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A NEW SPECIES OF THE DEVONIAN ACTINOPTERYGIAN FISH *MOYTHOMASIA* FROM BELARUS

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Abstract. A new species of early actinopterygian fishes, *Moythomasia lebedevi* sp. nov., is described based on numerous isolated scales occurring in Middle Devonian (Givetian, Polotskian Regional Stage) marine deposits (Goryn, Stolin and Moroch Beds) of Belarus. These scales characterize different ontogenetic stages (adult and subadult) of the fish. Few additional scales from Upper Devonian (Famennian) marine deposits of Russia (Perm Krai) are attributed to *Moythomasia* cf. *lebedevi* sp. nov. based on the ornamentation, scale shape, and the type of scale-to-scale articulation. The new data add to our knowledge on the taxonomic composition of the Givetian and Famennian ichthyofaunas of the East European platform.

Introduction

Moythomasia Gross, 1950 is a genus of Devonian actinopterygian fishes described on the basis of fossils collected in a number of localities in Europe, Northern and Southern America, Asia and Australia (Choo 2015; Schultze et al. 2021). This genus is one of the rare examples of Devonian taxa having a global distribution. Fossils of this genus are known since the Late Eifelian of the Northern Hemisphere. Representatives of this genus reached their widest distribution in the Early Frasnian, both in Laurussia and Gondwana (Choo 2015). The type species of the genus was initially described by W. Gross as *Aldingeria perforata* (Gross, 1942) on the basis of two skulls and associated scales from Upper Devonian deposits of Kokenhusen (Latvia). Since the generic name *Aldingeria* was preoccupied (Moy-Thomas, 1942), the fish from Latvia was renamed as *Moythomasia* by Gross (1950).

Eight valid species of *Moythomasia* are known up to the present time. Three of them are described based on articulated fossils, while the other five have been established upon separate scales (Choo 2015; Schultze et al. 2021). The type species *M. perforata* (Gross, 1942) was described on the basis of more complete remains. This species occurs in

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the Snetnaya Gora and Pskov Beds of the Lower Frasnian Plavinas Regional Stage of the Baltic region and Russia, as well as in the Skrygalovo and Saria Beds of the Lower Frasnian Sargaevian Regional Stage of the Republic of Belarus. The species *M. nitida* Gross, 1953 and *M. lineata* Choo, 2015 are known from the upper beds of the Plattenkalk Quarry of Heiligenstock and from the fish-bearing beds of Bergisch Gladbach, North Rhine-Westphalia (Upper Givetian to Lower Frasnian), Germany (Gross 1953; Jessen 1968; Choo 2015). The species *M. durgaringa* Gardiner et Bartram, 1977 is known from outcrops of the Gogo Formation near the Fitzroy Crossing settlement as well as from the Gneudna Formation of the Southern Carnarvon Basin, Western Australia (Trinajstic 1999). The species *M. devonica* (Clarke, 1885) has been described from the Upper Devonian of the USA based on a disarticulated skeleton. Species established upon isolated scales are *M. striata* Gross, 1953 and *M. laevigata* Gross, 1953, originating from Frasnian deposits of Bad Wildungen in Hessen, Germany (Gross 1953), as well as *M. antiqua* (Williams, 1886) from Givetian deposits of the USA. The last two species were described very briefly and they have never been revised.

The present paper is dedicated to the description of the new species *M. lebedevi* sp. nov., established also upon a collection of isolated scales originating from the Goryn, Stolin, and Moroch Beds of the Givetian Polotskian Regional Stage of the Republic of Belarus.

Geological setting

Record of new actinopterygian scales from Belarus

Scales presented in the description part of the paper have been collected from siliciclastic and carbonaceous-siliciclastic deposits of the Goryn, Stolin, and Moroch Beds of the Givetian Polotskian Regional Stage from Belarus, reached in the following boreholes: Pinsk 10, Zhitkovichi 2, Berdyzh 1, Klimovichi 4p, Smol'ki 6p, and North-Polotsk 1 (Fig. 1). According to the Stratigraphic Chart of Devonian deposits of Belarus (Obukhovskaya et al. 2010) (Fig. 2), the deposits of the Goryn and Stolin Beds should be attributed to the *Geminospora vulgata - Retispora archaeolepidophyta* palynomorph zone. This stratigraphic interval corresponds to the *Polygnathus hemiansatus* conodont zone and the lower part of the *Polygnathus varcus*. The Moroch Beds belong to the *Cristatisporites triangulatus – Corrystisporites serratus* palynomorph zone, which approximately equals the upper part of *Polygnathus varcus* conodont zone.

According to the ichthyofaunal data, the Goryn, Stolin, and Moroch Beds belong to the Polotskian Regional Stage of Belarus. This regional stage corresponds to the *Diplacanthus gravis* acanthodian zone (Valiukevičius 1994; Valiukevičius 1998; Plaksa 2008; Plax 2008). The Goryn Beds and the lower part of the Stolin Beds of the Polotskian Regional Stage are synchronous to the Aruküla Regional Stage of the Middle Devonian Givetian Stage of the Baltic and might possibly be correlated to the *Pycnosteus palaeformis* and *P. pauli* heterostracan zones (Sorokin et al. 1981; Mark-Kurik 2000; Ivanov & Lebedev 2011).

The upper part of the Stolin Beds and the Moroch Beds should be correlative to the Burtnieki Regional Stage of the Middle Devonian Givetian Stage of the Baltic. The upper part of the Stolin Beds is equivalent to the *Asterolepis dellei* placoderm zone of and the *Pycnosteus tuberculatus* heterostracan zone. The Moroch Beds belong to the *Microbrachius* placoderm zone (Plaksa 2008; Plax 2008). The Belarusian Polotskian Regional Stage corresponds to the Vorob'evkian, Ardatovian, and Mullinian Regional Stages of the Staryi Oskol Regional Superstage of the central regions of the East European platform, as well as to the *Diplacanthus gravis* acanthodian zone (Valiukevičius & Kruchek 2000), and to the Podliptsy unit of the upper part of the Lopushany Formation, the Pelcha, Kryzhov, and Batyatych Formations of the Volyn-Podolia region (Ukraine) (Plax 2011). Scale finding localities, their lithological characteristics, and the taxonomical composition of the ichthyofauna found there are discussed in detail below.

