 16, 20, 21, 30 – Upper *K. disparilis* CZ; 9, 10, 12, 13, 15, 19, 22–24, 26, 28, 29, 31, 32, 34–39 – *S. norrisi* CZ; 25 – Upper *Po. varcus* CZ. 1–4 – *Phoebodus fastigatus* Ginter et Ivanov, 1992, teeth, occlusal views: 1 – PMSPU 97-1, 2 – PMSPU 97-2, 3 – PMSPU 97-3, 4 – PMSPU 97-4. 5–7 – *Ph. sophiae* St. John et Worthen, 1875, teeth, occlusal views: 5 – PMSPU 97-5, 6 – PMSPU 97-6, 7 – PMSPU 97-7. 8–10 – *Ph. curvatus* Ivanov, 2021, teeth, occlusal (8a, 9, 10) and labial (8b) views: 8 – PMSPU 74-2, 9 – PMSPU 74-4, 10 – PMSPU 74-5. 11–13 – *Ph. latus* Ginter et Ivanov, 1995, teeth, occlusal

views: 11 – PMSPU 97-8, 12 – PMSPU 97-9, 13 – PMSPU 97-10. 14–22 – Chondrichthyan scales, crown views: 14, 15 – *Ohiolepis* type, 14 – PMSPU 97-11, 15 – PMSPU 97-12; 16–21 – Ctenacanth type, 16 – PMSPU 97-13, 17 – PMSPU 97-14, 18 – PMSPU 97-15, 19 – PMSPU 97-16, 20 – PMSPU 97-17, 21 – PMSPU 97-18; 22 – Tessera-like scale, PMSPU 97-19. 23 – Acanthodiformes indet., scale, oblique crown view, PMSPU 97-20. 24, 25 – Ptyctodontida indet.: 24 – upper tooth plate, lingual view, PMSPU 97-21; 25 – dermal clasping element, ventral view, PMSPU 97-22. 26–29 – Struniiformes indet.: 26 – jaw fragment, lingual view, PMSPU 97-23; 27 – parasymphysial whorl, lateral view, PMSPU 97-24; 28, 29 – teeth, 28 – lateral view, PMSPU 97-25, 29 – lingual view, PMSPU 97-26. 30–32, 39 – Actinopterygii indet.: 30 – jaw fragment, labial view, PMSPU 97-27; 31 – skull bone, external view, PMSPU 97-28; 32 – fulcral scale, external view, PMSPU 97-29; 39 – flank scale, external view, PMSPU 97-30. 33–36 – *Moythomasia* sp., flank scales, external views: 33 – PMSPU 97-31, 34 – PMSPU 97-32, 35 – PMSPU 97-33, 36 – PMSPU 97-34. 37, 38 – *Mimipiscis* sp., flank scales, external views: 37 – PMSPU 97-35, 38 – PMSPU 97-36. Scale bars: 1–23 – 100 µm; 24–29 – 500 µm; 30–39 – 300 µm

including *Moythomasia* sp. and *Mimipiscis* sp. (Fig. 1.31, 32, 34–39). A number of fish remains were recovered from the Upper *M. falsiovalis* CZ: the teeth of *Phoebodus fastigatus*, *Ph. latus* (Fig. 1.1, 11), and *Ph. sp.*; chondrichthyan scales of protacrodontid and ctenacanthid types (Fig. 1.17, 18); osteolepiform scale fragments; struniiform teeth, fragments of jaws, and scales (Fig. 1.27); teeth, jaw fragments, and scales of actinopterygians, including *Moythomasia* sp. and *Mimipiscis* sp. (Fig. 1.33). The record of *Omalodus* teeth in the Pokrovskoe section is erroneous [8] – there are no known findings of omalodontids in the Urals.

**Baronskaya section.** An assemblage of diverse fishes from the Frasnian of the Lower *Palmatolepis rhenana* CZ of the Baronskaya section comprises the following remains: the teeth of the chondrichthyans *Phoebodus bifurcatus* (Fig. 2.1), *Ph. curvatus*, *Ph. fastigatus* (Fig. 2.2), *Ph. latus*, *Ph. sp.*, *Diademodus* sp. (Fig. 2.3), and *Protacodus* sp. (Fig. 2.4); chondrichthyan scales of the ctenacanthid type; acanthodiform scales; struniiform teeth; scales of the actinopterygians *Moythomasia* sp. and *Mimipiscis* sp. The teeth of *Phoebodus bifurcatus* and the fragments of actinopterygian scales were found in the *Palmatolepis linguiformis* CZ of the section, and a tooth of *Cladodoides* sp. was obtained from the Famennian of the Middle *Palmatolepis triangularis* CZ (Fig. 3).

