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New Chondrichthyan Assemblages from the Upper Devonian–Carboniferous of Belarus

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Abstract—New chondrichthyan assemblages are described from the Frasnian (Upper Devonian)–Bashkirian (Carboniferous) of Belarus. Chondrichthyan remains are found for the first time in the Upper Frasnian Voronezhian Regional Stage; the Famennian Tonezhian, Tremlian, Turovian and Kalinovichian Regional Stages; the Viséan Mikhailovian Regional Stage; the Serpukhovian Sozhian and Yastrebkian Regional Stages; the Bashkirian Pripyatian Regional Stage. The most taxonomically diverse assemblages are recorded in the Famennian Petrikovian, Tournaisian Cherepetian, Serpukhovian Sozhian and Bashkirian Pripyatian Regional Stages. Ten chondrichthyan taxa have been never found earlier on the territory of Belarus.

Keywords: chondrichthyans, Devonian, Carboniferous, Belarus
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INTRODUCTION

First chondrichthyan assemblages had been reported from the Famennian–Viséan of Belarus by Esin and al. (2000). Those included Ctenacanthidae gen. 1, Ctenacanthidae gen. 3, Ctenacanthidae gen. indet., *Protacrodus* sp. nov. 1, *Ageleodus* sp.—from the Famennian Polessian Regional Stage; Ctenacanthidae gen. 1, Ctenacanthidae gen. 2, Ctenacanthidae gen. indet., *Listracanthus* sp.—from the Tournaisian Malevkian Regional Stage; Ctenacanthidae gen. indet.—from the Tournaisian Upian Regional Stage; *Protacrodus* sp. nov. 1, Ctenacanthidae gen. indet., *Listracanthus* sp.—from the Viséan Gostovian Regional Stage. The taxa were mentioned but neither described nor illustrated. Lebedev (2001) described a new species *Venustodus arcuatus* Lebedev, 2001 from the Upper Bashkirian of Petrikov 523 borehole.

The descriptions of diverse chondrichthyan microremains collected from 18 boreholes of the Emsian (Lower Devonian) to Lower Tournaisian (Lower Carboniferous) of Belarus are presented earlier by the authors (Ivanov, Plax, 2018). The teeth of phoebodontiforms *Phoebodus* cf. *typicus* Ginter et Ivanov, 1995, *Ph. turnerae* Ginter et Ivanov, 1992, *Ph.* sp., ctenacanthiforms *Tamiobatis elgae* Ivanov, 2018, *T.* sp.; *Cladodoides* cf. *wildungensis* (Jaekel, 1921); euselachians *Protacrodus aequalis* Ivanov, 1996, *P.* sp., Protacrodontidae indet.; chondrichthyans of uncertain systematic position *Karksiodus mirus* Ivanov et Märss, 2011 and *Ageleodus* sp.; and scales of various types were described there.

A result of study of the new chondrichthyan specimens of collected during the last five years from 18 boreholes from the Upper Frasnian, Upper Devonian–Bashkirian, Pennsylvanian, Carboniferous of Belarus are presented in this paper.

MATERIAL AND METHODS

The new chondrichthyan specimens were collected from four boreholes (Brinev 6, Knyshevichi 7, Krasnoselskaya 215, Ostashkovichi 2R) mentioned earlier (Ivanov, Plax, 2018) and from new 14 boreholes (Komarovka 91z/10, Kormyanskaya 4, Oktyabrskaya (Zelenkovichi) 30, Ostashkovichi 7R, Ostashkovichi 16R, Petrikov 12, Petrikov 364D, Petrikov 469, Rechitsa 18R, Rechitsa 19R, Starobin 1, Turov 1R, Zaozernaya 29-p, Zaozernaya 31-p). Komarovka 91z/10 borehole is located in the Volyn Monocline, all other boreholes in the Pripyat Trough (Fig. 1).

Studied chondrichthyan microremains were found in the Upper Frasnian Voronezhian Regional Stage; the Famennian Tonezhian, Tremlian, Turovian, Drozdovian, Petrikovian, and Kalinovichian Regional Stages; the Tournaisian Malevkian, Upian, and Cherepetian Regional Stages; the Viséan Mikhailovian Regional Stage; the Serpukhovian Sozhian and Yastrebkian Regional Stages; the Bashkirian Pripyat-

Fig. 1. Location map of the boreholes in Belarus in which studied chondrichthyan remains are recorded: (1) Komarovka 91z/10; (2) Turov 1R; (3) Petrikov 12; (4) Petrikov 469; (5) Brinev 6; (6) Petrikov 364D; (7) Starobin 1; (8) Oktyabrskaya (Zelenkovichi) 30; (9) Knyshevichi 7; (10) Kormyanskaya 4; (11) Ostashkovichi 2R; (12) Ostashkovichi 7R; (13) Ostashkovichi 16R; (14) Rechitsa 19R; (15) Rechitsa 18R; (16) Krasnoselskaya 215; (17) Zaozernaya 29-p; (18) Zaozernaya 31-p.

ian Regional Stage (Tables 1 and 2). The Devonian and Lower Carboniferous subdivisions of Belarus are presented in the last approved stratigraphic chart (*Stratigraficheskie Skhemy*,... 2010).

The microremains are represented by isolated teeth, tooth files, denticles and scales. They were extracted from limestone, marl and siltstone samples by 10% acetic acid, as well as from clay samples by washing in warm water.

The SEM images of the chondrichthyan microremains were prepared using the scanning electron microscope JSM-5610 LV (JEOL, Japan). Studied specimens are housed in the palaeontological collection of the Department of Mining, Belarusian National Technical University, Minsk.