The Pinsk 10 borehole, located in the Starobin Centrocline within the western part of the Pripyat Trough, reached platy fine-grained siltstones of light-grey and greenish to blue-grey color, quartz-dominated, well-cemented with clayey cement and locally carbonate at depths of 146.0 m and 142.9 m, belonging to the Stolin Beds deposits. The siltstones yielded fish remains, i.e., 17 isolated scales of *M. lebedevi* sp. nov., scales and dentine tubercles of *Psammolepis* sp., *Ganosteus* sp., Psammo-

Fig. 1 - Geographic map showing the location of the boreholes yielding scales of *Moythomasia lebedevi* sp. nov.: 1) Pinsk 10, 2) Zhitkovichi 2, 3) Berdyzh 1, 4) Klimovichi 4p, 5) Smol'ki 6p, 6) North-Polotsk 1.

steoidei indet., scales of *Holonema* sp., a fragment of a right mixilateral plate and an indeterminate plate fragment of *Asterolepis* sp. 1, small indeterminate fragments of plates of *Asterolepis* sp., small plate fragments of Antiarcha gen. indet., scales of *Cheiracanthus latus* Egerton, 1861, *C. brevicostatus* Gross, 1973, *Diplacanthus gravis* Valiukevičius, 1988, *D. tenuistriatus* Traquair, 1894, *Acanthodes* ? sp., fragments of fin spines of *Haplacanthus* sp., *H. marginalis* Agassiz, 1845, scale fragments of *Glyptolepis* sp., *Onychodus* sp., Osteolepididae gen. indet., Actinopterygii indet., small indeterminate bones and teeth of Sarcopterygii indet., scales of *Cheirolepis* sp., *C.* cf. *gaugeri* Gross, 1973, *Orvikuina vardiaensis* Gross, 1953 (Plax & Kruchek 2014; Plax & Newman 2021; Plax & Newman 2022).

At depths of 131.5 m and 122.0 m, the same drilling penetrated light-grey, fine-grained, dense, weakly cemented, platy quartz-feldspar sandstones belonging to the Moroch Beds deposits. Thirteen scales of *M. lebedevi* sp. nov. were found in these sandstones. Five scales of *M. lebedevi* sp. nov. were found in the same borehole at the depth of 99.0 m in light grey, fine-grained, dense, weakly cemented, platy siltstones of the Moroch Beds with clayey-carbonate cement. Together with the scales of the new species noted above, this unit yielded shell fragments of lingulid brachiopods, dentine tubercles and scales of *Psammolepis* sp., Psammosteoidei indet., small fragmentary plates of Antiarcha indet., scales of *Cheiracanthus* sp., *C. brevicostatus* Gross, 1973, *C. latus* Egerton, 1861, *C. intricatus* Valiukevičius, 1985, *Diplacanthus gravis* Valiukevičius, 1988, *D. tenuistriatus* Traquair, 1894, *Rhadinacanthus longispinus* (Agassiz, 1844), *Acanthodes* ? sp., *Glyptolepis* sp., Osteolepididae gen. indet., *Cheirolepis* sp., *Orvikuina* sp., *O. vardiaensis* Gross, 1953, Actinopterygii indet., fin spine fragments of *Haplacanthus* sp., Acanthodii gen. indet., teeth of *Onychodus* sp., and Sarcopterygii indet. (Plax & Kruchek 2014; Plax & Newman 2021).

The Zhitkovichi 2 borehole located in the Starobin Centrocline of the western part of the Pripyat Trough penetrated a light grey to grey, locally with motley color spots, dense, unclearly laminated clays of the Stolin Beds at depths of 86.2 m, 88.7 m, and in the 98.0-103.0 m interval. 19 isolated scales of *M. lebedevi* sp. nov. were discovered in these clay layers. Together with these scales in the same clays the tubercles, scales, tesserae, and small plate fragments of *Schizosteus* sp., *S.* cf. *asatkini* Obruchev,

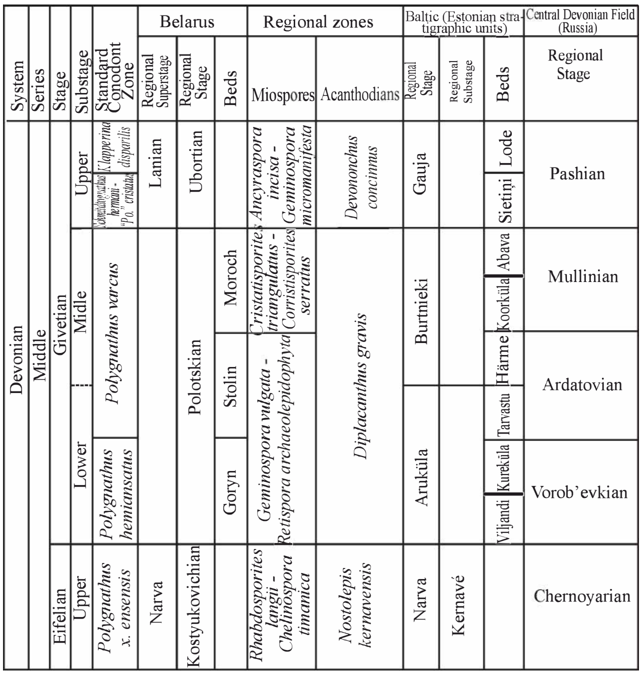

Fig. 2 - Stratification of the Givetian deposits in Belarus with underlying sediments and the correlation with synchronous deposits of adjacent territories (according to Obukhovskaya et al. 2010).

1940, *Pycnosteus* sp., *Ganosteus* sp., *Psammolepis* sp., Psammosteoidei indet., a nuchal plate, a fragment of lateral plate, a fragment of a Cd1 plate of proximal segment of the pectoral fin and a fragment of a Cd3 or Cv3 plate of distal segment of the pectoral fin of *Asterolepis* sp. 2, scales of *Acanthodes* ? sp., fin spine fragments of *Haplacanthus marginalis* Agassiz, 1845, scales of Chondrichthyes gen. indet., teeth of *Onychodus* sp., scales of *Glyptolepis* sp., Osteolepididae gen. indet., Sarcopterygii indet., *Orvikuina* sp., *O. vardiaensis* Gross, 1953, and Actinopterygii indet. (Plax & Kruchek 2010, 2014; Plax & Newman 2022) were identified.

The Berdyzh 1 borehole drilled within the Zhlobin Saddle contains at depths of 234.0 m, 233.0 m, 232.4 m, 232.0 m, 231.7 m, 231.6 m, 231.2 m, and 230.8 m grey to light-grey, greenish-blue-grey or violet-brown, fine- to middle-grained, feldspar and mica-bearing, clayey, well-cemented platy sandstones; light-grey to bluish-, yellowish-, brown-, brownish- or greenish-grey fine- and medium-grained, feldspat-quartz, micaceous, mainly clayey platy siltstones; and light-grey to greenish-grey, lilac, sandy-silty, dense lympy clays of the Stolin Beds. 79 isolated scales of *M. lebedevi* sp. nov. were found in these clays, siltstones and sandstones. Together with these scales, small fragments of lingulid shells, dentine tubercles, small plates, tesserae, and scales of *Schizosteus* ? sp., *Pycnosteus* sp., *Psammolepis* sp., *P.* ? sp., *Psammosteus* ? sp., *Ganosteus* sp., *G. stellatus* Rohon, 1901, Psammosteoidei indet., a tritor of Ptyctodontida gen. indet., a single spinal plate of Actinolepidae gen. indet., small plates of Coccosteidae gen. indet., small indeterminate plates of Holonematidae gen. indet. 4, a small infragnathal plate of Euarthrodira gen. indet., the fragment of a medioventral plate of *Asterolepis* sp. 2, small plates of *Byssacanthus* sp., *Asterolepis* sp., *A. dellei* Gross, 1940, Antiarcha gen. indet., Placodermi indet., scales of *Cheiracanthus* sp., *C. brevicostatus* Gross, 1973, *C. latus* Egerton, 1861, *Diplacanthus gravis* Valiukevičius, 1988, *D. tenuistriatus* Traquair, 1894, *Ptychodictyon* sp., *Rhadinacanthus* sp., *R. deltosquamosus* Pinakhina et Märss, 2018, *Acanthodes* ? sp., fin spine fragments of *Haplacanthus* sp., *H. marginalis* Agassiz, 1845, *Diplacanthus* sp., *Devononchus* sp., *D. concinnus* (Gross, 1930), *Archaeacanthus* sp., Ischnacanthiformes indet., Acanthodii gen. indet., scales of Chondrichthyes indet., teeth of *Protacrodus* sp., *Protacrodus* ? sp., *Phoebodus* ? sp., scale fragments of *Glyptolepis* sp., Osteolepididae gen. indet., scales of *Cheirolepis gaugeri* Gross, 1973, *C.* cf. *gaugeri* Gross, 1973, *Orvikuina* sp., *O. vardiaensis* Gross, 1953, Sarcopterygii indet., Actinopterygii indet., and teeth of *Onychodus* sp. and Sarcopterygii indet. (Plax 2015; Plax & Newman 2022) were found.