**Sulem section.** The fish remains from the Sulem section were discovered in four levels: Frasnian of the Lower *Pa. rhenana*, *Pa. linguiformis*, Famennian of the Lower and Upper *triangularis* CZ. The teeth of *Phoebodus bifurcates* and *Ph. latus* (Fig. 2.5, 6) and the struniiform teeth occurred in the Lower *Pa. rhenana* CZ. The chondrichthyan scales of the ctenacanthid type, placoderm scale, acanthodiform and actinopterygian scales were collected in the *Pa. linguiformis* CZ. The chondrichthyan teeth of *Cladodoides* sp. and the unidentified cladodontomorph, actinopterygian bone fragments were found in the Lower *Pa. triangularis* CZ. The teeth of *Wellerodus* sp. (Fig. 2.7) and *Cladodoides* sp. (Fig. 2.8), struniiform teeth, and actinopterygian scales were obtained from the Upper *Pa. triangularis* CZ.

**Pershino section.** A tooth of *Phoebodus curvatus* was recorded in the Lower *Pa. rhenana* CZ of the Pershino section. The teeth of *Protacodus* sp., scales of the ctenacanthid type, and placoderm fragments occurred in the Lower *Pa. triangularis* CZ of same section. The assemblage of the Middle–Upper *Pa. triangularis* CZ of the section