CHONDRICHTHYAN DIVERSITY

Phoebodontiforms. Phoebodontiforms are represented by teeth of *Phoebodus bifurcatus* Ginter et Ivanov, 1992, *Ph. typicus* Ginter et Ivanov, *Ph.* cf. *turnerae* Ginter et Ivanov, *Ph.* sp., *Thrinacodus ferox* (Turner, 1982). The tooth of *Phoebodus bifurcatus* is reported from the Strelichevo Beds of the Voronezhian Regional Stage, Upper Frasnian of the Starobin 1 borehole. This tooth (Fig. 2.1) has a phoebodont crown with five ornamented cusps and cusplets, a typ-

Table 1. List of borehole and samples containing the described Late Devonian chondrichthyan remains

Name of borehole	Depth (m)	Stratigraphical level	Lithology
Starobin 1	867	Strelichevo B., Voronezhian R.S., U. Frasnian, U. Devonian	Limestone dark gray, platy
Rechitsa 19R	2264.87–2269.5	Tonezhian R.S., Zadonskian R.SS., L. Famennian, U. Devonian	Limestone gray, massive, lumpy
Turov 1R	3015.85–3022.25	Tonezhian R.S., Zadonskian R.SS., L. Famennian, U. Devonian	Limestone gray
Ostashkovichi 7R	2928–2931.3	Tonezhian R.S., Zadonskian R.SS., L. Famennian, U. Devonian	Limestone dark gray, massive, organogenic
Kormyanskaya 4	3480.9	Tonezhian R.S., Zadonskian R.SS., L. Famennian, U. Devonian	Limestone clayey gray, solid
Rechitsa 18R	2284.5–2290.5	Tremlian R.S., Zadonskian R.SS., L. Famennian, U. Devonian	Limestone gray, solid, massive
Petrikov 469	776.2	Tonezhian R.S., Zadonskian R.SS., L. Famennian, U. Devonian	Limestone gray, massive, dense
	769.2	Tremlian R.S., Zadonskian R.SS., L. Famennian, U. Devonian	Limestone gray, nodular
	743–747		Limestone light gray, platy
	546–551	Drozdovian R.S., Eletsian R.SS., L. Famennian, U. Devonian	Limestone gray, nodular
	394.7	Petrikovian R.S., L. Famennian, U. Devonian	Limestone gray, nodular
	284–289		
Knyshevichi 7	2081.7	Turovian R.S., Eletsian R.SS., L. Famennian, U. Devonian	Limestone gray, organogenic
	2060.3	Drozdovian R.S., Eletsian R.SS., L. Famennian, U. Devonian	Limestone light gray, organogenic
	2054.7		
	1989.9	Petrikovian R.S., L. Famennian, U. Devonian	Limestone gray, organogenic
	1968.8		
Ostashkovichi 2R	2634–2641	Drozdovian R.S., Eletsian R.SS., L. Famennian, U. Devonian	Limestone light gray, massive
	2630	Petrikovian R.S., L. Famennian, U. Devonian	Limestone dark gray to black, massive, platy
Brinev 6	446.7	Petrikovian R.S., L. Famennian, U. Devonian	Limestone light gray, platy
Krasnoselskaya 215	3176–3184	Petrikovian R.S., L. Famennian, U. Devonian	Limestone clayey dark gray
Ostashkovichi 16R	2742.2–2747.45	Petrikovian R.S., L. Famennian, U. Devonian	Limestone gray, organogenic
Petrikov 12	305.2–310	Velizhie B., Kalinovichian R.S., U. Famennian, U. Devonian	Clay gray, dense

Abbreviations: B.—Beds; Fm.—Formation; L.—Lower; M.—Middle; R.S.—Regional Stage; R.SS.—Regional Superstage; U.—Upper.

Table 2. List of borehole and samples containing the described Carboniferous chondrichthyan remains

Name of borehole	Depth, m	Stratigraphical level	Lithology
Petrikov 12	305.2–310	Velizhie B., Kalinovichian R.S., U. Famennian, U. Devonian	Clay gray, dense
	283.4–285	Malevkian R.S., L. Tournaisian, Mississippian. Carboniferous	Clay gray, dense, thin-bedded
	275–280	Upian R.S., L. Tournaisian, Mississippian. Carboniferous	Clay gray, dense, thin-bedded
	266–270	Slavinsk B., Cherepetian R.S, U. Tournaisian, Mississippian. Carboniferous	Siltstone clayey brown, dense
	261–266		Clay gray, dense
Petrikov 364D	252.5–252.3	L. Tournaisian, Mississippian. Carboniferous	Sandstone argillaceous greenish-gray, dense, fine-grained, carbonaceous
Oktyabrskaya (Zelenkovichi) 30	393 386.2 385	Maleshevo B., Cherepetian R.S, U. Tournaisian, Mississippian. Carboniferous	Limestone clayey light gray, gray and greenish-gray, thin-bedded
Komarovka 91z/10	336.7 335.9	Dregovichi Fm., Mikhailovian R.S, U. Viséan, Mississippian, Carboniferous	Limestone clayey brownish-gray, organogenic, dense
Zaozernaya 31-p	818 817 812	Sozhian R.S, L. Serpukhovian, Mississippian. Carboniferous	Limestone light gray Limestone clayey gray
	795	Yastrebkian R.S, U. Serpukhovian, Mississippian. Carboniferous	Limestone light gray
Zaozernaya 29-p	355.3 354.6	Dvizhki Fm., Pripyatian R.S., Bashkirian, Pennsylvanian, Carboniferous	Clay greenish-gray, dense

Abbreviations: B.—Beds; Fm.—Formation; L.—Lower; M.—Middle; R.S.—Regional Stage; R.SS.—Regional Superstage; U.—Upper.

ical bifurcated, arched base with extended linguo-lateral ends and prominent, oval apical button. The small tooth of *Phoebodus typicus* (Fig. 2.2) occurs in the Famennian Drozdovian Regional Stage of the Ostashkovichi 2p borehole, and possesses the pentacuspid phoebodont crown and the oval base with large apical button occupying almost all the occlusal surface. The incomplete,poorly preserved tooth of *Phoebodus* cf. *turnerae* was found in the Petrikovian Regional Stage, Famennian of the Krasnoselskaya 215 borehole. The incomplete tooth of *Phoebodus* sp. (Fig. 2.3) resembling the teeth of *Ph. rayi* Ginter et Turner, 1999 and *Ph. turnerae* was recorded in the Famennian Drozdovian Regional Stage of the Petrikov 469 borehole.