The Klimovichi 4p borehole situated in the Orsha Depression penetrated platy sandstones of light grey color, fine-grained, quartz-bearing, weakly containing mica, well-cemented, with carbonate-clayey cement, massive, dense, breccia-like, belonging to the Stolin Beds at depths of 235.5 and 235.0 m. 23 separate scales of *M. lebedevi* sp. nov. were found in these beds. Together with the scales, rare small fragments of brachiopods, tubercles and small indeterminate plates of *Psammolepis* sp., *Pycnosteus* sp., Psammosteoidei indet., fragmentary preserved plates of *Asterolepis* sp., Placodermi indet., rounded scales of *Holonema* ? sp., scales of *Cheiracanthus* sp., *C. latus* Egerton, 1861, *C. brevicostatus* Gross, 1973, *C. intricatus* Valiukevičius, 1985, *Nostolepis gaujensis* Valiukevičius, 1998, *Acanthodes* ? sp., fin spine fragments of *Diplacanthus* sp., a tooth plate of Dipteridae gen. indet., teeth and scales of *Glyptolepis* sp., Onychodontidae gen. indet., Osteolepididae gen. indet., Porolepiformes indet., Sarcopterygii indet., as well as scales of *Cheirolepis* cf. *gaugeri* Gross, 1973, *Orvikuina* sp., and Actinopterygii indet. were found (Plax & Bahdasarau 2023).

The Smol'ki 6p borehole is located within the Surazh Buried Ridge of the Voronezh Anteclise. At a depth of 279.2 m, it penetrated a platy marlstone of light-grey color, dense, unclearly laminated, solid, sand-bearing, belonging to the Goryn Beds. Eleven isolated scales of *M. lebedevi* sp. nov. were found in this marl. Together with these scales, rare scolecodonts, numerous small fragments of lingulid shells, rare small fragments of indeterminate plates and a spinal plate of Placodermi indet., two tritors of Ptyctodontida gen. indet., rare scales of *Cheiracanthus brevicostatus* Gross, 1973, teeth of Onychodontiformes indet., and numerous scales of *Orvikuina vardiaensis* Gross, 1953 were found.

The North-Polotsk 1 borehole, located in the Latvian Saddle, reached at a depth of 231.0 m platy clayey sandstones of light grey color, quartz to mica-containing, fine-grained, well-cemented, belonging to the Stolin Beds. These sandstones yielded three isolated scales of *M. lebedevi* sp. nov. Together with them, rare coalified plant remains, fragments of lingulid shells, rare tubercles of *Ganosteus* sp., plate fragments, tesserae and scales of *Tartuosteus* cf. *maximus* Mark-Kurik, 1965 (in Obruchev & Mark-Kurik 1965), scales of *Holonema* sp., small plate fragments of Placodermi indet., scales of *Rhadinacanthus longispinus* (Agassiz, 1844), *Diplacanthus tenuistriatus* Traquair, 1894, *Ptychodictyon rimosum* Gross, 1973, *P. sulcatum*? Gross, 1973, *Nostolepis gaujensis* Valiukevičius, 1998, *Cheiracanthus latus* Egerton, 1861, *Acanthodes*? sp., fin spine fragments of *Rhadinacanthus* sp., Acanthodii gen. indet., rare scales (or small platelets) of *Karksilepis parva* Märss, 2008, polygonal platelets of *Karksilepis* sp., scale fragments of Osteolepididae gen. indet., Porolepiformes gen. indet., Sarcopterygii indet., teeth of Onychodontidae gen. indet., Sarcopterygii indet., scales of *Orvikuina* sp., Actinopterygii indet. (Plax & Newman 2021, 2022) have been found.

Records of new actinopterygian scales from Russia

The study material was collected from the Gubakha locality (Figs. 3 and 4), situated somewhat downstream opposite the Koksokhim Bridge (thus abbreviated as the OKB section), on the left bank of the Kosva River, opposite the Koksokhim industrial area of the City of Gubakha, Perm Krai (=Perm Region), Russia.

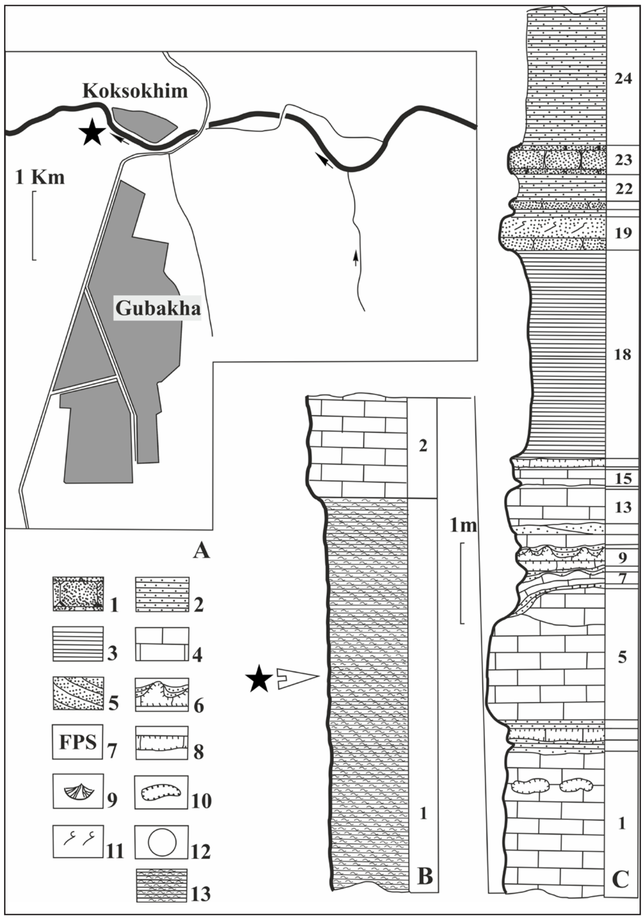

Fig. 3 - Geographical and stratigraphic position of the Gubakha Opposite Koksokhim Bridge (OKB), section (marked by an asterisk). A) geographical position of the section (asterisk); B) stratigraphic column of the Gubakha, Opposite Koksokhim Bridge (OKB) section; C) stratigraphic column of the Gubakha–Stary Most (b) sections. Legend: 1 – sandstones; 2 – siltstones; 3 – claystones; 4 – limestones; 5 – cross-bedding; 6 –build-ups; 7 –palaeosols; 8 – chert layer; 9 – marine invertebrates; 10 – chert concretions; 11 – fossil roots; 12 – plant macro- and microfossils; 13 – oil-bearing siltstones of "Domanic"-facies.