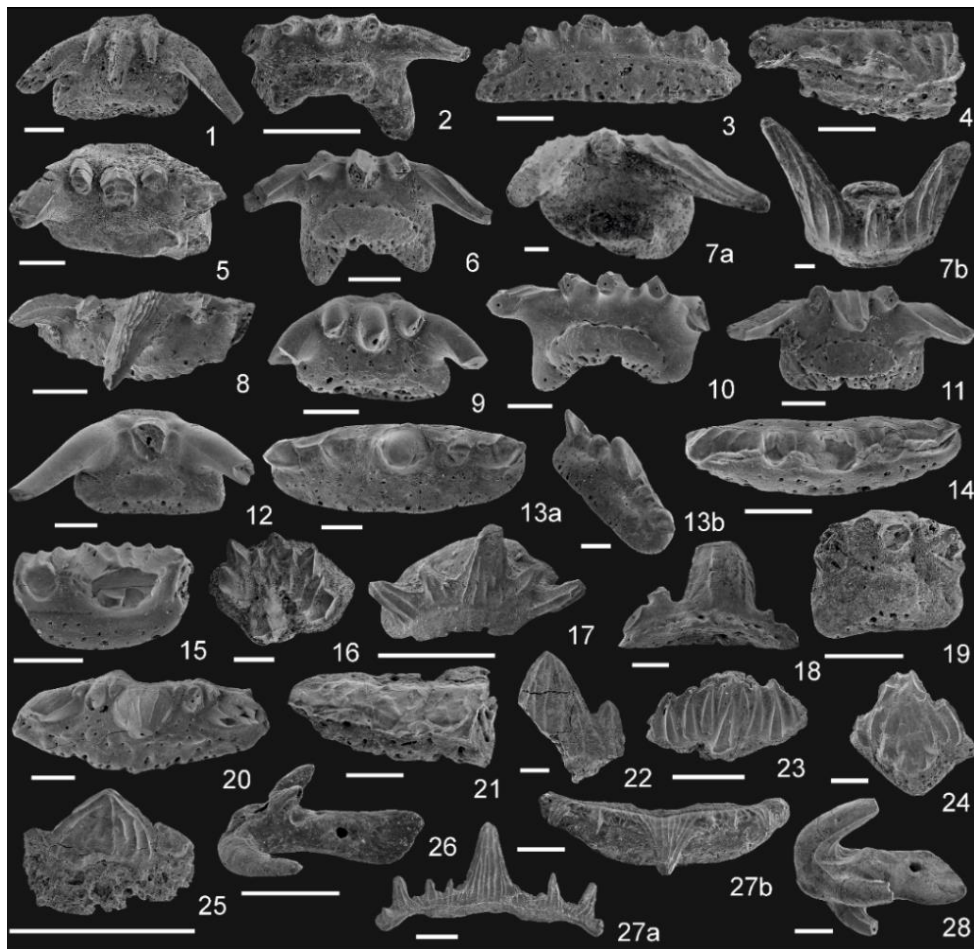


Fig. 2. The chondrichthyan teeth (1–15, 17–22, 25–28) and scales (16, 23, 24) from the Late Devonian of the Baronskaya section (1–4), Sulem section (5–8), Vilva section (9–17), Pershino section (18–24), and Yokva section (25–28). 1–6, 9–15 – Lower *Pa. rhenana* CZ; 7, 8, 16 – Upper *Pa. triangularis* CZ; 17 – Uppermost *Pa. crepida* CZ; 18–24 – Middle–Upper *Pa. triangularis* CZ; 25 – *Pa. linguiformis* CZ; 26, 27 – *Pa. postera*–Middle *Pa. expansa* CZ; 28 – Middle *Pa. expansa*–Middle *S. praesulcata* CZ. 1, 9 – *Phoebodus fastigatus* Ginter et Ivanov, 1992, occlusal views: 1 – PMSPU 97-37, 9 – PMSPU 97-45. 2, 6, 10 – *Phoebodus bifurcatus* Ginter et Ivanov, 1992, occlusal views: 2 – PMSPU 97-38, 6 – PMSPU 97-42, 10 – PMSPU 97-46. 3, 13 – *Diademodus* sp.: 3 – oblique occlusal view, PMSPU 97-39; 13 – occlusal (13a) and oblique lateral (13b) views, PMSPU 97-49. 4, 15, 21, 22, 25 – *Protacodus* sp., occlusal (4, 15, 21) and labial (22, 25) views: 4 – PMSPU 97-40, 15 – PMSPU 97-51, 21 – PMSPU 97-56, 22 – PMSPU 97-57, 25 – PMSPU 97-60. 5, 11 – *Phoebodus latus* Ginter et Ivanov, 1995, occlusal views: 5 – PMSPU 97-41, 11 – PMSPU 97-47. 7 – *Wellerodus* sp., occlusal (7a) and labial (7b) views, PMSPU 97-43. 8 – *Cladodoides* sp., occlusal view, PMSPU 97-44. 12 – *Phoebodus curvatus* Ivanov, 2021, occlusal view, PMSPU 97-48. 14 – Protacrodontidae indet., occlusal view, PMSPU 97-50. 16, 23 – Ctenacanth type scales, crown views: 16 – PMSPU 97-52, 23 – PMSPU 97-58. 17 – cf. *Cladodoides* sp., oblique labial view, PMSPU 97-53. 18 – Symmoriiformes indet., labial view, PMSPU 97-54. 19 – *Phoebodus typicus* Ginter et Ivanov, 1995, occlusal view, PMSPU 97-54. 20 – *Squatina* sp., occlusal view, PMSPU 97-55. 24 – Protacrodontid type scale, crown view, PMSPU 97-59. 26 – *Thrinacodus tranquillus* Ginter, 2000, oblique occlusal view, PMSPU 97-61. 27 – *Squatina* sp., labial (27a) and occlusal (27b) views, PMSPU 97-62. 28 – *Thrinacodus ferox* (Turner, 1982), oblique occlusal view, PMSPU 97-63. Scale bars: 300  $\mu$ m

