Estonian Journal of Earth Sciences
2025, **74**, 2, 96–119

https://doi.org/10.3176/earth.2025.07

www.eap.ee/earthsciences
Estonian Academy Publishers

RESEARCH ARTICLE

Received 29 November 2024
Accepted 12 March 2025
Available online 2 June 2025

Keywords:
taxonomy, biostratigraphy, Vertebrata, Silurian and Lower Devonian, Ufa Amphitheatre, Central Urals

Corresponding author:
Tiiu Märss
Tiiu.Marss@taltech.ee

Citation:
Märss, T. 2025. On the Silurian and lowermost Devonian vertebrates of the Ufa Amphitheatre, the Central Urals, with emphasis on agnathans and correlations with the East Baltic. *Estonian Journal of Earth Sciences*, **74**(2), 96–119. https://doi.org/10.3176/earth.2025.07

On the Silurian and lowermost Devonian vertebrates of the Ufa Amphitheatre, the Central Urals, with emphasis on agnathans and correlations with the East Baltic

Tiiu Märss

Department of Geology, Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia

ABSTRACT

The vertebrate microremains from the Wenlock (lower Silurian) to the Lower Lochkovian (Lower Devonian) of the Ufa Amphitheatre, on the western slope of the Central Urals, have been studied. This investigation discusses vertebrate taxonomy and biostratigraphy, with an emphasis on the agnathan groups Thelodonti, Heterostraci, Osteostraci, and Anaspida. The thelodont species identified in the region include *Paralogania martinssoni* (Gross), *Phlebolepis elegans* Pander, *Thelodus laevis* (Pander), *Thelodus carinatus* (Pander), *Thelodus parvidens* Agassiz, *Thelodus sculptilis* Gross, *Thelodus trilobatus* (Hoppe), *Turinia pagei* (Powrie), *Boreania minima* Karatajūtė-Talimaa, and *Talivalia elongata* (Karatajūtė-Talimaa). Representatives of Heterostraci – Eriptychiiformes with *Oniscolepis* Pander, and Traquairaspidiformes with ‘*Traquairaspis*’ sp. – are briefly discussed along with recently described cyathaspidid heterostracans (*Archegonaspis lindstroemi* Kiaer, *Archegonaspis integra* (Kunth), *Cyathaspis alexanderi* Märss, and *Cyathaspis alexanderi*? Märss). Osteostracans comprise *Tremataspis schmidti* Rohon, *Tremataspis rohoni* Robertson, *Thyestes*? sp. ind., *Procephalaspis* sp. ind., *Tahulaspis ordinata* Märss, Afanassieva et Blom and *Tahulaspis praevia* Märss, Afanassieva et Blom, the latter two being assigned to a new family, Tahulaspididae fam. nov. A few birkeniid anaspids (*Schidiosteus mustelensis* Pander, *Septentrionia mucronata*? Blom, Märss et Miller, and *Liivilepis curvata* Blom, Märss et Miller) have also been included to bring together all Silurian and Lower Devonian agnathans of the Ufa Amphitheatre in a single publication. Vertebrate distribution data have been used to determine the age of the strata and correlate the beds with those of the East Baltic. A reversed succession of vertebrate distribution was discovered in a section on the southern bank of Mikhailovsk Pond, and the recurrence of the bonebed complex was detected in the Tabuska Hill section (right bank of the River Ufa).

Introduction

The Silurian and Lower Devonian vertebrates of the Ufa Amphitheatre, located on the western slope of the Central Urals (Fig. 1A), have been insufficiently studied. Research on these fossils began in the 1970s when Dr V. A. Nasedkina (Sverdlovsk, now Yekaterinburg) provided the author of this paper with the first sample (N. 3182) from the locality in the southern area of Mikhailovsk Pond. The sample contained scales of the thelodont *Phlebolepis elegans* Pander, a common taxon in the Ludlow of the Baltic Sea region but also found elsewhere (Welsh Borderland, Great Britain; Poland; Gotland Island, Sweden; Timan-Pechora region, Komi, and the Severnaya Zemlya Archipelago, Russia). Recognising the potential of vertebrate microremains for correlating Uralian sections with western regions of the East European Platform, further studies were undertaken.