The deposits outcropping at the cliff are represented by black, dark-grey to brownish fine-laminated oil-bearing siltstones of so called "Domanic facies" enriched in organic matter, which belong to the Upper Devonian (Famennian; for further information see Naugolnykh, 2009). In terms of structural geology, the locality is in the core area of the Kizel anticlinal zone. The siltstones contain shells of clymeniids preliminary determined as *Clymenia laevigata* (Münster, 1831) and *Clymenia* sp. Several clymeniid jaws, rare orthoconch nautilids, numerous rhynchonellid brachiopods and ichnofossils were found in the same strata as well. The scales of species of *Moythomasia* described in the present paper were collected from these deposits. The general

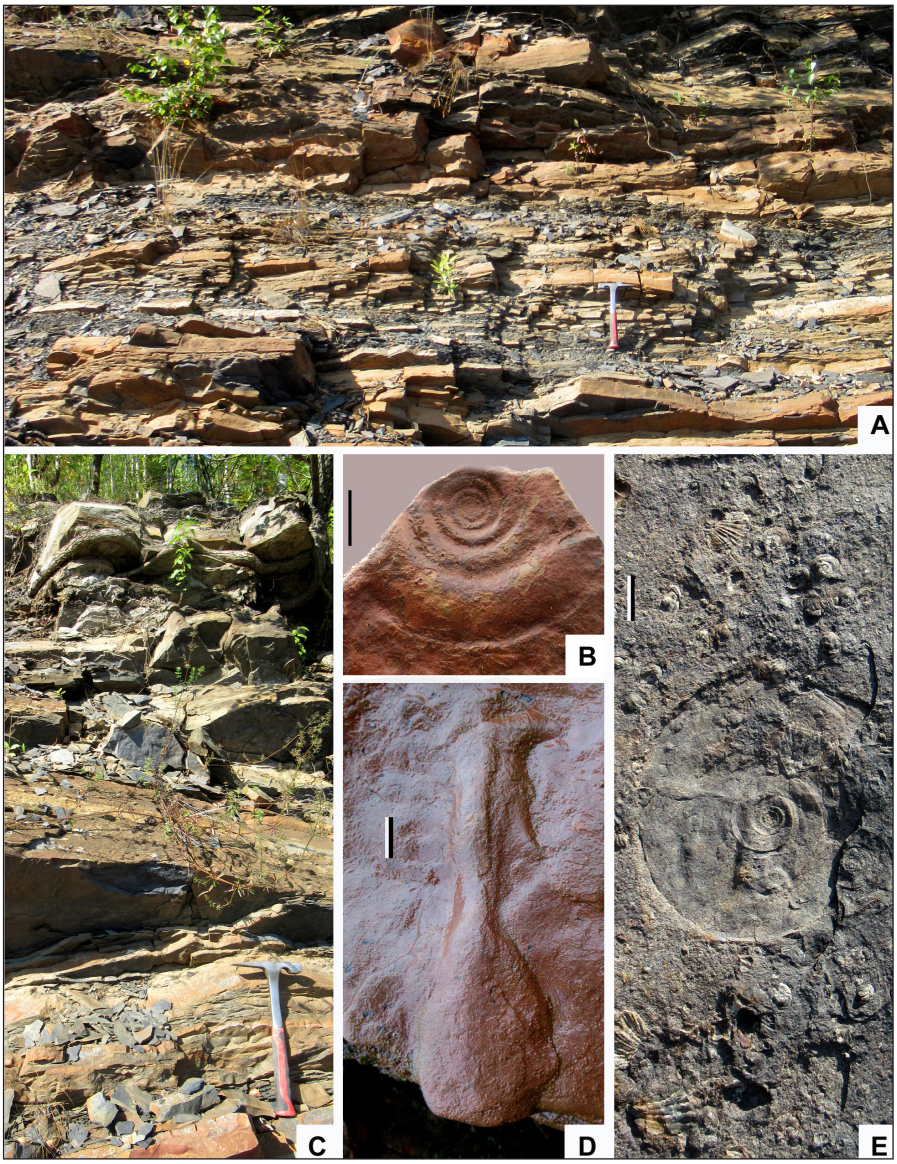

Fig. 4 - A, C) Views of the Gubakha Opposite Koksokhim Bridge (OKB) section; B) *Clymenia laevigata* (Münster, 1831); D) a pear-shaped burrow ichnofossil (putative dipnoan burrow; E) *Clymenia* sp. and rhynchonellid brachiopods. Scale bar for B, D, E is 1 cm.

thickness of the Famennian deposits in this section is about 15 m.

The Famennian deposits are covered upstream the Kosva River by grey and greyish-yellow mudstones of Early Carboniferous (Tournasian) age. In contrast to the relatively deep-marine the Famennian siltstones, the Tournasian mudstones represent shallow-water marine environments with a taxonomically rich fauna of corals (Tabulata and Rugosa), bryozoans, brachiopods and mollusks (Naugolnykh 2022; see this paper for further references). The Tournasian mudstones are covered by Viséan sandstones and limestones, often with paleosols (FPS-profiles) and remains of terrestrial plants, mostly lepidodendrids. Thus, the general succession of the Famennian to Viséan deposits in this area records a prominent regressive trend.

Materials and methods

All remains attributed to the new species described below are isolated scales. They derive from Givetian (Middle Devonian) deposits of Belarus. Numerous scales have been discovered both in clastic and clastic-carbonatic deposits of Middle Devonian age. Samples containing the studied scales were collected from the boreholes: Pinsk 10, Zhitkovichi 2, Berdyzh 1, Klimovichi 4p, Smol'ki 6p, and North-Polotsk 1. Several similar scales were found in Gubakha, opposite the Koksokhim Bridge, in Russia, in Famennian deposits (see below).

The studied specimens are kept in the palaeontological collection at the Department of Mining of the Belarusian National Technical University (BNTU), and at the Borissiak Palaeontological Institute of the Russian Academy of Sciences, collection number 5912.

5 % formic acid and 9–10% acetic acid were used for the extraction of fish scales from the drill cores. Rock was dissolved in acid during three to five days. The residual sediment was washed through several times to remove the clayey particles. The washed sediment was dried and then carefully checked under a MBS-1 binocular microscope. Scales were selected by hand using fine brushes and collected in Franke cameras.

