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# Middle Devonian actinopterygians from Lithuania and Belarus

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**Abstract:** In the Baltic States and Belarus, the Middle Devonian period is characterised by an abundant fossil record of invertebrates such as scolecodonts, brachiopods, ostracods, trilobites, bivalves, crinoids, gastropods, and tentaculites. On the other hand, there was limited diversity in the conodont and other vertebrate fauna. In this study, we introduce a newly refined ichthyofaunal assemblage from the Eifelian and Givetian epochs from the present-day regions of Belarus and Lithuania. The isolated scales of *Cheirolepis* are identified as *C. gaugeri*, *C.* cf. *gaugeri*, *C. aleshkai*, *C.* cf. *aleshkai*, and *Cheirolepis* sp., while *Orvikuina* is represented by the isolated scales of *O. vardiaensis* and *Orvikuina* sp. The histological analyses for the scales of *Orvikuina* are provided here. Moreover, *Orvikuina* and *Cheirolepis* taxa are now recognised to be widely distributed throughout the Baltic States, especially Lithuania and Belarus, as a result of these findings. Thus, this ichthyofaunal data markedly improved the biostratigraphic correlation within the study region and expanded the paleogeographic distribution of these taxa during the Eifelian and Givetian time in Laurasia.

**Keywords:** *Cheirolepis*; *Orvikuina*; scales; histology; Eifelian; Givetian; biostratigraphy; palaeogeography

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## 1. Introduction

The Devonian period is known as one of the most transformative episodes in the history of the biosphere [1]. In particular, the Middle Devonian period saw significant evolutionary changes in aquatic ecology. Placoderms were the predominant inhabitants of the oceans, signalling a major biotic dispersal event between the southern and northern supercontinents [1]. This biotic dispersal event also influenced other fish groups, such as the actinopterygians from eastern Laurasia, that are the focus of this research.

Middle Devonian rocks are extensively distributed in the territories of the Baltic States and Belarus [2,3]. These rocks comprised a diversity in lithology and facies characteristics [3,4]. The Aruküla, Burtnieki, and Gauja Stages comprise the Givetian Stage, while the Pärnu and Narva Regional Stages are part of the Eifelian Stage (see Figure 1). In contrast, the Adrov, Osveya, Gorodok, and Kostyukovichi Formations define Belarus Eifelian. Together with the Ubort Formation, the Polotsk Formation (which includes the Goryn, Stolin, and Moroch Subformations) represents the Givetian in Belarus (Figure 1).

Sorokin (1981) [5], Valiukevičius et al. (1986) [6], Kurss (1992) [7], Lyarskaya and Lukševičs (1992) [8], Valiukevičius (1994) [9], Kleesment (1994, 1995) [9,10], Kleesment and Mark-Kurik (1997) [11], Mark-Kurik (2000) [12], Šečkus (2000) [13], Märss et al. (2008) [14], Ivanov et al. (2011) [15], and Plax (2008, 2020, and 2022) [4,16,17] had previously studied the Middle Devonian ichthyofauna across the Baltic States (Estonia, Latvia, and Lithuania) and Belarus. In Lithuania, less research has been carried out on the Devonian ichthyofauna than in Estonia, Latvia, or Belarus. Therefore, the discovery of a new assemblage of Eifelian and Givetian actinopterygians will fill the gap in the area under study (Figure 2). One of the oldest actinopterygian genus for which the full skeleton is known is *Cheirolepis*, whose species was discovered by isolated material in the examined area here. Moreover, the majority of the *Orvikuina* material that is known from this genus in actinopterygians is what is provided here by isolated scales. This fish assemblage consists of *Cheirolepis gaugeri*, *C.* cf. *gaugeri*, *C. aleshkai*, *C.* cf. *aleshkai*, *Cheirolepis* sp., *Orvikuina vardiaensis*, and *Orvikuina* sp. (Figures 3–6). The histological examination of the *Orvikuina* taxon is provided (Figures 5 and 6). Moreover, we present a biostratigraphic correlation based on identified actinopterygian taxa for Lithuania and Belarus (Figure 7). Additionally, the species-level patterns of the ichthyofaunal assemblage from the area enhance our comprehension of the paleogeography of Middle Devonian actinopterygians in Laurasia.

## 2. Geological Settings

The Middle Devonian stratigraphic column is divided into the lower, middle, and upper segments of the Eifelian and Givetian Global Stages. The division within the Baltic States further categorises the Eifelian Stage into the Pärnu and Narva Regional Stages and the Givetian Stage into the Aruküla, Burtnieki, and Gauja Regional Stages. Meanwhile, the Amata Regional Stages is part of the lower Frasnian Stage. In contrast, Belarus's stratigraphy for the Eifelian encompasses the Adrov, Osveya, Gorodok, and Kostyukovichi Regional Stages, while the Givetian comprises the Goryn, Stolin, and Moroch Beds of the Polotsk Regional Stage, alongside the Ubort Regional Stage. Additionally, the Zhelon Regional Stage's deposits are identified with the Lower Frasnian, aligning with the research by Obukhovskaya et al. (2010) [18] (Figure 1).

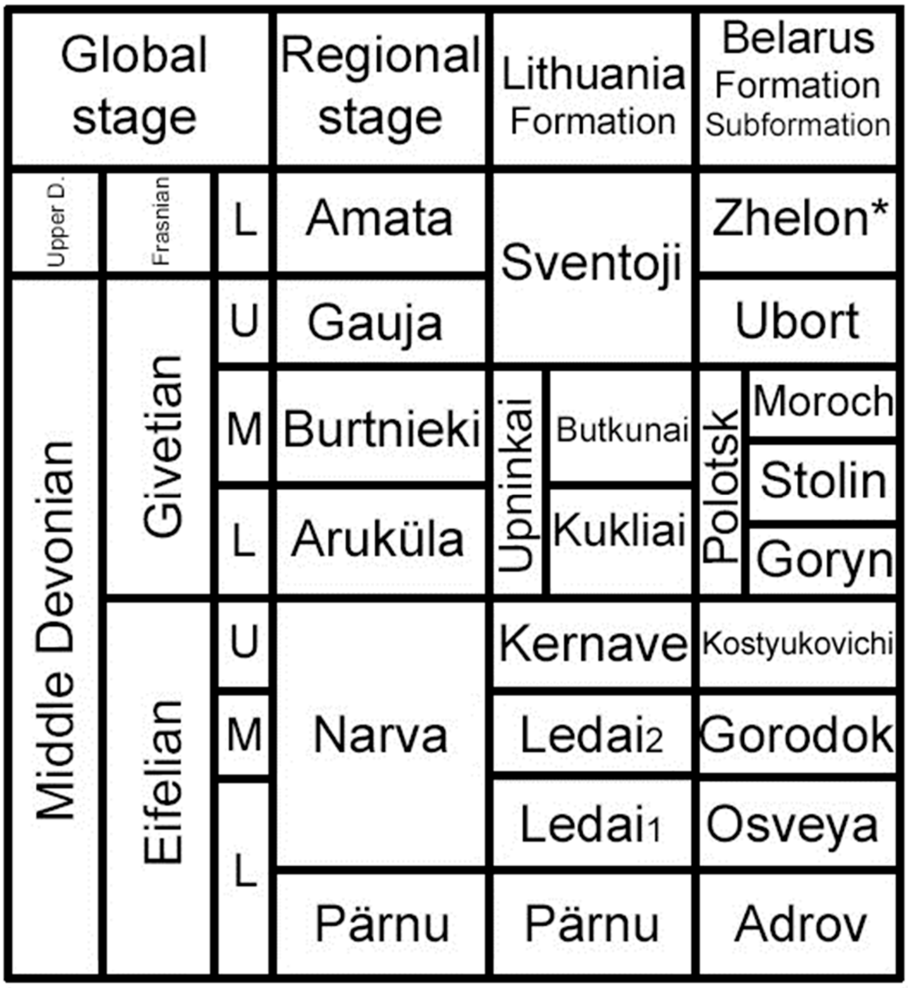


**Figure 1.** Middle and lower parts of Upper Devonian stratigraphy in Lithuania (modified after [2,19] and Belarus [12,20]). * According to the Devonian stratigraphic chart of Belarus since 2010, the Zhelon Formation is part of the Frasnian Stage (Upper Devonian).

The Narva Group in Lithuania consists of the Ledai 1, Ledai 2, and Kernave Formations, which are subsequently overlain by the Kukliai and Butkunai Formations of the Upninkai Group. During this time, most of the Baltic was covered by the marine–lagoonal basin of the Baltic Devonian, excluding the southernmost part of Lithuania and the northernmost section of Estonia, as documented by Paškevičius (1997) [2]. The Ledai Formation is particularly noted for its gypsum interbeds within sandy layers, indicative of a lagoonal environment with elevated salinity. The salinity gradient intensifies southward, with southern Latvia recording layer thicknesses between 116 and 150 m. Significant subsidence was observed in central and western Lithuania, characterised by sediment layers enriched with mudstones and sulphide minerals. Palaeontological finds within the Ledai Formation include brachiopods, ostracods, crustaceans, and occasional vertebrates. The Kernave Formation marks a time when the lagoonal environment began transitioning towards a marine setting with decreased salinity, facilitated by an enclosed shelf that supported the calm transportation of lagoonal sediments and marine fauna. In the west, with up to 40 m of thickness, the Baltic Devonian Basin experienced pronounced subsidence. The Upninkai Group reflects the Baltic Devonian Basin's regression, divided into the Kukliai and Butkūnai Formations. This time witnessed the complete transition of the lagoonal basin into a closed-shelf marine basin, characterised by lacustrine–alluvial–deltaic deposits. In the western Baltic, sediment thicknesses ranging from 50 to 103 m were recorded, attributed to the basin's low elevation and continuous tectonic subsidence [2].