The tooth of *Thrinacodus ferox* occurs in the Tournaisian Maleshevo Beds, Cherepetian Regional Stage of the Oktyabrskaya (Zelenkovichi) 30 borehole. The tooth (Fig. 2.4) is typically asymmetrical, possesses the tricuspid crown with large distal and small mesial cusps. The cusps are inclined lingually and strongly curved. The central cusp is wider than the mesial cusp. The striations and lateral carina are preserved on the larger distal cusp. The tooth base is narrow, twisted, strongly elongated lingually, with displaced lingual depression and labio-basal thickness. The base bears the opening of the main vascular canal in the mid of the occlusal surface.

Bransonelliformes. The teeth of bransonelliforms belong to *Bransonella lingulata* Ivanov et Ginter, 1996 and *Bransonella nebraskensis* (Johnson, 1984). The tooth of *Bransonella lingulata* (Fig. 2.6) has been found in the Serpukhovian Sozhian Regional Stage of the Zaozernaya 31-p borehole, and the one of *B. nebraskensis* (Fig. 2.5)—in the Bashkirian Pripyatian Regional Stage of the Zaozernaya 29-p borehole. *Bransonella* teeth have a tricuspid diplodont crown and an oval, lingually extended base, with small notch at the lingual edge. The large lateral cusps are rounded in the cross section, the central cusp is flattened mesiodistally. All cusps bear robust cristae forming an inverted "V"-nested ornamentation on the labial surface of the crown. Cristae are straight, sometimes bifurcated. Tooth base of *B. nebraskensis* bears prominent, compact, oval apical button located centrally. The tooth base of *B. lingulata* possesses the large, drop-shaped apical button occupying almost all the

occlusal surface of the base and reaching to the lingual edge.

Symmoriiforms. The symmoriiform microremains include teeth of *Denaea* cf. *fournieri* Pruvost, 1922, *Denaea wangi* Wang, Jin, et Wang, 2004, *Denaea* sp., *Stethacanthus* sp., Falcatidae indet., as well as the buccopharyngeal denticles of Symmoriiformes indet. Teeth of *Denaea* cf. *fournieri* are reported from the Tournaisian Maleshevo Beds, Cherepetian Regional Stage of the Oktyabrskaya (Zelenkovichi) 30 borehole. Those possess the cladodont crown consisting of five cusps and cusplets (Figs. 2.7, 8). Cusps are rounded in cross section, recurved and inclined lingually, ornamented with straight and parallel cristae on labial and lingual faces. The tooth base is trapezoid in shape, elongated mesio-distally and lingually extended. The oval, compact apical button is located on the prominent central part of the base, and penetrated by large foramen of vascular canal.

The incomplete tooth of *Denaea wangi* (Fig. 2.10) from the Serpukhovian Sozhian Regional Stage of the Zaozernaya 31-p borehole has a cladodont crown with smooth cusps and cusplets, and an asymmetrical triangular base. The incomplete and abraded tooth of *Denaea* sp. (Fig. 2.9) collected from the Tournaisian Maleshevo Beds, Cherepetian Regional Stage of the Oktyabrskaya (Zelenkovichi) 30 borehole possesses wide and high central cusp in the crown, triangular base with a small round apical button, and is rather similar to those of *D. williamsi* Ginter et Hansen, 2010.

The fragmentary teeth of *Stethacanthus* sp. (Figs. 2.12, 13) have been collected from the Famennian Tonezhian Regional Stage of the Turov 1R borehole and from the Bashkirian Pripyatian Regional Stage of the Zaozernaya 29-p borehole. A peculiar tooth of Falcatidae indet. (Fig. 2.11) occurs in the Famennian Tonezhian Regional Stage of the Rechitsa 19R borehole. This specimen possesses the tricuspid cladodont crown with smooth cusps bearing the distinct lateral carina. The central cusp is slightly higher than the lateral cusps. The tooth base is trapezoidal in shape, lacking the apical button and labio-basal projection on the occlusal and basal faces. The occlusal surface is penetrated by a large foramen of vascular canal located in the shallow median depression. This tooth resembles those of the falcatid *Stethacanthulus* but the latter has a triangular median depression extended at the lingual rim on the occlusal face and an arched transverse prominence located on the basal face and surrounded by two lateral depressions from each side (Ivanov et al., 2021).