Scanning electron micrographs were made at the Belarusian State Technological University (BSTU) with a JSM-5610 LV (JEOL, Japan) electron microscope and at the PIN Analytic Instrument Department with a TESCAN VEGA-III XMU electron microscope without coating. The micrographs were processed with Adobe Photoshop CS6 program. Figures were prepared using the software CorelDRAW 2019 Graphics Suite.

Scales are described following Esin's (1990) scheme, which subdivides the squamation into areas of sufficiently similar scale morphology (Fig. 5). Only flank scales from the anterior body half (areas A and B) are suitable for taxonomic description. This algorithm has been successfully used for describing the scale cover of the Devonian actinopterygians *Moythomasia* (Trinajstic 1999a, b), *Mimipiscis* (Trinajstic 1999b; Choo 2011), *Donnrosenia* (Long et al. 2008), and *Gogosardina* (Choo et al. 2009). Scale morphology has been described using the terminology of Schultze (1966), with modifications by Esin (1990), Burrow (1994), Qu et al. (2013), Bakaev & Kogan (2020, 2022) and Bakaev & Bulanov (2021).

Esin (1995) described three ontogenetic stages in the growth of palaeoniscoid-type ganoid scales: juvenile, subadult and adult, with transitional periods in between. Trinajstic (1999b) identified the same three ontogenetic stages for *M. durgaringa* scales. Our data suggest that the growth pattern of *M. lebedevi* sp. nov. scales are very similar to that of *M. durgaringa*. *M. lebedevi* sp. nov. scales described herein can be identified as adult (Fig. 6B, E-G, M-P), transitional (Fig. 6C, D) or subadult (Fig. 6A, I-L) based on their small size, marked boundaries between the ganoine ridges and absence or underdevelopment of the articular elements. According to Esin (1995), species-level taxonomic features develop towards the end of the subadult stage, making their observation in the scales described below possible. We

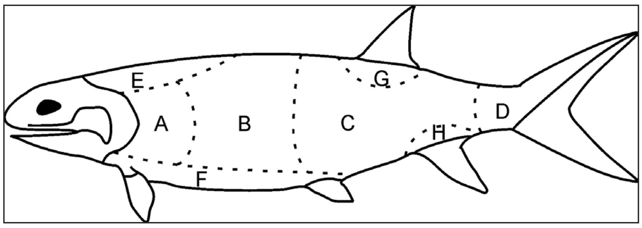

Fig. 5 - A generalized basal actinopterygian with typical squamation areas A–H according to Esin (1990).

describe both adult and subadult scales. However, the species is erected upon scales with completely developed "adult" characters (Fig. 6B). Thus, we give a diagnosis for adult scales in areas A and B.

Institutional abbreviations: BNTU: Belarusian National Technical University, Minsk, Belarus; PIN: Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia.

Systematic palaeontology

Class **OSTEICHTHYES** Huxley, 1880
Subclass **ACTINOPTERYGII** Cope, 1887 (*sensu* Goodrich, 1930)
Superorder **Palaeoniscimorpha** Lund, Poplin & Mccarthy, 1995
Family Moythomasiidae Kazantseva, 1971
Genus *Moythomasia* Gross, 1950

Moythomasia lebedevi sp. nov.

Figs. 6, 7

2008 *Moythomasia* ? sp. (pars). – Plax, p. 79, table. 1.
2010 *Moythomasia* ? sp. – Plax, Kruchek, p. 35 and 45, text-fig. 2, pl. II, figs. 9–11.
2013 *Moythomasia* ? sp. (pars). – Plax, p. 89.
2014 *Moythomasia* ? sp. – Plax, Kruchek, p. 34 and 36, text-fig. 3, text-fig. 4, table, pl. VI, figs.11, 12.
2014 *Moythomasia* ? sp. (pars). – Plax, p. 17 and 18.
2015 *Moythomasia* ? sp. – Plax, p. 31, table, text-fig. 3, pl. V, fig. 8.
2023 *Moythomasia* ? sp. – Plax, Bahdasarau, p. 165, pl. VII, figs. 6, 7 (?), 8, 9, 10, 11, 13, 14.
2023 *Moythomasia* sp. – Plax, p. 236.

Etymology: The name of the species is given in honor of the palaeoichthyologist Oleg Anatolevich Lebedev.

Holotype: Scale of area B, close to area C; collection number BNTU 143/4-12. (Fig. 6B).

Material: 170 isolated scales.

Type horizon and locality: Klimovichi 4p borehole, depth 235.0 m; Belarus, Klimovichi district, Mogilev region; Middle Devonian, Givetian, Polotskian Regional Stage, Stolin Beds.

Diagnosis: Rectangular scales, with a small and rounded anterodorsal corner and a weakly inclined anteroventral corner. Peg and socket well-developed. Depressed field very narrow (less than 1/10 the length of the scale). The anterior margin of the free field consists of vertically or subvertically aligned ridges with pronounced second-order ridges along the sloping leading edge. Towards the anteroventral corner, the ridges curve posterior and then follow the ventral margin to create a serration on the posterior margin. The posterior part of the free field bears coalesced ridges or is almost smooth with subhorizontally oriented rolls separated by shallow cannelures. Posteoventrally-facing large elliptical pores are concentrated in the grooves or cannelures and follow an approximately linear pattern. The free field terminates with short denticles.

Description. Area A (Fig. 6A, D). Rectangular scales, with a height/length ratio varying between 2:1 for midline anterior scales (Fig. 6A) and 1.5:1 for scales closer to area B (Fig. 6D) and to the dorsal and ventral margins. The anterior and posterior margins are straight. The anterodorsal corner is small and rounded and does not extend significantly above the dorsal scale margin. The anteroventral corner has a weak (less than 30°) dorsal inclination. The peg and socket are high and deep, and the peg base is ca. 1/5 the length of the scale. The keel is well-developed. The depressed field is very narrow, ca. 1/10 the length of the scale. The anterior margin of the free field consists of vertically aligned; narrow ridges flattened-triangular in cross-section with pronounced second-order ridges along the sloping leading edge. The ridges curve posteriad in the area of the anteroventral corner to create a serrated posterior margin of the scale. The grooves separating the ridges are wide and long. The posterior part of the free field consists of ganoine ridges well-separated by long grooves, which do not anastomose in the subadult scale (Fig. 6A), but consist of coalesced ridges in the adult-subadult scale (Fig. 6D). There are deep elliptical pores between the ridges. The ganoine ridges terminate with up to nine short denticles along the caudal margin.

Area B (Fig. 6B, C, I, L, O). Scales with a height equal to or slightly exceeding the length. The keel, peg and socket are well-developed in the adult scale (Fig. 6B), poorly developed in a subadult scale (Fig. 6L), and broken in others (Fig. 6C, I). The anterior margin of the free field consists of vertically aligned ridges (like in area A scales). The posterior part of the free field of the adult scale (Fig. 6B) is made of an almost smooth surface (on the periphery) and flattened subhorizontally oriented rolls (in the central part) separated by shallow cannelures. In contrast, the anterior part of the free field is ornamented with of coalesced ridges in the adult-subadult scale (Fig. 6C) and well-separated ridges that do not anastomose in the subadult (Fig. 6L) and juvenile-subadult (Fig. 6I) scales. Numerous moderately large pores are located on the smooth surface (concentrated in the cannelures) or in the grooves between the ridges. All pores have higher anterodorsal than posteroventral margins, forming a posteroventrally-facing slope for each pore. In both cases, pores follow an approximately linear pattern towards the serrations along the caudal margin. The free field terminates in up to six denticles along the posterior margin. Other characters are as in area A.