The Middle Devonian stratigraphy of Belarus aligns closely with that of Lithuania, as illustrated in Figure 1. The Eifelian Stage in Belarus is represented by the Andov, Osveya, Gorodok, and Kostyvkovichi Formations, which are succeeded by the Givetian Stage's Goryn, Stolin, and Moroch Subformations of the Polotsk Formation, followed by the Ubort Formation, as delineated by Obuhovskaya et al. (2010 and 2013) [18,21]. The Zhelon Formation falls within the Frasnian Stage (Upper Devonian), adhering to the Devonian stratigraphic framework of Belarus that was established in 2010. During the Adrov phase, according to Plax (2013) [3], the Belarusian sea was shallow and exhibited slight desalination, leading to the deposition of sandy, clayish, silty sediments with partial carbonate content. The Adrov Formation is noted for its diverse faunal assemblage, including vertebrates and invertebrates such as ostracods, conchostracans, and lingulids. The succeeding Osveya Formation experienced a gradual increase in salinity, favouring the formation of dolomites, often oolitic, along with dolomitic marls, sulphates, and sporadic terrigenous rocks. This saline environment began to desalinate during the Gorodok time, only for the seawater salinity to rise again, leading to dolostone formation and the presence of foraminifera, ostracods, gastropods, bivalves, lingulids, calcareous algae, and ichthyofauna. The Kostyukovichi time was characterised by water with regular salinity in the shallow epicontinental sea, resulting in the deposition of clayey, carbonate, and clay–carbonate sediments and an increased diversity of invertebrates, including scolecodonts, brachiopods, ostracods, trilobites, gastropods, bivalves, tentaculites, crinoids, and vertebrates such as conodonts. The Givetian deposits are distributed in a smaller area compared to the Eifelian deposits in Belarus. During the Givetian, a shallow marine environment prevailed, dominated by the mechanical accumulation of terrigenous sandy–silt material and clay particle sedimentation, with the sea experiencing significant freshening, likely due to the influx from freshwater rivers. The connection of the basin with the Lviv-Volynsky Basin in western Ukraine during the Polotsk time was through a shallow strait, as mentioned by Golubtsov et al. (1979 and 1981) [22,23], indicating a rich faunal presence, including foraminifers, scolecodonts, conchostracans, bivalves, gastropods, brachiopods, tentaculites, crinoids, and vertebrates like various agnathans and other fish. In the Ubort time, the sea remained shallow and possibly experienced desalination similar to that during the Polotsk time, with the continued accumulation of predominantly sandy and silty materials. The sea was inhabited mainly by the majority of fossil skeletons belonging to vertebrates.

## 3. Materials and Methods

This study presents 199 isolated fish scales collected from 10 boreholes across Belarus: North Polotsk; Lepel 1; Klimovichi 4п; Berdyzh 1; Pinsk 54; Pinsk 10; Pinsk 26; Smol'ki 6п; Bykhov 1; and Korma 1 (Figure 2). Part of this assemblage belongs to Dr. Dmitry Plax's personal collection, while others were stored at the Department of Mining at the Belarusian National Technical University (BNTU). Stratigraphically, this material spans the Osveya, Gorodok, and Kostyukovichi Formations, along with the Goryn, Stolin, and Moroch Subformations of the Polotsk Formation, all within the Middle Devonian period of Belarus (Figure 1).

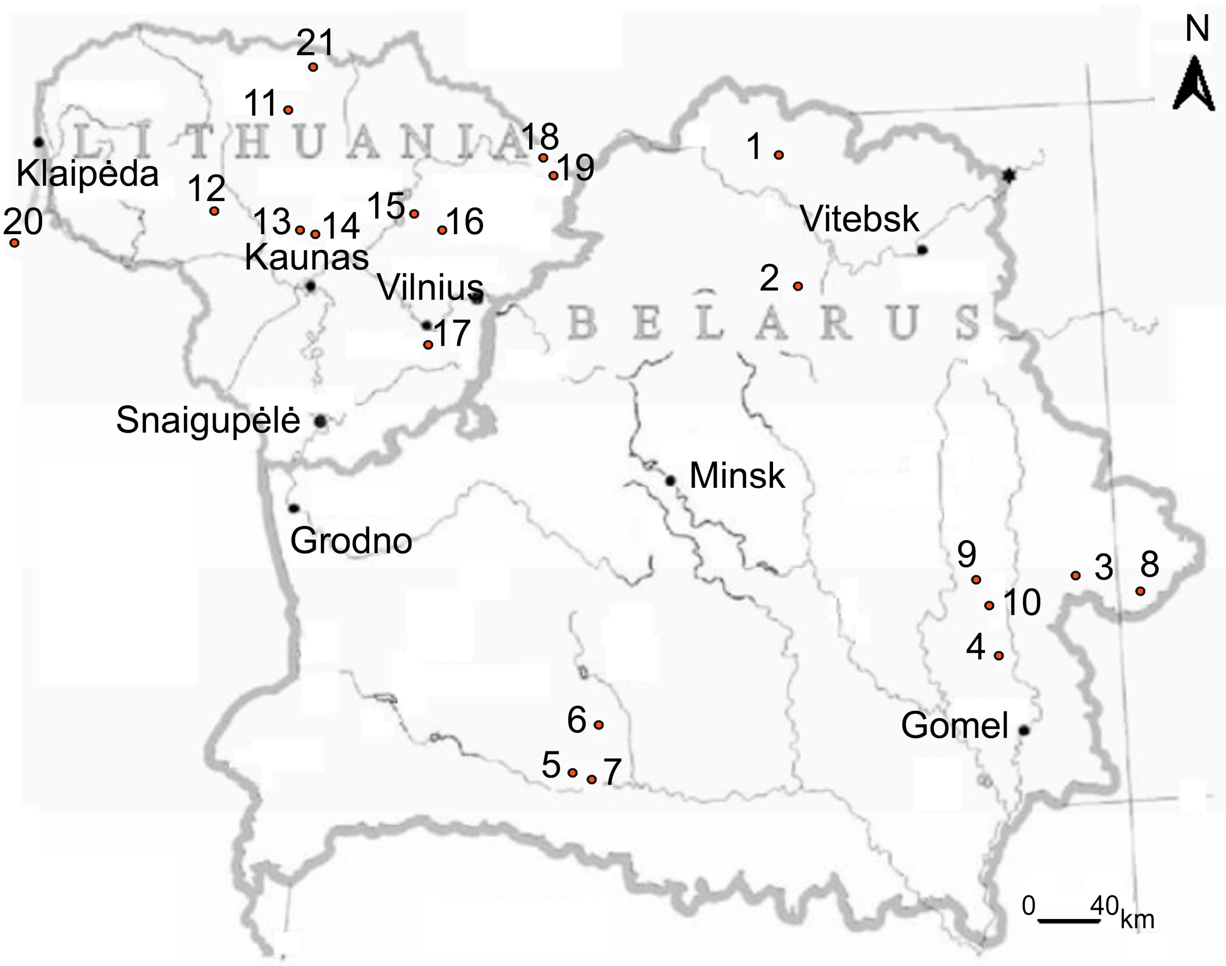


**Figure 2.** Geographic locations of the studied boreholes in Lithuania and Belarus (modified after Šeirienė et al., 2015 [24]). Black circles mark cities; red circles mark boreholes. 1. North Polotsk 1; 2. Lepel 1; 3. Klimovichi 4п; 4. Berdyzh 1; 5. Pinsk 54; 6. Pinsk 10; 7. Pinsk 26; 8. Smol'ki 6п borehole; 9. Bykhov 1; 10. Korma 1; 11. Stačiūnai-8; 12. Kunkojai-12; 13. Medininkai-126; 14. Ledai-179; 15. Stakiai-255; 16. Kaniūkai-261; 17. Vilnius-4; 18. Riešutynė-321; 19. Drūkšiai-51; 20. Dvorikai-2 in Sambia Peninsula; and 21. Kriukai-146 boreholes.

The comprehensive study of materials from Lithuania has examined 230 isolated fish scales. This collection includes contributions from the ichthyofaunal collections of Prof. Dr. Juozas Valiukevičius and Dr. Habil. Valentina Karatajūtė-Talimaa, in addition to specimens collected by Dr. Jonas Šečkus from 2000 to 2002. All studied fossils are preserved in the Geological Museum at the Institute of Geosciences of Vilnius University. Specimens were collected from 11 boreholes: Stačiūnai-8, Kunkojai-12, Medininkai-126, Ledai-179, Stakiai-255, Kaniūkai-261, Vilnius-4, Riešutynė-321, Drūkšiai-51, Dvorikai-2, and

Kriukai-146 (Figure 2). Stratigraphically, this material corresponds to the Ledai, Kernave, Kukliai, and Butkunai Formations of the Middle Devonian period of Lithuania (Figure 1).

Samples from Belarus were prepared chemically at the Belarusian National Technical University, whereas samples from Lithuania were processed at Vilnius University by applying Jeppsson et al.'s (1999) [25] technique using formic acid for carbonates and hydrogen peroxide for clayish sandstone. Later, the undissolved residue was placed into ceramic dishes, dried in a 60 °C oven, and sieved using the standard sieving technique [26] for fossil extraction, whose size ranged between 0.1 and 2.0 mm. After that, all materials were taxonomically studied under a binocular microscope.