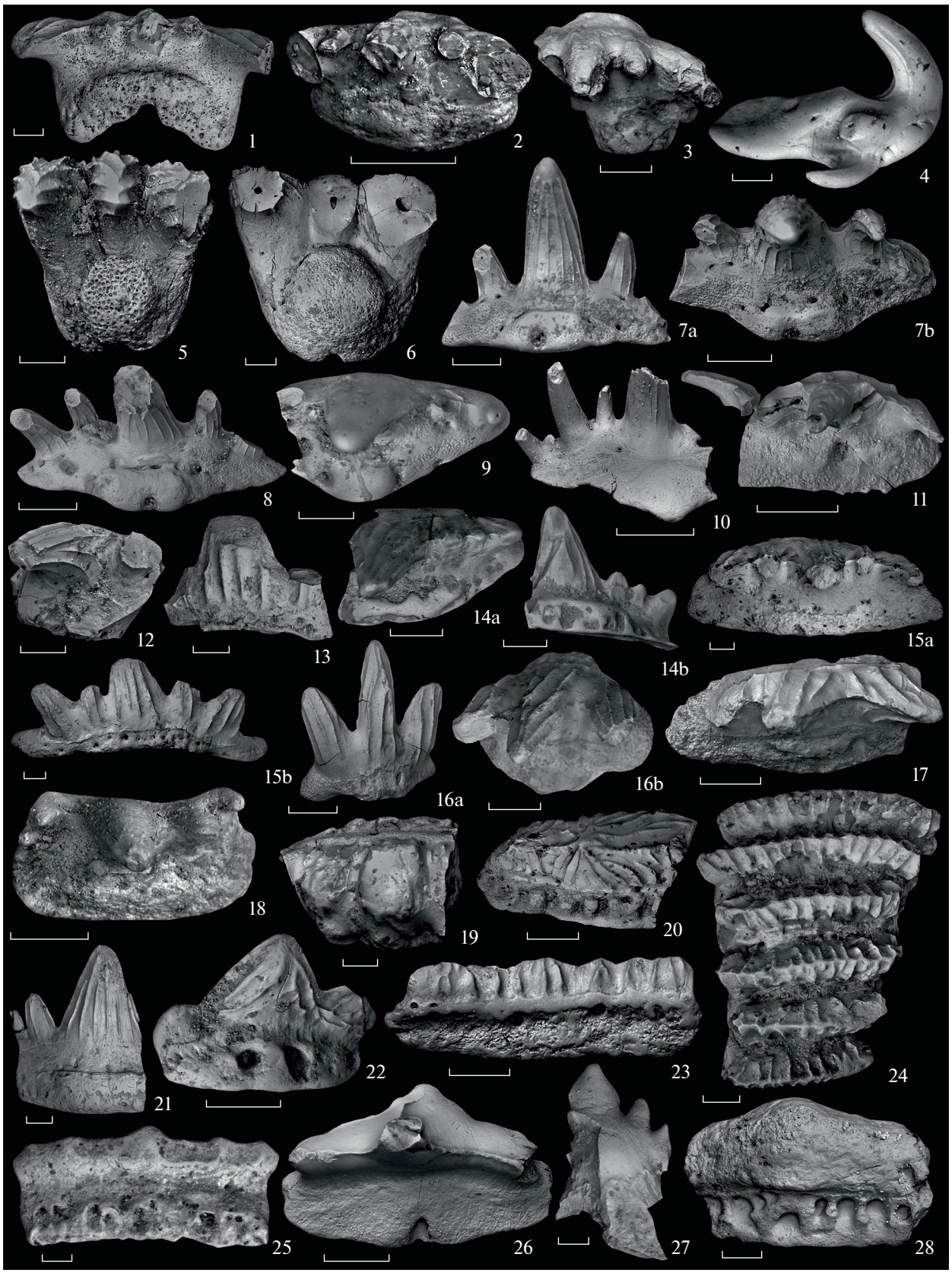
The buccopharyngeal denticles of symmoriiforms belong to *Stemmatias* type and their crowns bear a single or double rows of cusps (Figs. 3.1, 2). The crown includes the acuminate, recurved cusps, which consecutively overlap each other and increasing in size posteriorly. These denticles occur in the Serpukhovian Sozhian Regional Stage of the Zaozernaya 31-p borehole, and in the Bashkirian Pripyatian Regional of the Zaozernaya 29-p borehole. The similar buccopharyngeal denticles were described in several symmoriiform taxa, such as *Cobelodus* (Zangerl and Case, 1976), *Stethacanthus* (Coates and Sequeira, 2001), *Stethacanthulus* and *Symmorium* (Williams, 1985).

Ctenacanthiforms and Other Cladodontomorphs. The ctenacanthiform microremains include teeth of two different morphotypes. The tooth of Ctenacanthiformes indet. A (Fig. 2.16) has been found in the Famennian Tonezhian Regional Stage of the Petrikov 469 borehole, and possesses the tricuspid cladodont crown and the round base with weakly noticeable apical button and labio-basal projection. The labial face of the crown is ornamented by robust cristae bifurcating on the large central cusp. This tooth resembles the tricuspid teeth of Ctenacanthus terrelli (Newberry, 1889) but the latter has a prominent apical button and distinct, wide labiobasal projection (Ginter, 2010, fig. 3E, F). The tooth of Ctenacanthiformes indet. B (Fig. 2.17) was collected from the Famennian Petrikovian Regional Stage of the Ostashkovichi 16p borehole. It is elongated mesio-distally and flattened labio-lingually, has a cladodont crown with three cusps connected by distinct lateral carina. The cusp ornamentation consists of robust, straight cristae. The tooth base isshort lingually and bears a narrow apical button.

The teeth of a cladodontomorph *Cladodoides* sp. (Figs. 2.14, 15) occur in the Famennian Tremlian Regional Stage of the Petrikov 469 borehole, as well as in the Tournaisian Malevkian and Cherepetian Regional Stages of the Petrikov 12 borehole. These teeth possess the cladodont crown with high and wide central and moderate lateral cusps, as well as small intermediate cusplets. The tooth base is trapezoidal or lanceolate in shape, extended mesio-distally, with elongated and narrow apical button placed at the lingual rim. These teeth differ from those of *C.* cf. *wildungensis* (Jaekel, 1921) described from the Malevkian Regional Stage of Belarus (Ivanov, Plax, 2018) by its narrow apical button and weakly developed labiobasal projection.

The slightly abraded peculiar cladodont tooth (Fig. 2.18) has been found in the Bashkirian Pripyatian Regional Stage of the Zaozernaya 29-p borehole. In this tooth the cusps and cusplets are smooth, the subrectangular base bears a wide labial depression and an oval apical button with poorly defined edges. Some cusplets are irregularly displaced lingually. This tooth resembles some squatinactiform teeth, such as *Squatinactis glabrum* (Ginter, 1999), *S. multicuspidatus* Ivanov, 2023, *S.* sp. (Ivanov, 1996; Ginter, 1999; Ivanov et al., 2023) and is attributed here to Squatinactiformes indet.

Euselachians. The euselachian microremains are represented by teeth of Protacrodontidae indet. A, Protacrodontidae indet. B, *Sphenacanthus* sp., *Reeso-*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dus sp., Hybodontiformes indet. A, Hybodontiformes indet. B, and a tooth file of cf. *Dalmehodus* sp. The fragmentary tooth of Protacrodontidae indet. A (Fig. 2.19) from the Famennian Tremlian Regional Stage of the Petrikov 469 borehole has a crown with a rounded cusp and a labial row of accessory cusplets. Such crown type is typical for the protacrodontid *Deihim mansureae* Ginter, Hairapetian and Klug, 2002 (Ginter et al., 2002, 2010). An incomplete tooth of Protacrodontidae indet. B (Fig. 2.20) was collected from the Bashkirian Pripyatian Regional Stage of the Zaozernaya 29-p borehole, and possesses a pyramidal crown with low conical cusps ornamented by coarse ridges diverging from the cusp apex, and the distinct occlusal crest traced between cusps.