Area C (Fig. 6E-H, J, K, M). Rhombic scales, length exceeding height by 1.2–1.5 times. The peg and socket are poorly developed in scales close to area B and absent in scales close to area D. The free field is covered by coalesced, short, subvertically or diagonally aligned ridges in the anterior part and separate ridges in most of the posterior part. The ganoine ridges terminate in up to four short posterior denticles along the caudal margin. Other characters (and their evolution during ontogeny) are as in areas A and B.

Area D (Fig. 6P). Scales are rhomboid, more than twice as long as high, and become more elongate towards the caudal fin. The free field has fine second-order ridges along the anterior and dorsal margins. Keel, peg and socket are absent. The free field of adult scales is smooth, with a few posteroventrally-facing large pores in the center. The posterior margin of the scale bears one or two denticles. Other features as in area C.

Area F (Fig. 6N). Elongated rhombic scales. The depressed field is moderately developed, occupies approximately 1/4 of the scale and extends along the dorsal margin of the free field. Peg, socket and keel are small or absent. The anterior and dorsal margins of the free field are dissected by thin furrows. The ridges of the free field are sparse and short, with pronounced second-order ridges along the sloping leading edge. The surface of the free field is smooth with several pores, some linearly arranged in the center (Fig. 4G). The posterior margin of the free field bears one to three denticles. Other features as in area C.

Remarks. The type specimen BNTU 143/4-12 (Fig. 6B) represents the most anatomically informative specimen. Smaller scales are available, but they are inappropriate as holotype given their likely juvenile ontogenetic status.

Choo (2015) mentioned that *Moythomasia* spp. "…*do not share any unique squamation-based characters*