Scales from *Orvikuina* sp. and *O. vardiaensis* were used in histological studies to provide insights into their internal tissue structures. These specimens were encased in polyester resin and subsequently polished on both sides with 3H M-10 abrasive polishing powder. To detail the microstructure of *Orvikuina* scales, both transversal and longitudinal thin sections were prepared (as shown in Figure 5O,P and Figure 6K–M). The scanning electron microscopes (SEMs) located at Tallinn University of Technology in Estonia and the Belarusian State Technological University were used for capturing microphotographs of the scales and their respective thin sections. All images were processed using Adobe Photoshop CS6.

## 4. Systematic Palaeontology

Superclass: OSTEICHTHYES, Huxley, 1880 [27];
Class: ACTINOPTERYGII, Cope, 1887 [28];
Order: CHEIROLEPIDIFORMES, Kazantzeva-Selezneva, 1977 [29];
Family: CHEIROLEPIDIDAE, Pander, 1860 [30];
Genus: *Cheirolepis*, Agassiz, 1835 [31];
*Cheirolepis* cf. *gaugeri*, Gross, 1973 [32].
(Figure 3)

**Type species and holotype:** *Cheirolepis trailli* Agassiz, 1835 [31].

**Included species:** *C. aleshkai*, Plax, 2020 [4]; *C. canadensis*, Whiteaves, 1881 [33]; *C. gaugeri*, Gross, 1973 [32]; *C. gracilis*, Gross, 1973 [32]; *C. jonesi*, Newman et al., 2021 [34]; *C. schultzei*, Arratia and Cloutier, 2004 [35]; and *C. bychovensis*, Plax, 2022 [17].

**Type locality and horizon:** Pinsk 10 borehole, depth 142.9 and 122.0 m; Klimovichi 4п borehole, depth 235.5 and 235.0 m; Berdyzh 1 borehole, depth 233.0 and 231.2 m in Belarus; Middle Devonian, Givetian Stage, Polotsk Regional Stage, Stolin Beds. Dvorikai-2 borehole, depth 1009.2 m; Stačiūnai-8 borehole, depth 349.3 m; Drūkšiai-51 borehole, depth 178.2 m; Kunkojai-12, depth 529.0 m in Lithuania; Middle Devonian, Eifelian Stage, Narva Regional Stage, Kernave Formation and Givetian Stage, Aruküla and Burtnieki Regional Stages, Upninkai Group, Kukliai and Butkunai Formations (Figures 1, 2 and 7).

**Material:** 21 scales (13 scales from Belarus and 8 scales from Lithuania).

**Description:** Scales are rhomboidal, elongate–rhomboidal, and irregularly rectangular in shape (Figure 3A–Q). Crown dimensions vary from 0.25 mm to 0.7 mm in length, 0.18 to 0.5 mm in width, and 0.15 to 0.35 mm in height. The crown is slightly convex, with a rounded anterior margin. The crown surface is sculpted by distinct, well-defined, narrow, low, and little curved ridges. They are long and mostly reach the posterior part of the crown. Here, these ridges may converge into sharp and elongated forms of one to five and various lengths of tooth-like spikes (Figure 3A–D,G). Some of the ridges in the anterior portion of the crown could be split in two (Figure 3H,J–L). There may be five (Figure 3L) to twelve crown ridges (Figure 3D,H) in total. Different grooves of varying widths and depths divide them. The top of the scale consists of a shiny and thin layer of ganoine. The neck is short and clearly pronounced. The base has a rhomboidal, rectangular, or irregularly rectangular profile and slightly rounded corners. It is large and massive, with a relatively smooth surface. The keel is rather large and slightly displaced from the centre of the scale. The base is larger than the crown's outline (Figure 3A–C,E,H,J–P).

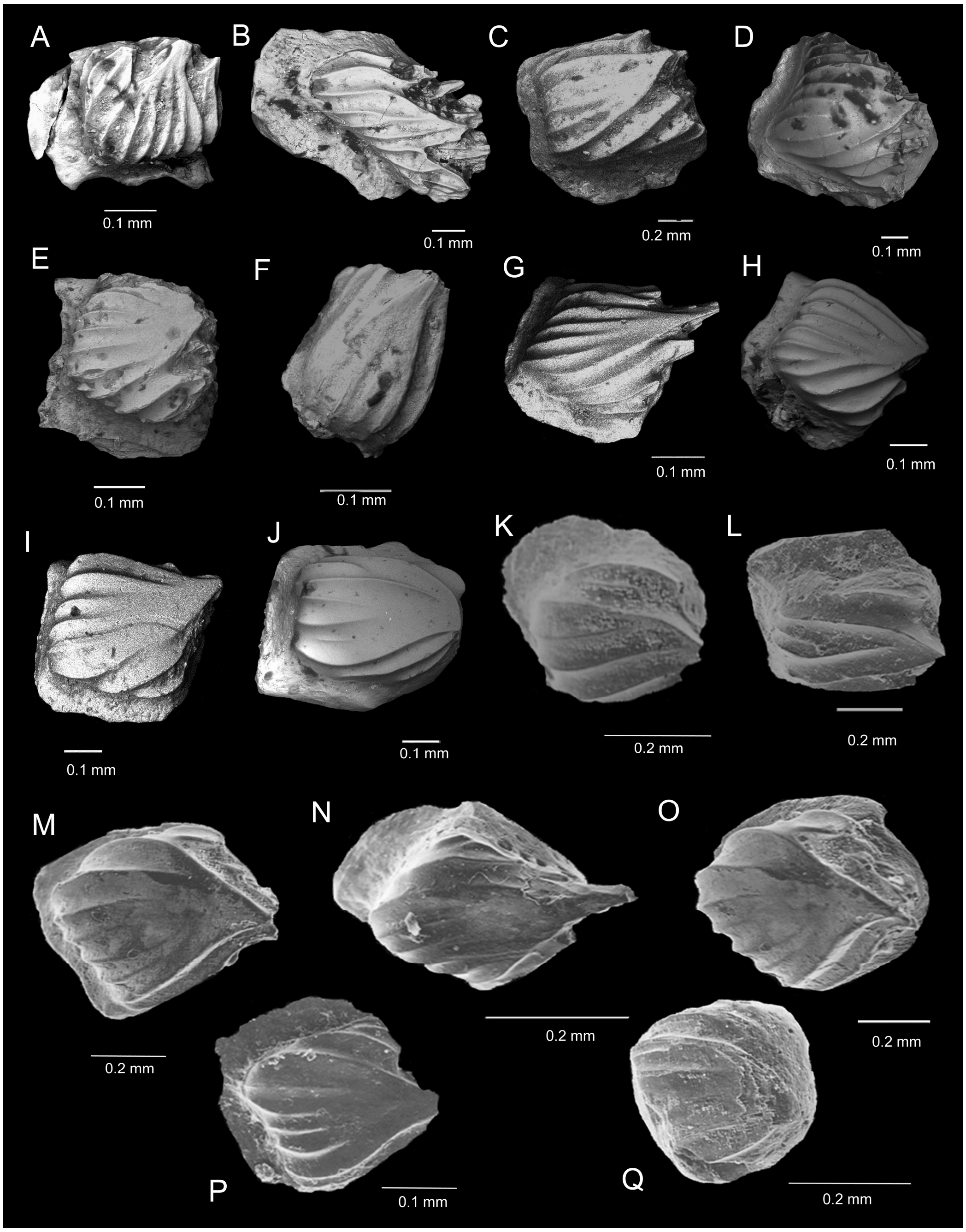


**Figure 3.** SEM pictures of isolated *Cheirolepis* cf. *gaugeri* scales in the studied area. (**A**) Specimen 85/16-10b from the Pinsk 10 borehole in Belarus, depth 142.9 m, in anterior crown view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**B**) Specimen 143/5-5 from the Klimovichi 4п borehole in Belarus, depth 235.5 m, in oblique crown view, Polotsk Formation, Stolin Subformation (Lower Givetian). (**C**) Specimen 86/28-2c from the Berdyzh 1 borehole in Belarus, depth 233.0 m, in crown view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**D**) Specimen 143/4-8 from the Klimovichi 4п borehole, depth 235.0 m, in oblique crown view, Polotsk Formation, Stolin Subformation (Lower Givetian). (**E**) Specimen 85/21-1f from the Pinsk 10 borehole, depth 122.0 m, in crown view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**F**) Specimen 85/16-10e from the Pinsk 10 borehole, depth 142.9 m, in crown view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**G**) Specimen 86/28-2b from the Berdyzh 1 borehole, depth 233.0 m, in crown view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**H**) Specimen 143/4-5 from the Klimovichi 4п borehole, depth 235.0 m, in crown view, Polotsk Formation, Stolin Subformation (Lower Givetian).

(**I**) Specimen 86/34-10a from the Berdyzh 1 borehole, depth 231.2 m, in crown view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**J**) Specimen 143/4-2 from the Klimovichi 4п borehole, depth 235.0 m, in oblique crown view, Polotsk Formation, Stolin Subformation (Lower Givetian). (**K**) Specimen LGI 25-P/54 from the Dvorikai-2 borehole in Lithuania, depth 1009.2 m, in oblique crown view, Kernave Formation (Upper Eifelian). (**L**) Specimen LGI 25-P/55 from the Dvorikai-2 borehole, depth 1009.2 m, in oblique crown view, Kernave Formation (Upper Eifelian). (**M**) Specimen LGI 25-P/53 from the Stačiūnai-8 borehole in Lithuania, depth 349.3 m, in crown view, Upninkai Group, Kukliai Formation (Lower Givetian). (**N**) Specimen LGI 25-P/62 from Drūkšiai-51 in Lithuania, depth 178.2 m, in oblique crown view, Kernave Formation (Upper Eifelian). (**O**) Specimen LGI 25-P/53 from the Stačiūnai-8 borehole in Lithuania, depth 349.3 m, in crown view, Upninkai Group, Kukliai Formation (Lower Givetian). (**P**) Specimen LGI 25-P/40 from Kunkojai-12 in Lithuania, depth 529.0 m, in crown view, Kernave Formation (Upper Eifelian). (**Q**) Specimen LGI 25-P/52 from the Stačiūnai-8 borehole, depth 349.3 m, in crown view, Upninkai Group, Butkunai Formation (Middle Givetian).