A well-preserved euselachian tooth file (Fig. 2.24) has been found in the Famennian Petrikovian Regional Stage of the Petrikov 469 borehole. This specimen includes six teeth fused by their bases and separated crowns. The monolithic crowns increase mesio-distally, and bear a slightly wavy, prominent occlusal crest. Coarse ridges diverge from the crest forming poorly defined cusps. The protacrodontid *Dalmehodus turnerae* Long et Hairapetian, 2000 was described by three isolate teeth from the Famennian of Iran possessing the crown with no prominent central cusp (Long, Hairapetian, 2000). However, the cusps in the type specimens are separated by notches and rather strongly fused basally. Later several authors (Hairapetian, Ginter, 2009; Ginter et al., 2011) illustrated the teeth of *D. turnerae* possessing more monolithic crown with very shallow notches between the distinct cusps and the tooth file with two crowns and fused bases (Ginter et al., 2011, text-Fig. 10H). The cusps in the tooth file described here are not developed. This protacrodontid tooth file is assigned to cf. *Dalmehodus* sp.

The tooth of *Sphenacanthus* sp. (Fig. 2.24) originates from the Tournaisian Cherepetian Regional Stage of the Oktyabrskaya (Zelenkovichi) 30 borehole, and is characterized by protacrodont crown and euselachian-type base. The crown is composed of pyramidal cusps ornamented by coarse ridges. The central cusp is slightly wider than the others. The cusps are separated by shallow notches. The ridges are straight or diverge towards the base. The tooth is similar to some teeth of *Sphenacanthus delepinei* Fournier et Pruvost, 1928 and *S. tenuis* Ginter, 2016 (Fournier, Pruvost, 1928; Ivanov, Derycke, 2005; Ginter, 2016).

Fig. 2. Chondrichthyan teeth from the Upper Devonian–Carboniferous of Belarus in occlusal (1–3, 5, 6, 9, 11, 14a, 15a, 16b, 17–20, 24, 26, 28), lingual (7, 10, 14b, 21, 22, 25), labial (13, 15b, 16a, 23, 27), oblique lingual (7b, 8), and oblique occlusal (12) views. (1) *Phoebodus bifurcatus* Ginter et Ivanov, 1992; 155/1-1, Starobin 1 borehole, depth 867 m, Strelichevo Beds, Voronezhian Regional Stage, Upper Frasnian, Upper Devonian. (2) *Phoebodus typicus* Ginter et Ivanov, 1995; 99/27-5a, Ostashkovichi 2R borehole, depth 2634–2641 m, Drozdovian Regional Stage, Famennian, Upper Devonian. (3) *Phoebodus* sp.; 164/75b-1, Petrikov 469 borehole, depth 546–551 m, Drozdovian Regional Stage, Famennian, Upper Devonian. (4) *Thrinacodus ferox* (Turner, 1982); 98/4g-8, Oktyabrskaya (Zelenkovichi) 30 borehole, depth 393 m, Maleshevo Beds, Cherepetian Regional Stage, Tournaisian, Mississippian, Carboniferous. (5) *Bransonella nebraskensis* (Johnson, 1984); 162/28-20, Zaozernaya 29-p borehole, depth 354.6 m, Dvizhki Formation, Pripyatian Regional Stage, Bashkirian, Pennsylvanian, Carboniferous. (6) *Bransonella lingulata* Ivanov et Ginter, 1996: 105/35-1, Zaozernaya 31-p borehole, depth 812 m, Sozhian Regional Stage, Serpukhovian, Mississippian, Carboniferous. (7, 8) *Denaea* cf. *fournieri* Pruvost, 1922; Oktyabrskaya (Zelenkovichi) 30 borehole, depth 385 m, Maleshevo Beds, Cherepetian Regional Stage, Tournaisian, Mississippian, Carboniferous: 7, 98/4-1, 8, 98/4-3. (9) *Denaea* sp.; 98/4g-7, Oktyabrskaya (Zelenkovichi) 30 borehole, depth 393 m, Maleshevo Beds, Cherepetian Regional Stage, Tournaisian, Mississippian, Carboniferous. (10) *Denaea wangi* Wang, Jin, et Wang, 2004; 105/38-5, Zaozernaya 31-p borehole, depth 817 m, Sozhian Regional Stage, Serpukhovian, Mississippian, Carboniferous. (11) Falcatidae indet.; 152/26-1, Rechitsa 19R borehole, depth 2264.87–2269.5 m, Tonezhian Regional Stage, Famennian, Upper Devonian. (12, 13) *Stethacanthus* sp.; 12, 162/28-21, Zaozernaya 29-p borehole, depth 354.6 m, Dvizhki Formation, Pripyatian Regional Stage, Bashkirian, Pennsylvanian, Carboniferous; (13) 146/38-1, Turov 1R borehole, depth 3015.85–3022.25 m, Tonezhian Regional Stage, Famennian, Upper Devonian. (14, 15) *Cladodoides* sp.: 14, 62/40-2b, Petrikov 12 borehole, depth 283.4–285 m, Malevkian Regional Stage, Tournaisian, Mississippian, Carboniferous; (15) 164/118-1, Petrikov 469 borehole, depth 769.2 m, Tremlian Regional Stage, Famennian, Upper Devonian. (16) Ctenacanthiformes indet. A; 164/119-1, Petrikov 469 borehole, depth 743–747 m, Tremlian Regional Stage, Famennian, Upper Devonian. (17) Ctenacanthiformes indet. B; 150/18-1, Ostashkovichi 16R borehole, depth 2742.2–2747.45 m, Petrikovian Regional Stage, Famennian, Upper Devonian. (18) Squatinactiformes indet.; 162/28-22, Zaozernaya 29-p borehole, depth 354.6 m, Dvizhki Formation, Pripyatian Regional Stage, Bashkirian, Pennsylvanian, Carboniferous. (19) Protacrodontidae indet. A; 164/113-2, Petrikov 469 borehole, depth 743–747 m, Tremlian Regional Stage, Famennian, Upper Devonian. (20) Protacrodontidae indet. B; 162/29-4, Zaozernaya 29-p borehole, depth 355.3 m, Dvizhki Formation, Pripyatian Regional Stage, Bashkirian, Pennsylvanian, Carboniferous. (21) Hybodontiformes indet. A; 62/45-10a, Petrikov 12 borehole, depth 266–270 m, Slavinsk Beds, Cherepetian Regional Stage, Tournaisian, Mississippian, Carboniferous. (22) Hybodontiformes indet. B; 98/4g-3, Oktyabrskaya (Zelenkovichi) 30 borehole, depth 393 m, Maleshevo Beds, Cherepetian Regional Stage, Tournaisian, Mississippian, Carboniferous. (23) *Sphenacanthus* sp., 98/4b-2, Oktyabrskaya (Zelenkovichi) 30 borehole, depth 386.2 m, Maleshevo Beds, Cherepetian Regional Stage, Tournaisian, Mississippian, Carboniferous. (24) cf. *Dalmehodus* sp., 164/46a-1, Petrikov 469 borehole, depth 394.7 m, Petrikovian Regional Stage, Famennian, Upper Devonian. (25) *Reesodus* sp.; 79/3-2, Komarovka 91z/10 borehole, depth 336.7 m, Dregovichi Formation, Mikhailovian Regional Stage, Viséan, Mississippian, Carboniferous. (26) *Cooleyella fordi* (Duffin et Ward, 1983); 105/38-3, Zaozernaya 31-p borehole, depth 817 m, Sozhian Regional Stage, Serpukhovian, Mississippian, Carboniferous. (27) Petalodontiformes indet.; 79/2-1s, Komarovka 91z/10 borehole, depth 335.9 m, Dregovichi Formation, Mikhailovian Regional Stage, Viséan, Mississippian, Carboniferous. (28) Helodontiformes indet.; 105/39-2, Zaozernaya 31-p borehole, depth 818 m, Sozhian Regional Stage, Serpukhovian, Mississippian, Carboniferous. Scale bars: (1–19, 22–28) 200 μm, (20, 21) 500 μm.