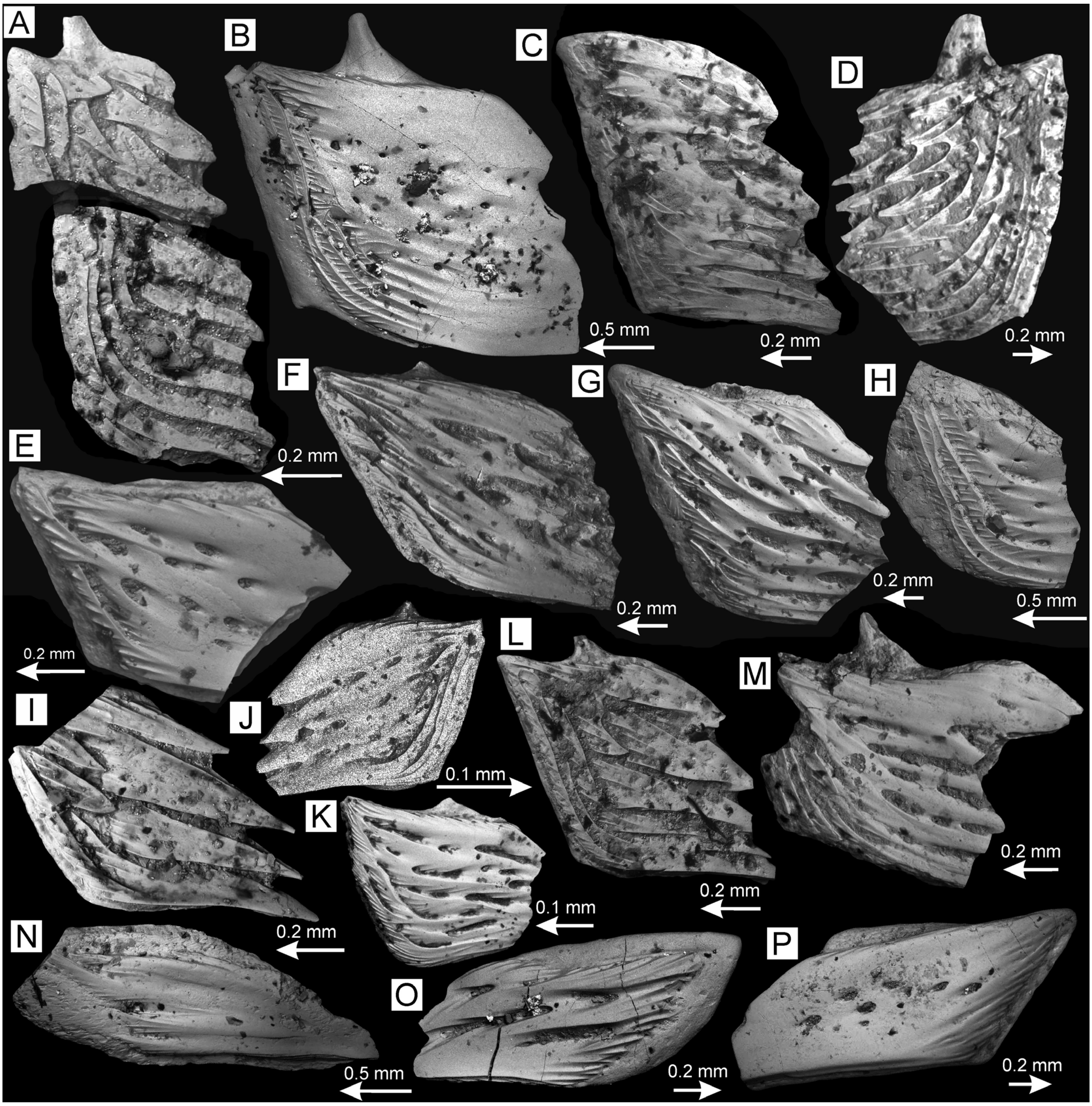

Fig. 6 - *Moythomasia lebedevi* sp. nov. scales in crown view, from the Givetian deposits of Belarus. A) subadult scale from area A, BNTU 86/34-22, Berdyzh 1 borehole, depth 231.2 m, Polotskian Regional Stage, Stolin Beds; B) holotype, adult scale from area B, close to area C, BNTU 143/4-12, Klimovichi 4p borehole, depth 235.0 m, Polotskian Regional Stage, Stolin Beds; C) transitional adult-subadult scale from area B, BNTU 57/31*б*-16*с*, Zhitkovichi 2 borehole, depth 86.2 m. Polotskian Regional Stage, Stolin Beds; D) transitional adult-subadult scale from area A, close to area B, BNTU 57/28g-66, Zhitkovichi 2 borehole, depth 98.0-103.0 м, Polotskian Regional Stage, Stolin Beds; E) adult scale from area C, close to area H, BNTU 86/27-24, Berdyzh 1 borehole, depth 234.0 m, Polotskian Regional Stage, Stolin Beds; F) adult scale from area C, close to area D, BNTU 86/35-23, Berdyzh 1 borehole, depth 230.8 m, Polotskian Regional Stage, Stolin Beds; G) adult scale from area C, close to area D, BNTU 86/32-12, Berdyzh 1 borehole, depth 231.6 m, Polotskian Regional Stage, Stolin Beds; H) fragmentary scale from area C, BNTU 143/5-14, Klimovichi 4p borehole, depth 235.5 m, Polotskian Regional Stage, Stolin Beds; I) transitional juvenile-subadult scale from area B, close to area C, BNTU 86/34-21, Berdyzh 1 borehole, depth 231.2 m, Polotskian Regional Stage, Stolin Beds; J) subadult scale from area C, BNTU 86/30-1b, Berdyzh 1 borehole, depth 232.0 m, Polotskian Regional Stage, Stolin Beds; K) subadult scale from area C, BNTU 85/21-2a, Pinsk 10 borehole, depth 122.0 m, Polotskian Regional Stage, Moroch Beds; L) subadult scale from area B, close to area C, BNTU 86/34-24, Berdyzh 1 borehole, depth 231.2 m, Polotskian Regional Stage, Stolin Beds; M) adult scale from area C, BNTU 86/32-18, Berdyzh 1 borehole, depth 231.6 m, Polotskian Regional Stage, Stolin Beds; N) adult scale from area F, BNTU 86/31-13, Berdyzh 1 borehole, depth 231.7 m, Polotskian Regional Stage, Stolin Beds; O) adult scale from area C, close to areas H and D, BNTU 143/4-19, Klimovichi 4p borehole, depth 235.0 m, Polotskian Regional Stage, Stolin Beds; P) adult scale from area D, BNTU 86/27-13, Berdyzh 1 borehole, depth 234.0 m, Polotskian Regional Stage, Stolin Beds. Arrows point anteriad.

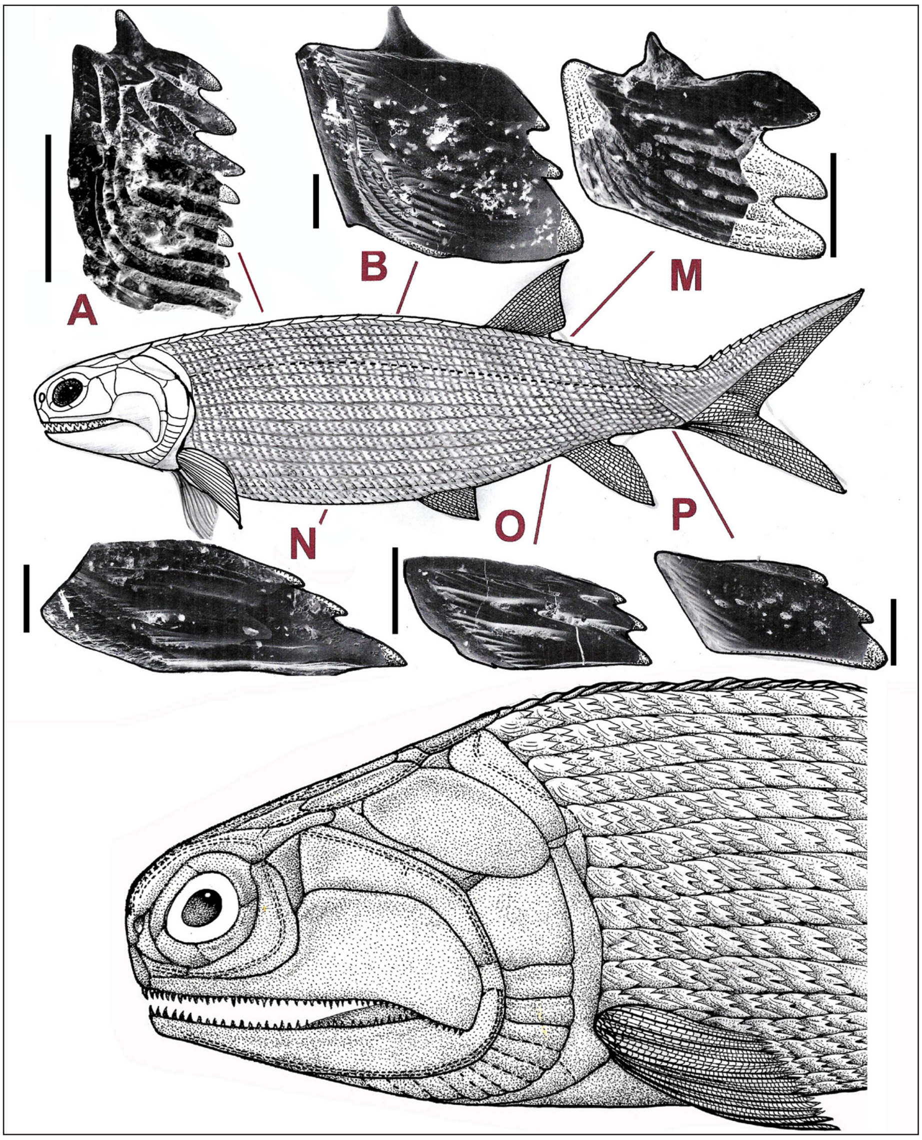

Fig. 7 - *Moythomasia lebedevi* sp. nov. Tentative restoration of the fish with the distribution of scale types over the body. Lettering corresponds to figure indexes in Fig. 6. General morphology of the fish skull is given after Jessen, 1968, with modifications. Scale bars are 0.5 mm.

exclusive to other Devonian actinopterygians". Therefore, we compare the scales of *Moythomasia lebedevi* sp. nov. across Devonian actinopterygians.

Unlike the scale cover of *M. lebedevi* sp. nov., the squamation of *Cheirolepis* (Zylberberg et al. 2016) and *Tegeolepis* (Dunkle & Schaeffer 1973) is micromeric. *Osorioichthys* (Taverne 1997), *Mimipiscis* (Trinajstic 1999b; Choo 2011), *Gogosardina* (Choo et al. 2009), *Krasnoyarichthys* (Prokofiev 2002), *Donnrosenia* (Long et al. 2008), *Howqualepis* (Long 1988; Choo et al. 2009), *Raynerius* (Giles et al. 2015) and *Palaeoneiros* (Giles et al. 2023) differ from *M. lebedevi* sp. nov. in the wider depressed field, in the lack of vertically aligned ridges and posteroventrally-facing large elliptical pores and the presence of diagonal, rarely or not anastomosing, non-coalesced ganoine ridges on the free field.

Vertically or subvertically aligned ridges along the leading edge of the free field are present on scales of the Famennian actinopterygians *Limnomis* (Daeschler 2000), *Cuneognathus* (Friedman & Blom 2006) and *Stegotrachelus* (Swartz 2009; Choo 2015). However, the adult scales of these fishes are squat (about as high as long even in the A and B areas) and have more pronounced and non-coalesced sculptural ridges in the posterior part of the free field, unlike *M. lebedevi* sp. nov. Additionally, *Limnomis* and *Cuneognathus* have a weakly developed peg and socket.