**Comparison:** The scales of the described species differ from those of *C. trailli* [31,36,37] in crown shape, elements of its sculpture, characteristics of the posterior part of the scale, and morphological details of the base. The scales of *Cheirolepis* cf. *gaugeri* differ significantly from those of *C. canadensis* [33,36,38,39] in crown shape and its sculpture, as there are a greater number of ridges and tooth-like spikes in the posterior part of the crown, as well as a base shape and profile with a little difference in the basal protrusion (keel). The scales of *C. gaugeri* Gross, 1973 [32] and the described species here slightly differ by crown shape, the number of ridges on the crown (up to 12), the posterior part of the crown, expression of the neck, and insignificantly by the morphology of the base. The scales of *C. gracilis* Gross, 1973 [32] and the scales of *Cheirolepis* cf. *gaugeri* very strongly differ by the sculpture on the crown and its posterior part, the smaller height of the neck, the outline of the base, and by the expression of basal protrusion through the base. The scales of the described species differ strongly from those of *C. schultzei*, Arratia and Cloutier, 2004 [35], in terms of their crown shape, different crown sculptures, the configuration of the posterior crown part, neck height, base shape, and profile, as well as their much better expression of basal projection. The scales of *Cheirolepis* cf. *gaugeri* differ from those of *C. aleshkai*, Plax, 2020 [4], in terms of their crown shape, the completely different character of the sculpture on the crown, the posterior part of the crown, better-developed neck, the base extending beyond the crown's outline and its convexity, and well-developed basal protrusion (keel). The scales of the described species differ strongly from those of *C. jonesi*, Newman et al., 2021 [34], in terms of their crown configurations, a different sculpture on the crown, a posterior crown part represented either by a single elongated spike or by several tooth-like spikes, a lower neck height, and a slightly different morphology of the base. The scales of the described species differ from those of *C. bychovensis*, Plax, 2022 [17], by a completely different sculpture on the crown, the absence of large pores on the scale's surface, the character of the posterior crown margin, a neck development, the shape of the base, and the level of its convexity.

**Remarks:** The scales of this species vary in shape and size. The crown sculpture differs in the number of different lengths of ridges. The number of tooth-like spines on the posterior edge of the crown can vary from one to five units. The clarity of the basal protrusion (keel) may be a little variable.

Genus: *Cheirolepis*, Agassiz, 1835 [31];
*Cheirolepis gaugeri*, Gross, 1973 [32].
(Figure 4A–C)

**Type locality and horizon:** Lepel 1 borehole, depth 194.0 m; Berdyzh 1, depth 231.2 and 232.4 m in Belarus; Middle Devonian, Eifelian Stage, Kostyukovichi Regional Stage and Givetian Stage, Polotsk Regional Stage, Stolin Beds (Figures 1, 2 and 7).

**Material:** Five scales from Belarus.

**Description:** The scales have a diamond shape. The crown has dimensions of 0.3 to 0.5 mm in width and 0.4 to 0.6 mm in length. The crown is smooth, massive, thick, and slightly convex in the anterior corner. Well-defined longitudinal ridges have sculpted the crown. The ridges are narrow, not high, smooth, more sharply distinguished at the anterior margin, and distributed partly (Figure 4A) or all over the crown (Figure 4B,C). The number of ridges is mainly up to eight units. They are divided by distinct grooves of various widths. A thin layer of glossy ganoine, which covers the crown, is present. The neck is short and poorly expressed. The base has an outline of a rounded square.

**Comparison:** These scales of the described species significantly differ from those of other species from the *Cheirolepis* in the crown shape, its pattern (number of ridges), ridges and grooves arrangement and configuration, length of ridges, division of the crown into lobes, distinctly developed spike-like characteristics in the posterior margin of the crown, the level of neck development, the base outline, size, and its convexity.

**Remarks:** The scales of this species are rare in the fossil record due to a lack of comparative material. A histological analysis of the studied material for tissue examination is necessary. Due to the scarcity of scale material, a histological analysis of the scales was not performed here.

Genus: *Cheirolepis* Agassiz, 1835 [31];
*Cheirolepis aleshkai*, Plax, 2020 [4].
(Figure 4D)

**Type locality and horizon.** Lepel 1 borehole, depth 244.9 m, Belarus; Middle Devonian, Eifelian Stage, Osveya Regional Stage (Figures 1, 2 and 7).

**Material:** Five scales from Belarus.

**Description:** The scales have a rectangular form in general. The crown has dimensions of 0.4–0.6 mm in width and 0.5–0.8 mm in length. The slightly convex crown is covered by well-marked, not high, smooth, and longitudinal ridges. These ridges have grown along the entire length of the crown's field, typically extending up to fifteen units. Up to seven spike-like structures developed on the crown's posterior margin. The crown's outer tissue is composed of a shiny, thin layer of ganoine. The neck has a low level of expression. The base is large, massive, and usually does not expand beyond the crown.

**Comparison:** The scales of the described species differ significantly from those of other species in the *Cheirolepis* genus in terms of the shape of the crown, its pattern (number of ridges), the arrangement and configuration of the ridges and grooves, the length of the ridges, the division of the crown into lobes, the level of neck development, the outline, size, and convexity of the base.

**Remarks:** Due to a scarcity of comparable specimens, the scales of this species are uncommon in the fossil records. In this case, a histological analysis of the scales was not possible due to a scarcity of scale material.

Genus *Cheirolepis*, Agassiz, 1835 [31];
*Cheirolepis* cf. *aleshkai* Plax, 2020 [4].
(Figure 4E,F)

**Type locality and horizon:** Riešutynė-321 borehole, depth 252.6 and 208.2 m, Lithuania; Middle Devonian, Eifelian Stage, Narva Regional Stage, Ledai Formation (Figures 1, 2 and 7).

**Material:** Four scales from Lithuania.

**Description:** The scales have mainly a diamond (Figure 4E,F) shape. The crown is 0.4–0.6 mm long and 0.4–0.8 mm wide. The crown is flat (Figure 4E,F) and sculptured by well-marked, relatively narrow, not high, smooth, longitudinal ridges developed all over the length of the crown field (Figure 4E,F). These ridges extend progressively to the posterior margin. Here, the crown shows up to 4–5 units of developed spike-like features (Figure 4E,F). Different but comparable-sized grooves clearly divide them. The crown's outer tissue consists of a shiny layer of ganoine. The neck has a low level of expression. The base is massive, thick, and does not exceed the crown margins.

**Comparison:** These scales differ from those of *Cheirolepis trailli*, Agassiz, 1835 [31], in the arrangement, length, and number of ridges on the crown. The sculpture of *C. canadensis*, Whiteaves, 1881 [33], scales significantly differ from the studied material in the size, distribution, and number of ridges on the crown, the developed pointy spikes like in the posterior margin of the crown, the narrower neck, and the outline of the base, which does not exceed the crown margins. The scales of the described species differ from those of *C. gaugeri*, Gross, 1973 [32], in the crown ornamentation as well as the arrangement, configuration, and number of ridges, depth of the grooves, differently developed spike-like characteristics in the posterior margin, the lower neck, and the base outline, which are not emerging beyond the crown borders. The scales of *C. gracilis*, Gross, 1973 [32], differ by the crown's ornamentation, the shorter neck, and the fact that the outline of the base is not extended beyond the margins of the crown. The scales of the described species differ from those of *C. schultzei*, Arratia and Cloutier, 2004 [35], by the shapes of their crowns, which are covered by a greater number of ridges, the arrangement and configuration of ridges, the less spike-like development in the posterior margin and their sizes, and the base outline, which does not extend beyond the margins of the crown.

**Remarks:** The scales of this material are taxonomically the most similar to *C. aleshkai*, Plax, 2020 [4], scales according to their general shape and size. The crown's sculpture has a similar number of ridges and length. The spike-like characteristic on the posterior edge of the crown can vary from one to five units. The clarity of the basal protrusion (keel) may be slightly varied. The revision of the inner structure and more comprehensive samples are necessary for the accurate identification of the examined material. The histological study of the scales is out here because of the scarcity of scale material.

Genus: *Cheirolepis*, Agassiz, 1835 [31];
*Cheirolepis* sp.
(Figure 4G–J)

**Type locality and horizon:** Pinsk 10 borehole, depth 122.0 and 103.7 m, Belarus; Middle Devonian, Givetian Stage, Polotsk Regional Stage, Moroch Beds; Dvorikai-2 borehole, depth 1009.2 m, Lithuania; Middle Devonian, Eifelian Stage, Narva Region Stage, Kernave Formations, and Givetian Stage, Aruküla and Burtnieki Regional Stages, Upninkai Group, Kukliai and Butkunai Formations (Figures 1, 2 and 7).

**Material:** 28 scales (11 scales from Belarus and 17 scales from Lithuania).

**Description:** *Cheirolepis* sp. is represented here by diamond-shaped (Figure 4G,I,J) and elongated diamond-shaped (Figure 4H) scales. The crown is smooth, massive, and thick, sometimes high (Figure 4G,H). Five to ten ridges are covered by the crown's surface. There are two types of ridge arrangements: transversely crossed (Figure 4G,J) and longitudinally directed (Figure 4H,I), in general. The ridges differ in their length as they are distributed partly (Figure 4I,J) or all over the crown (Figure 4G,H). The neck is short and poorly expressed. The base outline has a form of rounded square (Figure 4G,I) and rounded rectangular (Figure 4H), which is strongly emerging beyond the crown borders.