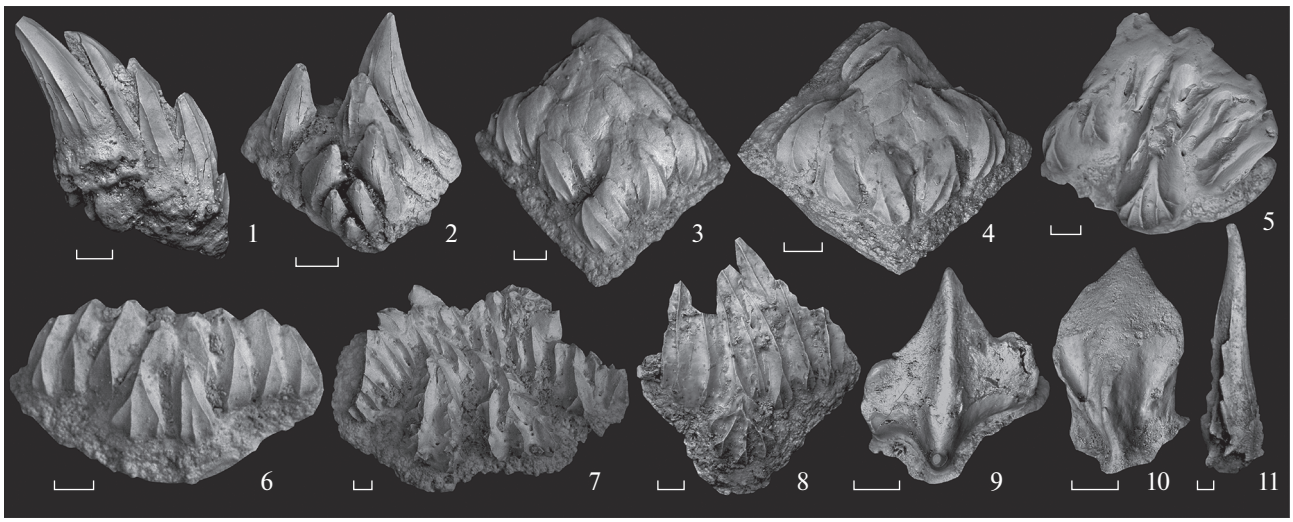

Fig. 3. Chondrichthyan buccopharyngeal denticles (1, 2) and scales (3–11) from the Upper Devonian–Carboniferous of Belarus in lateral (1, 11), crown (2–8) and anterior (9, 10) views. (1, 2) Symmoriiformes indet. (*Stemmatias* type): (1) 105/39-1, Zaozernaya 31-p borehole, depth 818 m, Sozhian Regional Stage, Serpukhovian, Mississippian, Carboniferous; (2) 162/28-12, Zaozernaya 29-p borehole, depth 354.6 m, Dvizhki Formation, Pripyatian Regional Stage, Bashkirian, Pennsylvanian, Carboniferous. (3, 4) *Cladolepis* type, Petrikov 469 borehole, depth 284–289 m, Petrikovian Regional Stage, Famennian, Upper Devonian: (3) 164/28-2, (4) 164/28a-1. (5–8) Ctenacanthid type: (5) 62/45-10f, Petrikov 12 borehole, depth 266–270 m, Slavinsk Beds, Cherepetian Regional Stage, Tournaisian, Mississippian, Carboniferous; (6, 7) Petrikov 469 borehole, depth 284–289 m, Petrikovian Regional Stage, Famennian, Upper Devonian: (6) 164/28-3, (7) 164/28-1; (8) 97/1a-2, Brinev 6 borehole, depth 446.7 m, Petrikovian Regional Stage, Famennian, Upper Devonian. (9, 10) Euselachian type, Zaozernaya 31-p borehole, depth 817 m, Sozhian Regional Stage, Serpukhovian, Mississippian, Carboniferous: 9, 105/38-1, 10, 105/38-4. (11) Hybodontid type, 162/28-4, Zaozernaya 29-p borehole, depth 354.6 m, Dvizhki Formation, Pripyatian Regional Stage, Bashkirian, Pennsylvanian, Carboniferous. Scale bars: 100 μm.

An incomplete tooth of Hybodontiformes indet. A (Fig. 2.21) from the Tournaisian Cherepetian Regional Stage of the Petrikov 12 borehole has a large conical central and small intermediate cusps separated by deep notches and ornamented with straight cristae on the labial and lingual faces. The tooth base bears a ridge-like apical button. The tooth resembles some morphotype of hybodontid *Ossianodus* (Ginter, 2016) but differs in the presence of an apical button.