In the summer of 1973, the first Estonian expedition to the geological sections of Mikhailovsk Pond took place, during which the sections of both southern and northern banks of the pond were described and sampled bed by bed. Additionally, several small, scattered outcrops along the rivers Serga, Ufa, and Kuba were visited and sampled. Vertebrate remains were recovered from deposits ranging from the Wenlock (lower Silurian) to the Emsian (Lower Devonian). In 1983, A. Zhivkovich and P. Chekhovich (then of the Institute of Lithosphere, Moscow, Russia) discovered the first large fragments of the head shields of cyathaspidid heterostracans (Agnatha)

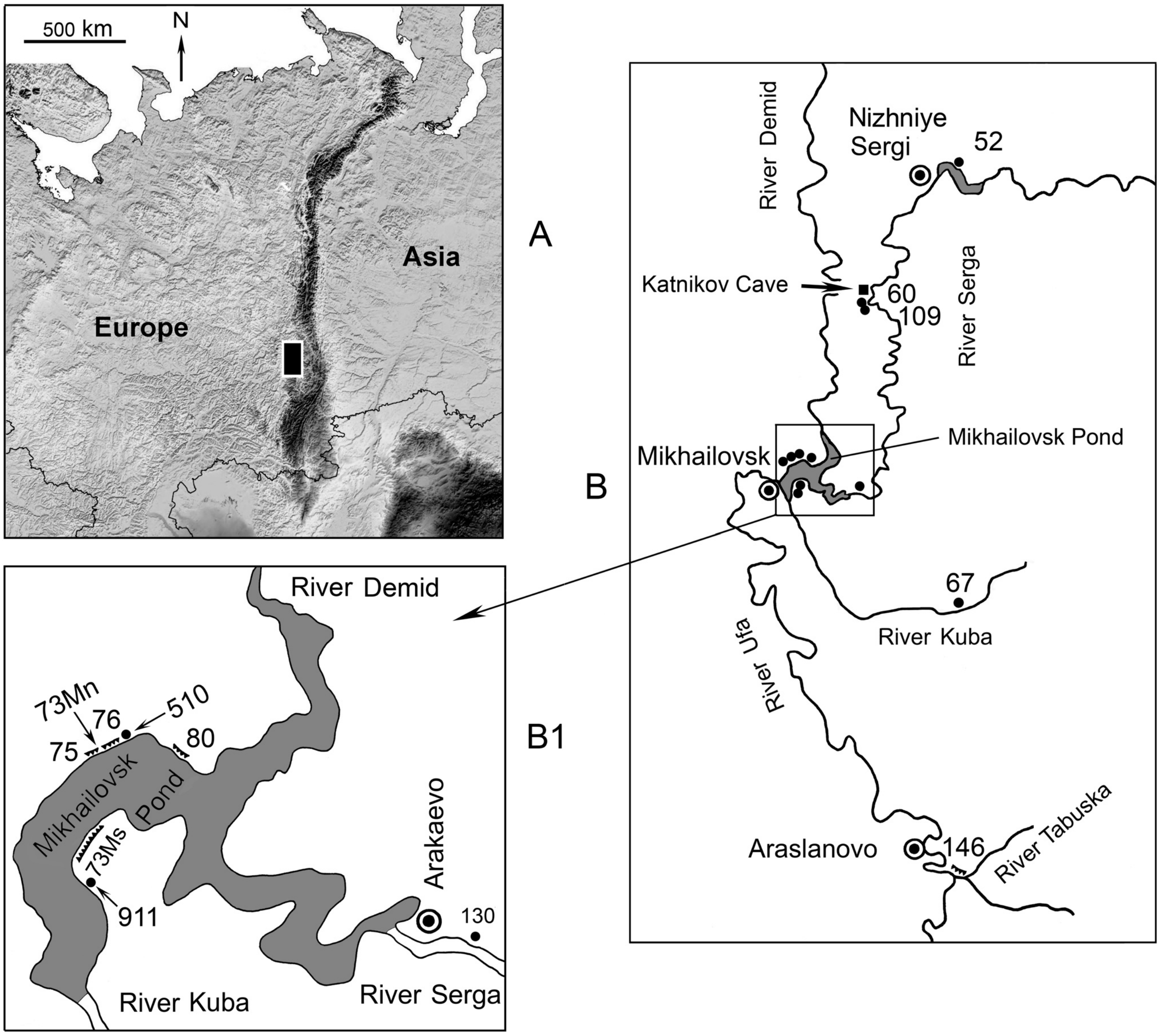

Fig. 1. **A** – map showing the location of the Ural Mountains and the Ufa Amphitheatre (Plateau) in the Central Urals. **B** – localities (simple black dots) containing vertebrate remains; B1 – enlarged extract of the area labelled in the black square. Mn, Ms – geological sections on the northern and southern banks of Mikhailovsk Pond, respectively. The simplified geographical maps in schematics B and B1 are based on Chekhovich et al. (1994, fig. 1), with minor additions from Google Maps (rivers north and south from Mikhailovsk, Sverdlovsk Oblast). The geographical positions of the localities (marked by numbers or combinations of number and letter) were provided by P. Chekhovich (pers. comm., 25.03.1992 and 26.11.2023).

in the outcrops on Tabuska Hill, on the right bank of the River Ufa. These findings spurred subsequent expeditions in 1985 and 1987, involving geologists from Tallinn, St Petersburg, and Moscow. Fieldworks conducted between 1973 and 1987 resulted in the processing of about 400 samples, mostly in Tallinn, forming the foundation for studies on Silurian and Lower Devonian vertebrates from the Ufa Amphitheatre.

In this paper, the Silurian agnathans from the Ufa Amphitheatre are systematically described and illustrated. In addition to agnathans, several jawed vertebrates (acanthodians, elasmobranchs, and osteichthyans) have been used for biostratigraphic purposes. Together with the new material, some specimens from earlier publications have also been included due to their biostratigraphic significance, providing the most comprehensive overview of agnathans in the region. In this context, images of certain thelodont, heterostracan, and anaspid scales have been reused in the taxonomic section.