**Comparison:** The material of this genus is different from its known species: *Cheirolepis trailli*, Agassiz, 1835 [31]; *C. canadensis*, Whiteaves, 1881 [33]; *C. gaugeri*, Gross, 1973 [32]; *C. gracilis*, Gross, 1973 [32]; *C. schultzei*, Arratia and Cloutier, 2004 [35]; *C. aleshkai*, Plax, 2020 [4]; *C. jonesi*, Newman et al., 2021 [34]; and *C. bychovensis*, Plax, 2022 [17] in shape and ornamentation of the crown, the pattern of the crown's sculpture (number of ridges), characteristics of the posterior part of the scale (number of spikes), the different levels of neck development (size and height), and morphology of the base outline, extending beyond the crown and its convexity.

**Remarks:** The taxonomical identification of the studied material at the species level requires inner structure revealing, which should be performed using well-preserved scales. The histological analysis of the scales was not performed due to the scarcity of scale material here.

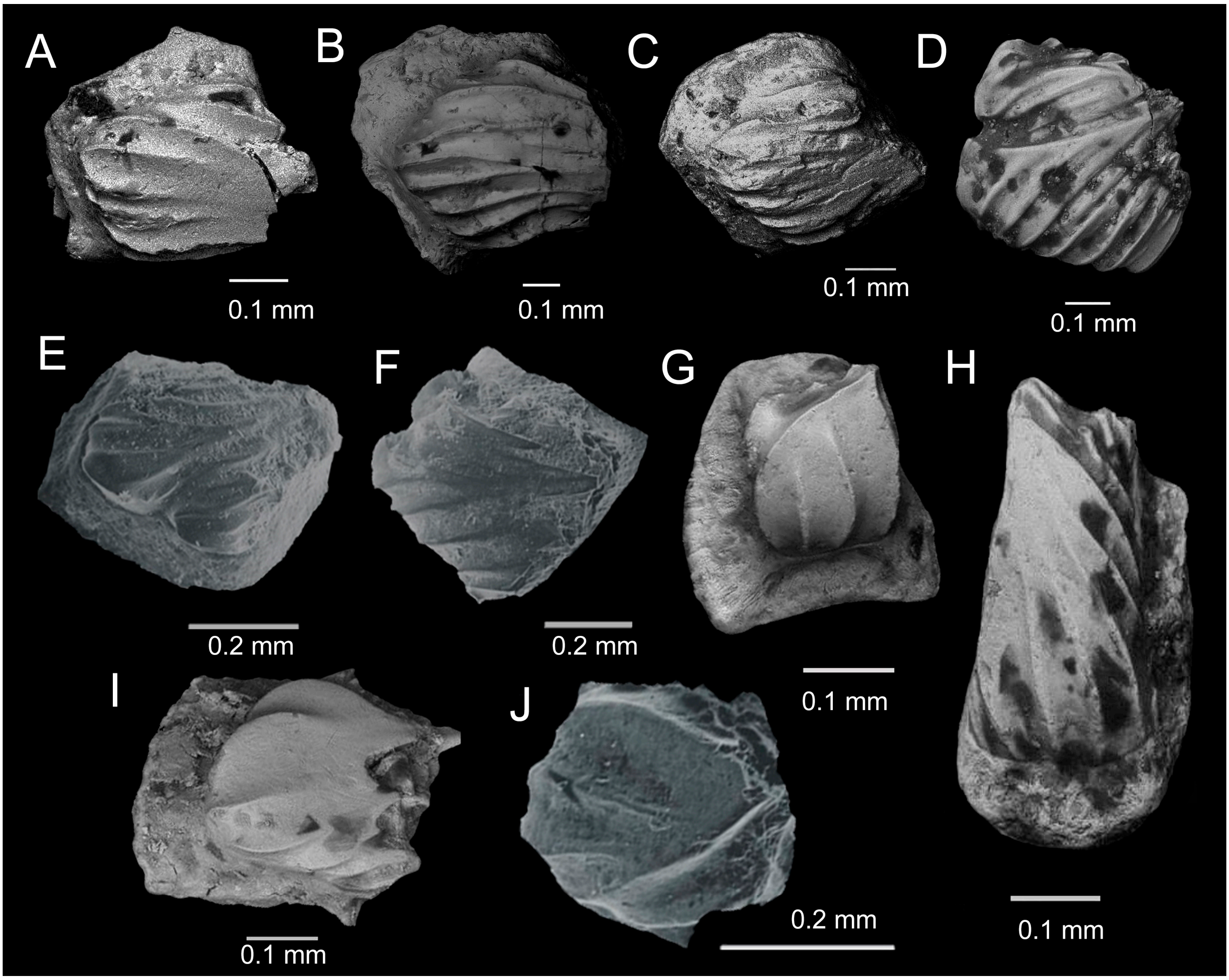


**Figure 4.** SEM pictures of isolated *Cheirolepis* scales in the studied area. (**A**) Specimen 47/19-50h of *C. gaugeri* Gross from the Lepel 1 borehole in Belarus, depth 194.0 m, in crown view, Kostyukovichi Formation (Upper Eifelian). (**B**) Specimen 86/29-32 of *C. gaugeri* Gross from the Berdyzh 1 borehole in Belarus, depth 232.4 m, in crown view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**C**) Specimen 86/34-10b of *C. gaugeri* Gross, 1973 [31], from the Berdyzh 1 borehole, depth 231.2 m, in crown view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**D**) Specimen 47/55-1a of *Cheirolepis aleshkai* Plax, 2020 [4], from the Lepel 1 borehole, depth 244.9 m, in crown view, Osveya Formation (Lower Eifelian). (**E**) Specimen LGI 25-P/58 of *Cheirolepis* cf. *aleshkai* Plax, 2020 [4], from the Riešutynė-321 borehole in Lithuania, depth 252.6 m, Ledai Formation (Eifelian). (**F**) Specimen LGI 25-P/59 of *Cheirolepis* cf. *aleshkai* Plax, 2020 [4], from the Riešutynė-321 borehole, depth 208.2 m, Ledai Formation (Eifelian). (**G**) Specimen 85/21-2g of *Cheirolepis* sp. from the Pinsk 10 borehole in Belarus, depth 122.0 m, in crown view, Polotsk Formation, Moroch Subformation (Middle Givetian). (**H**) Specimen 85/21-2b of *Cheirolepis* sp. from the Pinsk 10 borehole in Belarus, depth 122.0 m, in crown view, Polotsk Formation, Moroch Subformation (Middle Givetian). (**I**) Specimen 85/23-7d of *Cheirolepis* sp. from the Pinsk 10 borehole, depth 103.7 m, in crown view, Polotsk Formation, Moroch Subformation (Middle Givetian). (**J**) Specimen LGI 25-P/57 of *Cheirolepis* sp. from the Dvorikai-2 borehole in Lithuania, depth 1009.2 m, in crown view, Kernave Formation (Upper Eifelian).

Order: PALAEONISCIFORMES, Hay, 1902 [40];
Family: STEGOTRACHELIDAE, Gardiner, 1963 [41];
Genus: *Orvikuina*, Gross, 1953 [42];
*Orvikuina vardiaensis*, Gross, 1953 [42].
(Figure 5)

**Type species and holotype:** *Orvikuina vardiaensis*, Gross, 1953 [42]

**Included species:** *Orvikuina vardiaensis*, Gross, 1953 [42]; *Orvikuina* sp., Schultze, 1968 [43].

**Type locality and horizon:** Pinsk 26 borehole, depth 421.2 m; Berdyzh 1 borehole, depth 234.0 m; Pinsk 54 borehole, depth 465.0–460.0 m; Pinsk 10 borehole, depth 142.9 m; and Smol'ki 6п borehole, depth 279.2 m in Belarus; Middle Devonian, Eifelian Stage, Kostyukovichi Regional Stage and Givetian Stage, Polotsk Regional Stage, Goryn, Stolin, and Moroch Beds. Stakiai-255 borehole, depth 200.0 m; Riešutynė-321 borehole, depth 252.6 m; Medininkai-126 borehole, depth 368.6 m; and Stačiūnai-8 borehole, depth 511.35 m in Lithuania. Middle Devonian, Eifelian Stage, Narva Region Stage, Ledai and Kernave Formations, and Givetian Stage, Aruküla and Burtnieki Regional Stages, Upninkai Group, and Kukliai and Butkunai Formations (Figures 1, 2 and 7).

**Material:** 167 scales (100 scales from Belarus and 67 scales from Lithuania).

**Description:** *O. vardiaensis* scales have a highly expressed rhombic shape. Their measures for length are typically two to four times bigger than those for width. The crown is smooth, thick, and massive, with the sculptured surface characterised by two or three solid ridges. These ridges cover 3/4 of the length of the scale overall. The exposed field is positioned at the tip of the posterior corner, which may be mildly twisted (Figure 5A,B,L,N) or significantly twisted (Figure 5C,D,G,J,M). Some of them in the upper row of the crown's posterior region may be divided into two ridges (Figure 5B,E,H). The ridge in the posterior corner is sculptured by up to 12 units of brightly marked serrations (Figure 5A,C,H,J,K). Small, low, and thin serrations of varying lengths are spread longitudinally. In the middle field, the internal portion of the scale is massive, smooth, and convex (Figure 5F,G). There is no ornamentation seen on the scale's surface.