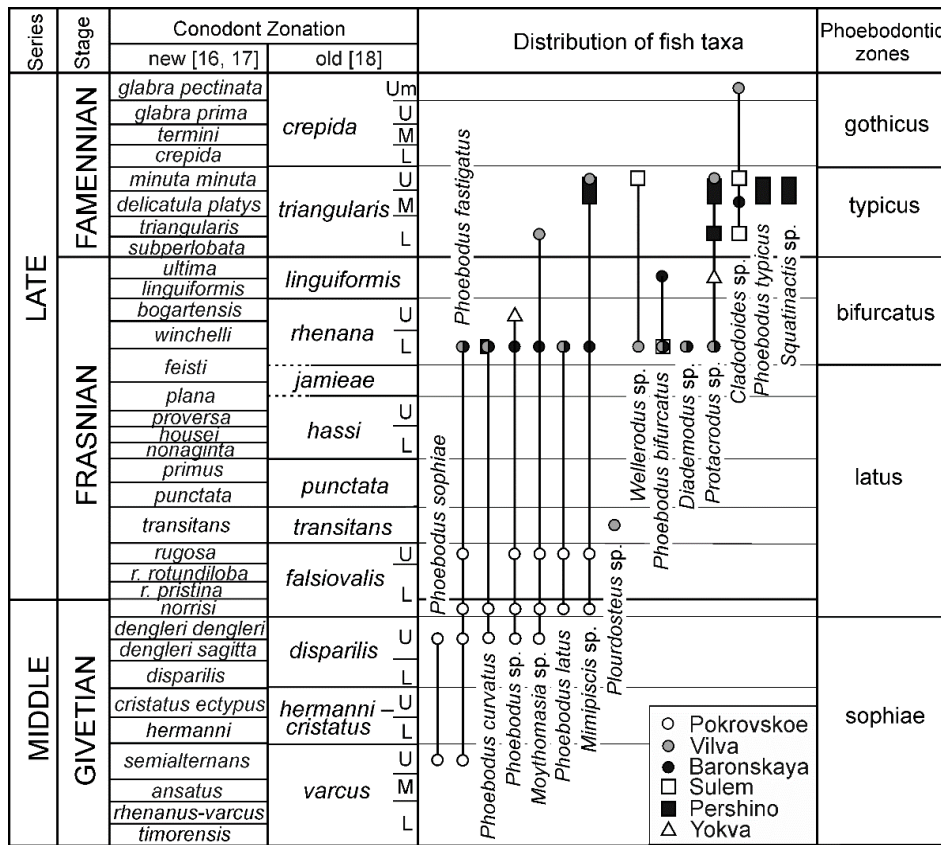


Fig. 3. Distribution of fish taxa in the sections of the Middle Urals. List of conodont zones: *Polygnathus timorensis*, *Polygnathus rhenanus*, *Polygnathus varcus*, *Polygnathus ansatus*, “*Ozarkodina*” *semialternans*, *Schmidtoognathus hermanni*, *Polygnathus cristatus*, *Polygnathus cristatus ectypus*, *Klapperina disparilis*, *Polygnathus dengleri sagitta*, *Polygnathus dengleri dengleri*, *Skeletognathus norrisi*, *Ancyrodella rotundiloba pristina*, *Ancyrodella rotundiloba soluta*, *Ancyrodella rotundiloba rotundiloba*, *Ancyrodella rugosa*, *Mesotaxis falsiovalis*, *Palmatolepis transitans*, *Palmatolepis punctata*, *Ancyognathus primus*, “*Ozarkodina*” *nonaginta*, *Palmatolepis housei*, *Palmatolepis proversa*, *Palmatolepis plana*, *Palmatolepis hassi*, *Palmatolepis feisti*, *Palmatolepis jamieae*, *Palmatolepis winchelli*, *Palmatolepis bogartensis*, *Palmatolepis rhenana*, *Palmatolepis linguiformis*, *Palmatolepis ultima*, *Palmatolepis subperlobata*, *Palmatolepis triangularis*, *Palmatolepis delicatula platys*, *Palmatolepis minuta minuta*, *Palmatolepis crepida crepida*, *Palmatolepis crepida*, *Palmatolepis termini*, *Palmatolepis glabra prima*, *Palmatolepis glabra pectinata*

includes: the teeth of *Phoebodus typicus* (Fig. 2.19), *Squatinactis* sp. (Fig. 2.20), *Protacodus* sp. (Fig. 2.21, 22), and Symmoriiformes indet. (Fig. 2.18); scales of the ctenacanthid and protacrodontid types (Fig. 2.23, 24); fragments of ptyctodontid plates; scales of *Mimipiscis* sp. and bone fragments of actinopterygians.