History of regional vertebrate research

Since the mid-1970s, data of early vertebrates from the Ufa Amphitheatre have been used in some biostratigraphic analyses (Zhivkovich and Goreva 1976; Karatajūtė-Talimaa 1978; Shurygina et al. 1981; Zhivkovich and Chekhovich 1985; Märss 1986, 1989, 1992; Modzalevskaya and Märss 1991; Chekhovich et al. 1994; Chekhovich 2007). When publishing the distribution data of vertebrates from the Přidoli and Silurian–Lower Devonian boundary beds in Europe, Märss (1997) listed and illustrated several agnathans, thelodonts, and heterostracans, as well as some gnathostomes (elasmobranchs, an actinopterygian, and acanthodians) from the northern bank of Mikhailovsk Pond. Later, the actinopterygian taxa were revised, and new species were established (Märss 2001; Schultze and Märss 2004). The available distribution data for thelodonts from the region were included in the *Handbook of Palaeoichthyology: Agnatha II: Thelodonti*

(Märss et al. 2007). More recently, cyathaspidid heterostracans have been described from both the Central and Southern Urals, as well from the North Timan and the Novaya Zemlya Archipelago, with their locality data presented alongside other cyathaspidid taxa from northern Eurasia (Märss 2019). Osteostracans, although relatively scarce, have been used in taxonomy and biostratigraphic analyses (Modzalevskaya and Märss 1991; Märss 1992, table 2; Märss et al. 2014, pp. 84 and 86). Anaspid species found in the Central Urals have been shortly characterised and included in a monographic paper on Silurian and Lower Devonian anaspids from the Northern Hemisphere (Blom et al. 2001). Our data on microvertebrate distribution, as well as the described lithology and illustrations of the lithological sections along the southern bank of Mikhailovsk Pond, have been used in reconstructing the lithofacies model of the region (Chekhovich 2007; Chekhovich and Zhivkovich 2024).

Historically, it is also noteworthy that for the first time, data on the Silurian and Lower Devonian vertebrate scale morphology from the Ufa Amphitheatre were presented on a poster at the Early/Lower Vertebrate Meeting in Tallinn in 1989 (with a summary published a year later, see Zhivkovich et al. 1990). The poster demonstrated the first scanning electron microscopy (SEM) images of early fish specimens from this region.