**Histology:** The histological analyses of *O. vardiaensis* scales in the transverse (Figure 5O) and longitudinal cross-sections (Figure 5P) reveal three main layers: ganoine (g); dentine (d); and bony plate (bp). The crown consists of orthodentine (a branching pattern of vertical canals that perpendicularly cut dentine tissue) and ganoine (densely packed horizontal layers without any vertical canals), while the base is a bony plate (the widest tissue without enclosed cells by bone substance). The base has a well-developed diagonal channel system (Figure 5O) and many straight-shaped Sharpey's fibres (Sf), which are thinner than the canals of Williamson (Figure 5(P1)). Also, the slightly curved-shaped and weakly meandering canals of Williamson (W) are very densely packed at the base of scale and vertically distributed through the bone plate without connection with the dentine layer (Figure 5(P2)), which are exceptional characteristics for this genus.

**Comparison:** Gross (1953) [42] identified the low-shaped, elongated scales from the ventral part of the fish as *O. vardiaensis*. The notable similarities are that they share traits with the material under study, such as their description of inner structure. The scales were sharply pointed, curved upward in the posterior corner without ornament, and generally straight in the anterior part, indicating the presence of ganoine ridges.

**Remarks:** Some crowns have stronger development of outer sculpture as ridge serrations in the posterior part of the scale, while others do not have this characteristic.

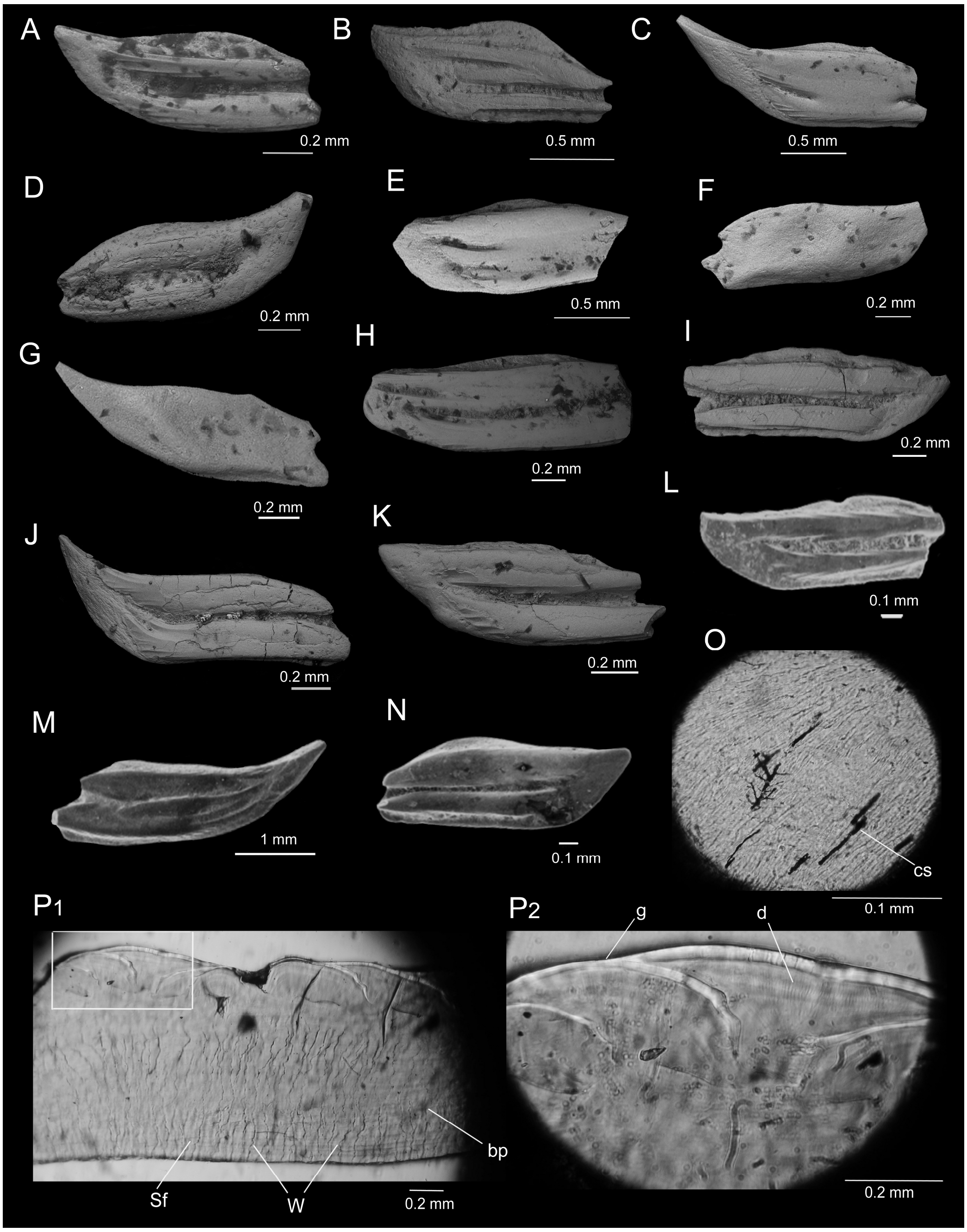


**Figure 5.** SEM pictures of isolated *Orvikuina vardiaensis* Gross, 1953 [42], scales in the studied area. (**A**) Specimen 41/4a-1 from the Pinsk 26 borehole in Belarus, depth 421.2 m, in external view, Kostyukovichi Formation (Upper Eifelian). (**B**) Specimen 86/27-12 of from the Berdyzh 1 borehole in Belarus, depth 234.0 m, in external view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**C**) Specimen 58/956-2a from the Pinsk 54 borehole in Belarus, depth range of 460.0–465.0 m, in external view, Kostyukovichi Formation (Upper Eifelian). (**D**) Specimen 86/27-38 from the Berdyzh 1 borehole, depth 234.0 m, in external view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**E**) Specimen 58/956-1a of from the Pinsk 54 borehole, depth range of 460.0–465.0 m, in external, Kostyukovichi Formation (Upper Eifelian). (**F**) Specimen 58/956-2c from the Pinsk 54 borehole, depth range of 460.0–465.0 m, in internal view, Kostyukovichi Formation (Upper Eifelian). (**G**) Specimen 58/956-2b from the Pinsk 54 borehole, depth range of 460.0–465.0 m, in internal view, Kostyukovichi Formation (Upper Eifelian). (**H**) Specimen 85/16-13 from the Pinsk 10 borehole, depth 142.9 m, in external view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**I**) Specimen 158/11-9 from

the Smol'ki 6п borehole, depth 279.2 m, in externa view, Polotsk Formation, Goryn Subformation (Lower Givetian). (**J**) Specimen 158/11-3 from the Smol'ki 6п borehole, depth 279.2 m, in external view, Polotsk Formation, Goryn Subformation (Lower Givetian). (**K**) Specimen 158/11-7 from the Smol'ki 6п borehole, depth 279.2 m, in external view, Polotsk Formation, Goryn Subformation (Lower Givetian). (**L**) Specimen LGI 25-P/16 from the Stakiai-255 borehole in Lithuania, depth 200.0 m, in external view, Kernave Formation (Upper Eifelian). (**M**) Specimen LGI 25-P/13 from the Riešutynė-321 borehole in Lithuania, depth 252.6 m, in external view, Ledai Formation (Eifelian). (**N**) Specimen LGI 25-P/13 from the Riešutynė-321 borehole in Lithuania, depth 252.6 m, in external view, Ledai Formation (Eifelian). O–P, thin sections of *O. vardiaensis* specimens. (**O**) A transverse sectioned specimen LGI 25-H/1 from the Medininkai-126 borehole in Lithuania, depth 368.6 m, Ledai Formation (Eifelian). (**P1**) A longitudinal sectioned specimen LGI 25-H/2 from the Stačiūnai-8 borehole in Lithuania, depth 511.35 m, Ledai Formation (Eifelian) in general view. (**P2**) The detailed view of the inner structure. bp, bony plate; cs, canal system; d, dentine; g, ganoine; Sf, Sharpey's fibres; and W, canals of Williamson.

Genus: *Orvikuina*, Gross, 1953 [42];
*Orvikuina* sp.
(Figure 6)

**Type locality and horizon:** Pinsk 10 borehole, depth 142.9 m; Berdyzh 1 borehole, depth 232.4 m; Klimovichi 4п borehole, depth 235.0 m; north Polotsk 1 borehole, depth 272.5 m; Korma 1 borehole, depth of 264.2 m; and Bykhov 1 borehole, depth of 201.4–202.4 m in Belarus; Middle Devonian, Eifelian Stage, Gorodok, and Kostyukovichi Regional Stages and Givetian Stage, Polotsk Regional Stage, and Stolin Beds. Ledai-179 borehole, depth 288.0 m; Kaniūkai-261 borehole, depth 204.6 m; Kriukai-146 borehole, depth 488.85 m; Medininkai-126 borehole, depth 368.6 m; and Stačiūnai-8 borehole, depth 511.35 m in Lithuania; Middle Devonian, Eifelian Stage, Narva Region Stage, Ledai and Kernave Formations, and Givetian Stage, Aruküla and Burtnieki Regional Stages, Upninkai Group, and Kukliai and Butkunai Formations (Figures 1, 2 and 7).

**Material:** 204 scales (70 from Belarus and 134 from Lithuania).

**Description:** *Orvikuina* sp. scales have elongated (Figure 6A–C,I), sometimes strongly elongated (Figure 6E) rhombic shapes, or partially fragmented scales (Figure 6F–H,J). Their length varied from 1 mm to 3 mm. The crown is smooth, thick, massive, and sculptured by massive ridges (mainly three units rather than two units). The posterior corner is flat (Figure 6A,B,E) or slightly twisted (Figure 6I). Every ridge is sculpted by the various number of serrations in the posterior corner (Figure 6A–C,E–G,I). These radiantly distributed serrations are small, thin, and placed in a random order. The internal part of the scale is smooth, massive, and mostly flat, without any ornamentation (Figure 6D).