M. lebedevi sp. nov. differs from all other species of *Moythomasia,* except for *Moythomasia* from the Middle or Late Devonian of Iowa, in the combination of a very narrow depressed field and vertically aligned ridges on the anterior margin of the free field. *M. striata* and *M. lineata* differ from *M. lebedevi* sp. nov. in a linear free-field ornament consisting of straight, separate ridges without the presence of pores. Additionally, *M. striata* differs from *M. lebedevi*

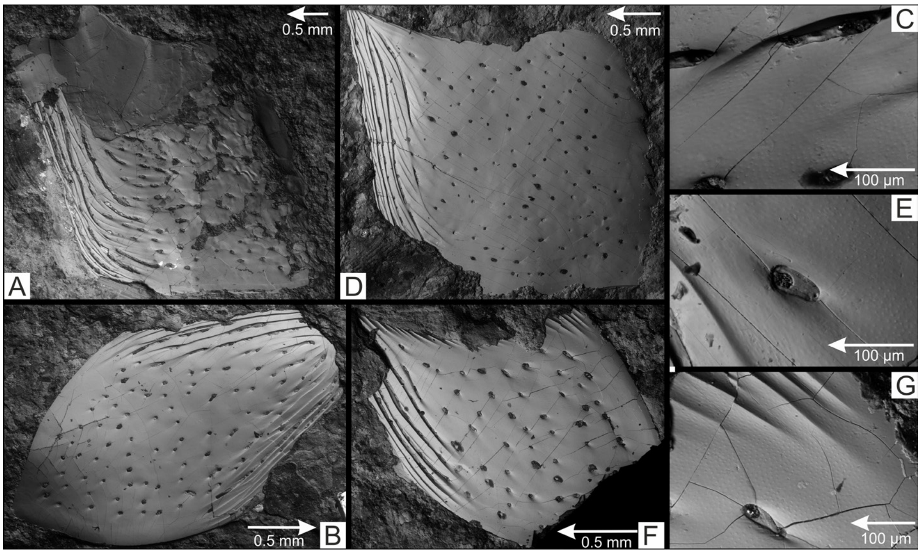

Fig. 8 - *Moythomasia* cf. *lebedevi* sp. nov. scales in crown view, from the Famennian deposits of Russia. City of Gubakha, Perm krai (=Perm region), Russia. A) scale from area A, close to area B, PIN 5912/1; B) ridge scale, PIN 5912/2; C) close-up of B; D) scale from area B, PIN 5912/3; E) close-up of D; F) scale from area B, PIN 5912/4; G) close-up of F.

sp. nov. in the much more prominent anterodorsal process (higher than the articular peg).

M. nitida and *M. durgaringa* resemble *M. lebedevi* sp. nov. in the free field sculpture (coalesced ridges or rolls with second-order ridges along the sloping leading edge and large posteroventrally-facing pores, which are concentrated in grooves or cannelures) and in the scale shape. However, they differ from *M. lebedevi* sp. nov. in the relatively more pronounced sculptural ridges (even in adult scales) and the lack of vertically aligned ridges along the leading edge of the free field.

The overall morphology of the scales of *M. lebedevi* sp. nov. is closest to that of *Moythomasia* from the Middle or Late Devonian of Iowa (Storrs 1987), from the Holy Cross Mountains of Poland (Liszkowski & Racki 1993) and from the Gubakha locality (Famennian of Perm Krai) (Fig. 8). The similarly aged scales of *Moythomasia* from Iowa and Poland may belong to *M. lebedevi* sp. nov., but they are too fragmentary and represented by a small sample. Therefore, we consider them as *M.* cf. *lebedevi* sp. nov. The more recent scales from Gubakha differ from *M. lebedevi* sp. nov. by the nearly smooth (except the vertically aligned ridges) free field, the finer and more numerous pores and denticles. However, these could be ontogenetic differences and we consider them too as *M.* cf. *lebedevi* sp. nov.

Thus, *M. lebedevi* sp. nov. is mostly similar to *M. nitida* and *M. durgaringa* among all Devonian ray-finned fishes. Morphological similarity (but with distinct differences) of *M. lebedevi* sp. nov. with two valid species of *Moythomasia* allows us to describe a new species, assigning it to this genus.

Geological age and geographical distribution. Middle Devonian, Givetian, Polotskian Regional Stage, Goryn, Stolin and Moroch Beds; Belarus, Luninets district of the Brest region, Soligorsk district of the Minsk region, Chechersk district of the Gomel region, Klimovichi and Kostyukovichi districts of the Mogilev region, Rossony district of the Vitebsk region.

Occurrence. Belarus, Luninets district, Brest region, Pinsk 10 borehole, depths 146.0 m, 142.9 m, 131.5 m, 122.0 m and 99.0 m; Soligorsk district, Minsk region, Zhitkovichi 2 borehole, depths 86.2 m, 88.7 m, and 98.0-103.0 m; Chechersk district, Gomel region, Berdyzh 1 borehole, depths 234.0 m, 233.0 m, 232.4 m, 232.0 m, 231.7 m, 231.6 m, 231.2 m and 230.8 m; Klimovichi district, Mogilev region, Klimovichi 4p borehole, depths 235.5 m and 235.0 m; Kostyukovichi district, Mogilev region, Smol'ki 6p borehole, depth 279.2 m; Rossony district, Vitebsk region, North-Polotsk 1 borehole, depth 231.0 m.

Discussion

Devonian actinopterygians are relatively less diverse, both taxonomically and ecologically, than coeval sarcopterygians (Anderson et al. 2011). However, already in the Devonian, the radiation of several actinopterygian lineages had occurred. These lineages continued their independent existence in the Carboniferous (Giles et al. 2015; Figueroa et al. 2021; Giles et al. 2023). Their divergence was not accompanied by an increase in ecological diversity.

Key modifications in the jaw and locomotion apparatus that allowed the inhabitation of new ecological niches had only appeared in the Carboniferous, just after the Hangenberg event (Giles et al. 2023).

The earliest evolution of actinopterygians, which branched off from the sarcopterygians in the Middle or Late Silurian, is still weakly studied. The most ancient findings of the actinopterygians originate in the Middle Devonian. However, by this time several independent and parallel evolved clades had already existed. *M. lebedevi* sp. nov. is the most ancient representative of the genus *Moythomasia*, and it is closely related to the two valid species *M. nitida* and *M. durgaringa*. Moreover, *M. lebedevi* sp. nov. is characterized by a wide geographic distribution in Laurussia, and by a wide stratigraphic range as well. Earlier, Choo (2015) suggested that the genus *Moythomasia* appeared in Gondwana in pre-Frasnian time for the first time. However, our data contradict to this assumption and point to a first appearance of this genus at least in the Middle Devonian of Laurussia, from where the genus spread out into Gondwana already by the beginning of the Late Devonian.

Conclusion

Numerous isolated scales form the base for the description of the new species *M. lebedevi* sp. nov. as a result of a careful revision of the palaeoichthyological collections at hand. Scales of the new species considerably differ from other previously described scales of *Moythomasia* species. Their characteristics are easily diagnosable. The new species adds new data on the taxonomic composition of the Middle and Upper Devonian palaeoichthyological assemblages of the East European Platform and the Urals of Russia.

Data Availability Statement

The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

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