A tooth attributed to Hybodontiformes indet. B (Fig. 2.22) from the Cherepetian Regional Stage of the Oktyabrskaya (Zelenkovichi) 30 borehole has a pyramidal, labio-lingually flattened crown with three wide cusps and a distinct lateral carina. The large central cusp is dominant. The cusps are ornamented by curved ridges richly branching towards the base. The tooth base is penetrated by two large foramina of vascular canals. The tooth is similar to the teeth of *Lamarodus* but in the latter the crown is labio-lingual flattened and the lateral cusps are high (Ivanov et al., 2020).

The slightly abraded tooth of a lonchidiid *Reesodus* sp. (Fig. 2.25) has been found in the Viséan Mikhailovian Regional Stage of the Komarovka 91z/10 borehole. The tooth is characterized by monolithic crown consisting of a slightly prominent central cusp and small others of same sizes. The tooth base is rectangular in shape, and perforated by numerous foramina of vascular canal. The tooth resembles some teeth of *Reesodus wirksworthensis* (Duffin, 1985) (Duffin, 2001; Habibi, Ginter, 2011).

Neoselachians. The typically anachronistid tooth of *Cooleyella fordi* (Duffin et Ward, 1983) from the Serpukhovian Sozhian Regional Stage of the Zaozernaya 31-p borehole (Fig. 2.26) possesses the crown with the occlusal crest separating the short lingual face from the extended, sloping labial face; the prominent central cusp; the labial flange, the lateral blades and deeply incised crown/base junction. The tooth base bears a rounded basal tubercle placed under the flange; the foramen of vascular canal opens at the lingual rim. A tiny, wavy ridge running from the central cusp to the labial flange is unknown in *C. fordi* teeth (Duffin, Ward, 1983; Ivanov et al., 2014).

Euchondrocephalians. The euchondrocephalian remains include teeth of Petalodontiformes indet. and Helodontiformes indet. An incomplete small petalodontid tooth (Fig. 2.27) from the Viséan Mikhailovian Regional Stage of the Komarovka 91z/10 borehole has a flat crown with triangular large central and small lateral cusps separated by deep notches, and an arched basally directed base. This tooth slightly resembles those of *Peripristis* and *Pristodus* (Ginter et al., 2010).

In an abraded tooth attributed to Helodontiformes indet. (Fig. 2.28) collected from the Serpukhovian

Sozhian Regional Stage of the Zaozernaya 31-p borehole the crown is elongated mesio-distally, bears a prominent central part, and a lingually extended and arched base perforated by numerous large foramina of vascular canals.

Chondrichthyan scales. Chondrichthyan scales belong to ctenacanthid-, hybodontid-, euselachian- and *Cladolepis*- types. Rare scales referred to *Cladolepis*-type (Figs. 3.3, 4) are recorded in the Famennian Petrikovian Regional Stage of the Petrikov 469 borehole. The hybodontid-type scales are recorded from the Famennian Kalinovichian Regional Stage of the Petrikov 12 borehole, the Tournaisian Cherepetian Regional Stage of the Petrikov 12 borehole; the Bashkirian Pripyatian Regional Stage of the Zaozernaya 29-p borehole.

Abundant ctenacanthid type scales (Figs. 3.5–8) are recorded from the Famennian Tonezhian, Tremlian, Turovian, Drozdovian, Petrikovian, and Kalinovichian Regional Stages; the Tournaisian Malevkian, Upian, and Cherepetian Regional Stages; the Serpukhovian Yastrebkian Regional Stage; and the Bashkirian Pripyatian Regional Stage of many boreholes. Euselachian type scales are reported from the Serpukhovian Sozhian Regional Stage of the Zaozernaya 31-p borehole and the Bashkirian Pripyatian Regional Stage of the Zaozernaya 29-p borehole.

DISCUSSION

Chondrichthyan Assemblages

Phoebodus bifurcatus occurs in the Strelichevo Beds of the Voronezhian Regional Stage (Upper Frasnian). An assemblage from the Famennian Tonezhian Regional Stage includes *Stethacanthus* sp., Falcatidae indet., Ctenacanthiformes indet. A. *Cladodoides* sp., Ctenacanthiformes indet. A, Protacrodontidae indet. A occur in the Famennian Tremlian Regional Stage. The Turovian Regional Stage contains only the ctenacanthid type scale. The assemblage from the Famennian Drozdovian Regional Stage comprises *Phoebodus typicus* and *Phoebodus* sp. Abundant chondrichthyans from the Famennian Petrikovian Regional Stage comprise *Phoebodus* cf. *turnerae,* Ctenacanthiformes indet. B, and cf. *Dalmehodus* sp. Rare remains from the Famennian Kalinovichian Regional Stage include ctenacanthid and hybodontid type scales, undetermined chondrichthyan scale.

In the Lower Carboniferous the chondrichthyan microremains have been found in three levels referred to the Tournaisian Stage: the tooth of *Cladodoides* sp. and ctenacanthid type scales in the Malevkian Regional Stage; ctenacanthid type scales in the Upian Regional Stage; the teeth of *Thrinacodus ferox*, *Denaea* cf. *fournieri*, *Denaea* sp., *Cladodoides* sp., *Sphenacanthus* sp., Hybodontiformes indet. A, Hybodontiformes indet. B, ctenacanthid and hybodontid type scales, as well as an undetermined chondrichthyan scale in the Cherepetian Regional Stage. *Reesodus* sp. and Petalodontiformes indet. ooccur in the Viséan Mikhailovian Regional Stage. The diverse assemblage from the Serpukhovian Sozhian Regional Stage contains *Bransonella lingulata*, *Denaea wangi*, *Cooleyella fordi,* Helodontiformes indet., Symmoriiformes indet. A ctenacanthid type scale was collected only from the Serpukhovian Yastrebkian Regional Stage.

Abundant chondrichthyan microremains from the Bashkirian Pripyatian Regional Stage include the teeth of *Bransonella nebraskensis*, *Stethacanthus* sp., Squatinactiformes indet., Protacrodontidae indet. B, symmoriiform denticles, ctenacanthid, hybodontid and euselachian type scales.