**Histology:** The histological analysis of *Orvikuina* sp. scales in the longitudinal sections (Figure 6K–M) reveals the typical inner structure of this genus, which mainly consists of ganoine, dentine, and bony plate. A densely packed horizontal ganoine layer covers the dentine tissue. The five growth generations of odontodes are observed in the studied material (from youngest to oldest): 1, 2, 3, 4, and 5 (Figure 6M). On the bottom of the bony plate, there are many straight-shaped Sharpey's fibres (Sf) and weakly meandering canals of Williamson (W) without connection with the dentine layer (Figure 6K–M). According to Currey (1961) [44], there are approximately 2300 canals of Williamson per mm$^2$ in *Orvikuina* scales, whose inner structures do not join with dentine tissue, while in other fish groups, up to 60 times less dense canals are connected with dentine. These are exceptional characteristics of this genus.

**Comparison:** The studied material morphologically is very similar to the material described by Schultze (1968), which was represented by mainly elongated and rare finds of rhombic-shaped *Orvikuina* sp. scales with analogues pattern of the ganoine crown.

**Remarks:** These *Orvikuina* sp. scales have flat or very little twisted posterior corners, mainly three massive ridges as the crown's sculpture, and randomly distributed serrations partly cut the ridge.

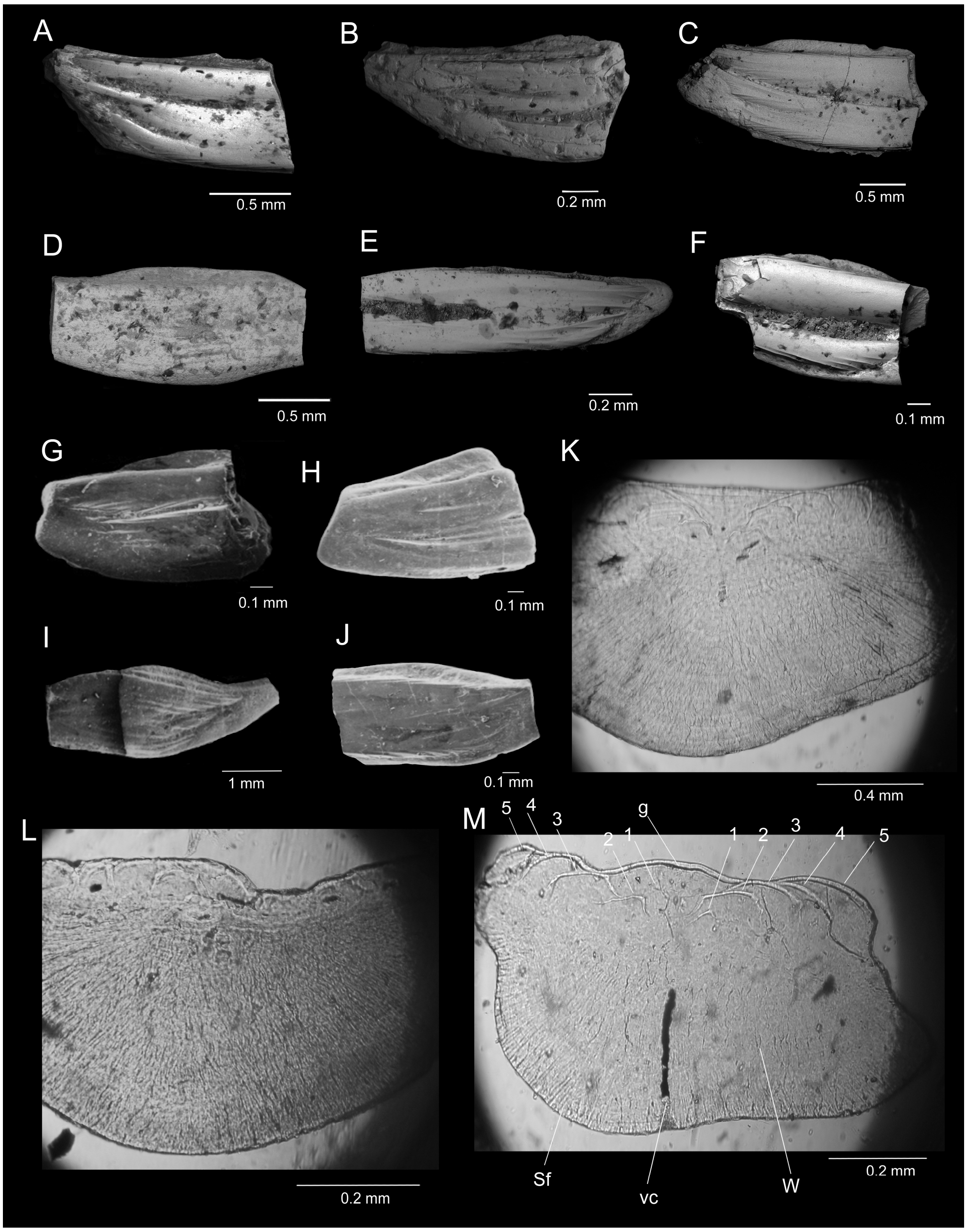


**Figure 6.** SEM pictures of isolated *Orvikuina* sp. scales in the studied area. (**A**) Specimen 85/16-16 from the Pinsk 10 borehole in Belarus, depth 142.9 m, in external view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**B**) Specimen 86/29-25 from the Berdyzh 1 borehole in Belarus, depth 232.4 m, in external view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**C**) Specimen 143/4-26 from the Klimovichi 4п borehole in Belarus, depth 235.0 m, in external view, Polotsk Formation, Stolin Subformation (Lower Givetian). (**D**) Specimen 126/8-2 from the north Polotsk 1 borehole in Belarus, depth 272.5 m, in internal view, Polotsk Formation, Stolin Subformation (Middle Givetian). (**E**) Specimen 121/10-2 from the Korma 1 borehole in Belarus, depth of 264.2 m, in external view, Gorodok Formation (Middle Eifelian). (**F**) Specimen (scale fragment) 116/16-9 from the Bykhov 1 borehole in Belarus, depth of 201.4–202.4 m, in external view, Kostyukovichi Formation (Upper Eifelian). (**G**) Specimen (scale fragment) LGI 25-P/31 from the Ledai-179 borehole in Lithuania, depth 288.0 m, in external view, Kernave Formation (Upper Eifelian). (**H**) Specimen (scale fragment) LGI 25-P/18 from the Kaniūkai-261 in Lithuania, depth 204.6 m, in external view, Kernave Formation (Upper Eifelian). (**I**) Specimen LGI 25-P/26 from the Kriukai-146 borehole in Lithuania, depth 488.85 m, in external view, Ledai Formation (Eifelian). (**K**–**M**) Thin sections of

*Orvikuina* sp. specimens. (**K**) A longitudinally sectioned specimen LGI 25-H/4 from the Medininkai-126 borehole in Lithuania, depth 368.6 m, Ledai Formation (Eifelian). (**L**) A longitudinally sectioned specimen LGI 25-H/5 from the Medininkai-126 borehole in Lithuania, depth 368.6 m, Ledai Formation (Eifelian). (**M**) A longitudinally sectioned specimen LGI 25-H/6 from the Stačiūnai-8 borehole in Lithuania, depth 511.35 m, Ledai Formation (Eifelian). g, ganoine; vc, vascular canal; Sf, Sharpey's fibres; W, canals of Williamson; and 1–5, the growth generations of odontodes (from youngest to oldest).

## 5. Discussion

The Middle Devonian actinopterygian collection, derived from 21 boreholes within the contemporary boundaries of Lithuania and Belarus (Figure 2), is predominantly made up of the genera *Orvikuina* and *Cheirolepis*. The isolated scales of *Cheirolepis* have been taxonomically classified as *C. gaugeri*, *C.* cf. *gaugeri*, *C. aleshkai*, *C.* cf. *aleshkai*, and *Cheirolepis* sp. (Figures 3 and 4). On the other hand, *Orvikuina* is represented by *O. vardiaensis* and *Orvikuina* sp., identified through their morphological features, along with histological examinations of the internal tissues (Figures 5 and 6). The specimens of *Orvikuina* and *Cheirolepis* were evaluated according to the encompassing crown, pattern, neck development, and base shape of the studied scales.

### *5.1. Palaeobiogeography*

The study of Middle Devonian fish fossils from the Baltic States (Estonia and Latvia) and Belarus has been extensively conducted by numerous researchers, including Sorokin (1981) [5], Valiukevičius et al. (1986) [6], Kurss (1992) [7], Lyarskaya and Lukševičs (1992) [8], Valiukevičius (1994) [9], Kleesment (1994 and 1995) [10,11], Kleesment and Mark-Kurik (1997) [45], Mark-Kurik (2000) [12], Märss et al. (2008) [14], Ivanov et al. (2011) [15], and Plax (2008, 2020, and 2022) [4,16,17]. The genus *Orvikuina*, exclusive to the Devonian period, has been identified in modern Ukraine [46], Belarus [12,16,47], Estonia [12], and Latvia [12,48], and has a fragmentary presence in Lithuania [13]. On the other hand, *Cheirolepis*, also from the Devonian period, exhibits a broader palaeogeographical distribution and is found in Belarus [12,16], Canada [49], Svalbard and Jan Mayen [34], the United Kingdom [37], the United States [35], Ukraine [46], Estonia [12], and Latvia [12,48]. Specific findings include *C. gaugeri* in Estonia [12] and Belarus [12,16], *C. aleshkai* exclusively in Belarus [4], and *C. gracilis* in both Estonia [12] and Belarus [12,16].