**Yokva section.** The fish remains in the Yokva section were found in two levels of the Upper Frasnian and two levels of Upper and Uppermost Famennian. A tooth of *Phoebodus* sp. was collected from the Upper *Pa. rhenana* CZ. The teeth of *Protacodus* sp. (Fig. 2.24) were found in the *Pa. linguiformis* CZ. The teeth of *Thrinacodus ferox*, *Th. tranquillus* (Fig. 2.26), *Squatinactis caudispinatus* (Fig. 2.27), along with scales of

the ctenacanthid type, placoderm fragments, actinopterygian teeth were recorded in the *Palmatolepis postera*–Middle *Palmatolepis expansa* CZ interval. The teeth of *Thrinacodus ferox* (Fig. 2.28), *Squatinactis caudispinatus*, and actinopterygian teeth were reported from in the Middle *Palmatolepis expansa*–Middle *Siphonodella praesulcata* CZ interval.

**Vilva section.** Diverse fish fossils were recorded in the Lower and Upper Frasnian, Lower Famennian of the Vilva section (Fig. 3).

The anterior supragnathal plate of *Plourdosteus* sp., plate fragments of arthrodiures and bothriolepids, osteolepiform scales were found in the *Palmatolepis transitans* CZ. The assemblage of the Lower *Pa. rhenana* CZ comprises the teeth of *Phoebodus bifurcatus* (Fig. 2.10), *Ph. curvatus* (Fig. 2.12), *Ph. fastigatus* (Fig. 2.9), *Ph. latus* (Fig. 2.11), *Wellerodus* sp., *Diademodus* sp. (Fig. 2.13), *Protacodus* sp. (Fig. 2.15), Protacrodontidae indet. (Fig. 2.14), and stethacanthid, as well as chondrichthyan scales of the ctenacanthid type, fragments of ptyctodontid and bothriolepid plates, struniiform teeth, osteolepiform scales, and actinopterygian teeth and scales. The fragments of placoderm plates, acanthodiform scales, fragments of struniiform scales, and scales of *Moythomasia* sp. were found in the Lower *Palmatolepis triangularis* CZ. A tooth of *Protacodus* sp., scales of the ctenacanthid type (Fig. 2.16), acanthodiform scales, fragments of struniiform scales, scales of *Mimipiscis* sp. were discovered in the Upper *Pa. triangularis* CZ. The fish remains from the Lower *Palmatolepis crepida* CZ include the chondrichthyan scales of the ctenacanthid and hybodontid types, acanthodiform scales, struniiform teeth, osteolepiform scales, and actinopterygian toothed plates. The tooth of cf. *Cladodoides* sp. (Fig. 2.17) was collected in the Uppermost *Pa. crepida* CZ.

### Conclusions

The fish assemblages from the Givetian–Famennian of the Middle Urals are taxonomically diverse and represented by widely distributed taxa. Among chondrichthyans, phoebodontids are dominant. Some taxa, such as *Diademodus*, *Wellerodus*, and *Mimipiscis*, were reported for the first time from the Urals. Data on the distribution of *Phoebodus* species in the Givetian–Frasnian of the Pokrovskoe section allow updating the boundary between the *Phoebodus sophiae* and *Ph. latus* phoebodontid zones [15]. The *Phoebodus sophiae* Zone corresponds to the Lower *Po. varcus*–*K. disparilis* CZ and the *Ph. latus* Zone to the Lower *M. falsovalis*–*Palmatolepis jamieae* CZ. The following phoebodontid zones can be recognized in the sections of the Middle Urals: *Phoebodus sophiae*, *Ph. latus*, *Ph. bifurcatus*, and *Ph. typicus*.

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ОРИГИНАЛЬНАЯ СТАТЬЯ

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**Комплексы рыб из среднего – верхнего девона  
Среднего Урала, Россия**

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**Аннотация**

Новые комплексы разнообразных рыб из живета – фамена описаны из шести разрезов Среднего Урала: Покровское, Баронская, Сулем, Першино, Йоква и Вильва. Представители *Diademodus*, *Wellerodus* и *Mimipiscis* впервые отмечены на Урале. Распространение видов *Phoebodus* в разрезе Покровское позволяет уточнить положение границы фободонтидных зон *Phoebodus sophiae* и *Ph. latus*. Полученные результаты свидетельствуют о том, что в разрезах Среднего Урала могут быть прослежены четыре фободонтидные зоны.

**Ключевые слова:** рыбы, девон, Средней Урал

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