Distribution of Chondrichthyans Taxa

The phoebodontiform *Phoebodus bifurcatus* is known from the Upper Frasnian (*rhenana–linguiformis* conodont zones) of Australia; China; Mauritania; Iran; Poland; Czech Republic; Belgium; Utah, USA; South Timan, Central Devonian Field, Middle and South Urals, Kuznetsk Basin, Gorny Altay in Russia (Ivanov, 2021). *Ph. typicus* occurs in the Lower and Middle Famennian (Lower *triangularis*–Uppermost *marginifera* conodont zones) of Australia, Morocco, Iran, Armenia and Belarus; North Timan, Middle and South Urals, Kuznetsk Basin of Russia (Ivanov, 2020, 2021). *Thrinacodus ferox* was reported from the Famennian (*expansa* conodont Zone)–Late Viséan of Australia, southern China, Iran, Morocco, Armenia, Poland, Germany, France, Belgium, England, Ireland, Utah (USA); Moscow Syneclise, South and Middle Urals, Timan-Pechora Province, Kuznetsk Basin of Russia, (Ginter et al., 2010; Ivanov, Lucas, 2011; Ivanov, 2022).

The bransonelliform *Bransonella lingulata* has been found in the Viséan–Bashkirian of the Moscow Region, South Urals and Kuznetsk Basin of Russia; Middle to Upper Pennsylvanian of Arizona, New Mexico and Oklahoma of USA (Ivanov, Lucas, 2019). *Bransonella nebraskensis* was recorded in the Viséan–Sakmarian of England, Belgium, Poland, Colombia, Arizona, Kansas, Nebraska and Oklahoma of USA; the Nearpolar and South Urals, Kaluga and Moscow regions, and Kuznetsk Basin of Russia (Ivanov, Lucas, 2019; Botella et al., 2020).

The symmoriiform *Denaea fournieri* was described from the Viséan of Belgium (Fournier and Pruvost, 1928), but *Denaea* cf. *fournieri* was also found in the Viséan–Serpukhovian of England, Germany, Poland, China; South Urals and Kuznetsk Basin of Russia (Ivanov et al., 2023). *Denaea wangi* was reported from the Viséan–Kasimovian of Belgium, Poland, China; Montana, USA; Samara Region and South Urals, Russia (Ivanov et al., 2023).

The neoselachian *Cooleyella fordi* occurs in the Viséan–Artinskian of Belgium, England, Ohio of

Global Stage	Regional Stage	Chondrichthyans
Bashkirian	Zaozerian	***Bransonella nebraskensis*, *Stethacanthus* sp., Symmoriiformes indet. (*Stemmatias* type denticles), Squatinactiformes indet., Protacrodontidae indet. B, ctenacanthid, euselachian and hybodontid type scales**
	Pripyatian	
	Khoinikian	
Serp.	Yastrebkian	**Ctenacanthid type scale**
	Sozhian	***Bransonella lingulata*, *Denaea wangi*, Symmoriiformes indet. (*Stemmatias* type denticles), *Cooleyella fordi*, Helodontiformes indet., euselachian type scales**
Viséan	Venevian	
	Mikhailovian	***Reesodus* sp., Petalodontiformes indet.**
	Aleksinian	
	Tulian	
	Bobrikian	
	Gostovian	
Tournaisian	Kizelovskian	***Thrinacodus ferox*, *Denaea* cf. *fournieri*, *D.* sp., *Cladodoides* sp., *Protacrodus* sp., *Sphenacanthus* sp., Hybodontiformes indet. A and B; ctenacanthid and hybodontid type scales, chondrichthyan scale**
	Cherepetian	
	Upian	*Tamiobatis* sp., *Cladodoides* cf. wildungensis, *Protacrodus* sp.; **ctenacanthid**, hybodontid, euselachian and *Ohiolepis* type scales
	Malevkian	*Tamiobatis elgae*, *Cladodoides* cf. *wildungensis*, ***C.* sp.,** *Protacrodus* sp., Protacrodontidae indet.; **ctenacanthid,** hybodontid and *Ohiolepis* type scales
Famennian	Kalinovichian	**Ctenacanthid and hybodontid type scales, chondrichthyan scale**
	Borovian	*Tamiobatis elgae*, *T.* sp., *Protacrodus aequalis*, *Ageleodus* sp.; ctenacanthid and euselachian type scales
	Stvigian	
	Starobinian	Euselachian type scales
	Streshinian	
	Oressian	
	Lebedyanian	*Phoebodus turnerae*, ***Ph.* cf. *turnerae***, *Ph.* cf. *typicus*, **Ctenacanthiformes indet. *B***, *Protacrodus aequalis*; **cf. *Dalmehodus* sp.,** ctenacanthid, protacrodontid and ***Cladolepis*** type scales, **chondrichthyan scale**
	Petrikovian	
	Drozdovian	***Phoebodus typicus*, *Ph.* sp., ctenacanthid** and protacrodontid type scales
	Turovian	**Ctenacanthid type scales**
	Vishanian	
	Tremlian	***Cladodoides* sp., Protacrodontidae indet. A, ctenacanthid type scale**
	Tonezhian	***Stethacanthus* sp., Falcatidae indet., Ctenacanthiformes indet. A, ctenacanthid type scales, chondrichthyan scale**
	Kuzmichian	*Phoebodus* cf. *typicus*
	Domanovichian	

Fig. 4. Distribution of chondrichthyan taxa in the Upper Devonian–Carboniferous of Belarus. Abbreviation: Serp.—Serpukhovian.

USA), Urals and Moscow Syneclise of Russia (Ivanov, 2011).

CONCLUSIONS

The chondrichthyan remains were found for first time in the Upper Frasnian Voronezhian Regional Stage; the Famennian Tonezhian, Tremlian, Turovian and Kalinovichian Regional Stages; the Viséan Mikhailovian Regional Stage; the Serpukhovian Sozhian and Yastrebkian Regional Stages; the Bashkirian Pripyatian Regional Stage. In respect to previously published data (Ivanov, Plax, 2018) the most taxonomically diverse assemblages are reported from the Famennian Petrikov, Tournaisian Cherepetian, Serpukhovian Sozhian and Bashkirian Pripyatian Regional Stages (Fig. 4). *Phoebodus bifurcatus, Thrinacodus ferox, Bransonella nebraskensis, B. lingulata, Denaea* cf. *fournieri, Denaea wangi, Stethacanthus*, *Sphenacanthus, Reesodus, Cooleyella fordi* have been never found earlier on the territory of Belarus.

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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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