In summary, these newly described actinopterygian fossil records notably broaden the recognised distribution of species within the genera *Orvikuina* and *Cheirolepis* across the Baltic States, now extending to include modern-day Lithuania and Belarus.

### *5.2. Biostratigraphy*

The fish taxa discussed in this study exhibit a stratigraphic range extending from the upper part of the Lower Eifelian to the Middle Givetian epochs (as illustrated in Figures 1 and 7). This work, in conjunction with previously published research on the Middle Devonian of Belarus by Plax (2008, 2015, and 2020) [4,16,44] and Šečkus (2000) [13], contributes to the biostratigraphic correlation between Lithuania and Belarus.

In Lithuania, *Cheirolepis* cf. *aleshkai* is exclusively documented from the Ledai Formation (highlighted in Figures 1 and 7) and was identified in the northern part of the country. The fossils were discovered within clayish carbonate rocks and sediments rich in sulphide minerals. *Orvikuina vardiaensis* and *Orvikuina* sp. display a stratigraphic presence spanning from the Ledai Formation through to the end of the Butkunai Formation of the Upninkai Group (as depicted in Figures 1 and 7). These taxa were located in specific sections of these formations, primarily in central and northern Lithuania, and were found in clays, dolomite marls with dolomite interlayers, sandstone, and gypsum rocks. *Cheirolepis* sp. has been identified from the Kernave Formation to the conclusion of the Butkunai Formation of the Upninkai Group (referenced in Figures 1 and 7), with a limited distribution in western Lithuania. The fossils from this taxon were extracted from sandy silty material, accompanied by carbonaceous clays, marls, and sandstones. *Cheirolepis* cf. *gaugeri*, spanning from the Kernave Formation to the end of the Butkunai Formation of the Upninkai Group (as shown in Figures 1 and 7), exhibits a broad geographic distribution within the country. The fossils of this taxon were located in environments indicative of lacustrine–alluvial–deltaic accumulation.

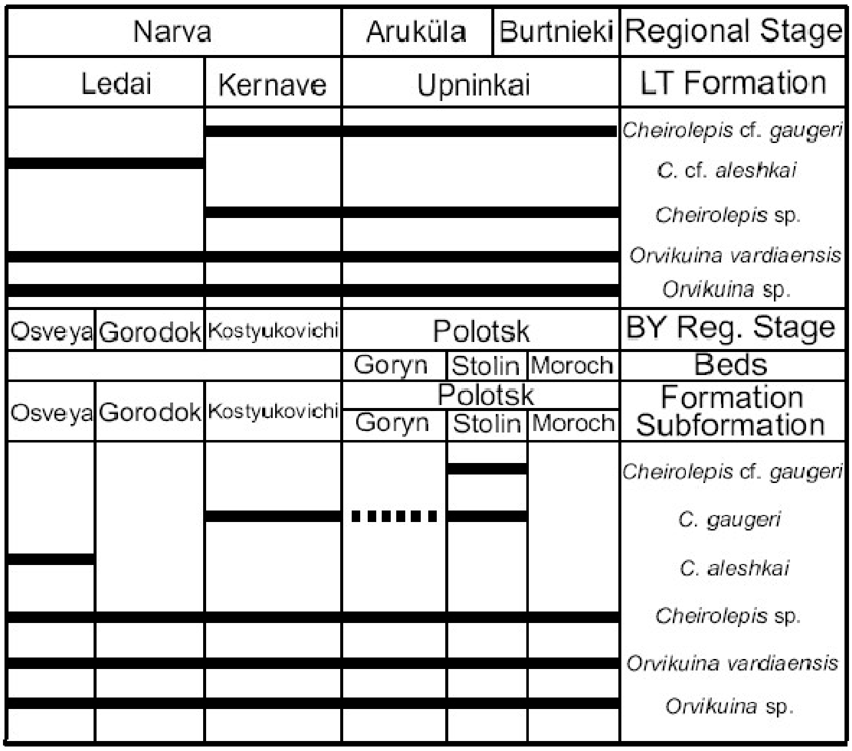


**Figure 7.** The biostratigraphic distribution of *Cheirolepis* and *Orvikuina* taxa spans the Narva, Aruküla, and Burtnieki Regional Stages in Lithuania, as well as the Osveya, Gorodok, Kostyukovichi, and Polotsk Regional Stages in Belarus.

In Belarus, *Orvikuina* sp. is recognised from the Adrov Formation through to the conclusion of the Moroch Subformation of the Polotsk Formation, showing a broad distribution within the country (as shown in Figures 1 and 7). The fossils of this taxon were discovered in various rock types that formed during the Middle Devonian period in the region. *O. vardiaensis* is identified from the Osveya Formation to the termination of the Moroch Subformation of the Polotsk Formation, with its presence noted across south–southwest, southeastern, east, northwest, north, and northeast Belarus (referenced in Figures 1 and 7). The fossils of this species were located in clays, siltstones, carbonates, and clayish carbonates. *Cheirolepis* sp. has a wide stratigraphic range from the Adrov Formation to the end of the Moroch Subformation of the Polotsk Formation, with a geographical spread across south–southwest, southeastern, east, north, and northeast Belarus (as shown in Figures 1 and 7). The fossils of this taxon were extracted from various rock types dating to the Middle Devonian period. *C. gaugeri* is recorded from the Kostyukovichi Formation to the Stolin Subformation of the Polotsk Formation, with a noted stratigraphical absence in the Goryn Subformation due to the lack of ichthyofaunal species, indicating its spread in northern and eastern Belarus (as illustrated in Figure 7). The discovered fossils were embedded in clays, carbonates, and clayish carbonate rocks. *Cheirolepis* cf. *gaugeri* is exclusively identified from the Stolin Subformation of the Polotsk Formation, found in the south–southwest and eastern parts of Belarus. The fossils of this taxon were obtained from silty and sandy sediments, highlighting the varied and rich ichthyofaunal history of the Middle Devonian period in the region.

In summary, the biostratigraphic correlation based on fish fossils reveals a complex pattern of ichthyofaunal distribution throughout the Middle Devonian period across the present-day territories of Belarus and Lithuania. The taxa *Orvikuina* sp., *O. vardiaensis*, and *Cheirolepis* sp. exhibit their broadest stratigraphic ranges during the Eifelian and Givetian series in both countries, as highlighted in Figure 7. However, the most favourable time for the abundance of *Cheirolepis* and *Orvikuina* species were identified as the late Narva time in Lithuania and the Kostyukovichi time in Belarus, according to Figures 1 and 7. During these times, the shallow epicontinental sea, characterised by normal salinity, supported a diverse ecosystem that included scolecodonts, brachiopods, ostracods, trilobites, bivalves, crinoids, gastropods, tentaculites, and vertebrates, among them rare conodonts. This indicates a rich and varied marine life that thrived in the conducive environmental conditions of the late Narva and Kostyukovichi times, as documented by Paškevičius (1997) [2] and Plax (2008 and 2013) [3,16].

## 6. Conclusions

The study of Eifelian and Givetian actinopterygian fossils from Lithuania and Belarus predominantly shows the presence of isolated scales of the genera *Orvikuina* and *Cheirolepis*. The genera are represented by species including *Orvikuina* sp., *O. vardiaensis*, *C. aleshkai*, *Cheirolepis* cf. *aleshkai*, *C. gaugeri*, *Cheirolepis* cf. *gaugeri*, and *Cheirolepis* sp. The introduction of this ichthyofaunal microfossil material has significantly broadened our understanding of the paleogeographic and environmental distribution of *Orvikuina* and *Cheirolepis* across the southeastern Baltic region and the eastern European margin of Laurasia. Prior to this research, *Orvikuina* was recognised in Ukraine, Belarus, Estonia, Latvia, and from sparse findings in Lithuania. Conversely, *Cheirolepis* exhibited a broader paleogeographic distribution during the Middle Devonian period, with known fossils primarily in Europe (including Svalbard and Jan Mayen, the United Kingdom, Ukraine, Belarus, Estonia, and Latvia) and, to a lesser extent, in North America (Canada and the US). Remarkably, the species of *Cheirolepis* had not been previously described within modern Lithuanian territory.

This study's biostratigraphic correlation of Middle Devonian ichthyofauna between Lithuania and Belarus yields significant insights at the species level. It reveals *Orvikuina* sp., *O. vardiaensis*, and *Cheirolepis* sp. as the most enduring actinopterygians throughout the Eifelian and Givetian stages in the region under study. The early to middle Givetian series, particularly in the Stolin Bed of the Polotsk Regional Stage in Belarus and the Upninkai Group in Lithuania, is pointed out as the most favourable time for these species, reflecting an environment highly conducive to their proliferation. This finding enhances our understanding of the evolutionary and environmental dynamics of the Middle Devonian period in this part of Laurasia, illustrating a complex pattern of ichthyofaunal distribution and adaptation in ancient aquatic ecosystems.

**Author Contributions:** Conceptualization, D.D. and D.P.P.; methodology, J.Š. and D.P.P.; software, D.D.; validation, D.D., J.Š. and D.P.P.; formal analysis, J.Š. and D.P.P.; investigation, D.D., J.Š. and D.P.P.; resources, J.Š. and D.P.P.; data curation, D.D. and D.P.P.; writing—original draft preparation, D.D.; writing—review and editing, D.D. and D.P.P.; visualization, D.D., J.Š. and D.P.P.; supervision, D.D. and D.P.P.; project administration, D.D.; funding acquisition, N/A. All authors have read and agreed to the published version of the manuscript.

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**Data Availability Statement:** The data are contained within this article.

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**Conflicts of Interest:** The authors declare no conflicts of interest.

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