Material and locality data

Material

Approximately 400 samples were obtained from various expeditions and institutions. The samples collected from the localities 73Ms and 73Mn by the palaeoichthyologists from the Institute of Geology, Tallinn, and the samples from the other localities with different locality numbers (Fig. 1B, B1), collected by scientists from the Institute of Mineral Raw Materials and its successor, the Institute of Lithosphere of the Russian Academy of Sciences, Moscow, have been utilised.

Not all samples contained vertebrate remains; only about a third of them included scales or shield fragments. The preservation of fish remains in the area varied. A dissolved bonebed from locality 911, with an original rock sample weight of 750 grams, yielded 10 grams of remains. This is one of the richest collections from the Ufa Amphitheatre, but its value was relatively low due to extensive microcracking of the bone material. Most of the remains consisted of pyritised and black scattered scales and shield fragments. Some localities yielded large, but pyritised, shield fragments of cyathaspidid heterostracans with perfectly preserved sculpture patterns. In some outcrops, only ocher-coloured powder remained in the matrix on the fresh rock surface, preserving the shape of the original phosphatic scales. However, these ‘scales’ would disintegrate upon touch. Energy-dispersive spectroscopy (EDS) analysis of some samples revealed that at certain stratigraphic levels, the surface layer of the scales contained only pyrite, with phosphate having completely disappeared from the structure.

Localities

The studied localities with vertebrate remains are mostly situated in three river basins (Serga, Ufa, and Kuba), as well as on the northern and southern banks of Mikhailovsk Pond (Fig. 1B, B1). The numbering of localities and samples can be quite complex due to multiple visits to these sites by different research groups over the years. In the text and figures, the collection year is abbreviated (73, 83, 85, or 87), followed by the locality number or an abbreviated locality name (Ms or Mn), then the section (or outcrop) number or a Cyrillic letter, and finally, the bed and sample numbers appear after a slash (Figs 2 and 3, and in the text).

The southern bank of Mikhailovsk Pond, locality 73Ms (Figs 1B1, 2A): sections 1–7.

Mikhailovsk Pond area south of the dam, near the railway, locality 911 (Figs 1B1, 2A, B): three excavations (sections A, Б, В); locality with sample N. 3182.

The northern bank of Mikhailovsk Pond, locality 73Mn (Fig. 1B, B1), samples 1–52; localities 75, 76, 80, 87510; P. Chekhovich, pers. comm., 25.03.1992.

The Tabuska Hill, right bank of the River Ufa, geological section about 1000 m downstream of the mouth of the River Tabuska (Fig. 1B): outcrops and samples in Fig. 3: 146-0 up to 146-10, 73146-0, 73146-2, 83022, 83024-11, 83042, 83146-5в, 83146-5д, 85042, 85146-0, 85146-5, and 85777 (Zhivkovich and Chekhovich 1985, fig. 20; P. Chekhovich, pers. comm., 25.03.1992 and 26.11.2023; levels added by Chekhovich are marked with an asterisk (*) in Fig. 3).

The River Serga, right bank. Four localities contained fish remains: 52, 60, 109 (Fig. 1B), and 130 (Fig. 1B1). Locality 52 was situated on Chapaev Street, Nizhniye Sergi town. Localities 60 and 109, situated close to each other, were about 500 m southward of the Katnikov Cave (Zhivkovich and Chekhovich 1985, pp. 83–84, fig. 23; P. Chekhovich, pers. comm., 25.03.1992). Locality 130 was on the right bank of the River Serga, in its lower reaches, near the village of Arakaevo (Zhivkovich and Chekhovich 1985, p. 70, fig. 18).

The River Kuba, right bank. Locality 67 (Fig. 1B) was located in the upper course of the river, downstream of the railway bridge (P. Chekhovich, pers. comm., 25.03.1992).

Methods

The carbonate rock samples were dissolved using a 10–15% non-buffered acetic acid solution. Despite the rather large number of samples (about 400), only a small fraction dissolved and contained vertebrate microremains. The beds were often barren, but bonebeds were present at certain levels. After dissolution with acetic acid, the residues of these samples were treated with bromoform to separate heavy and light fractions, and the specimens were picked up. The best-preserved scales were imaged under SEM.

Repository. The treated specimens are housed in the Department of Geology, Tallinn University of Technology. Additionally, one cyathaspid shield (Fig. 10B) was on loan from the Central Scientific Research Geological Museum, St Petersburg (CSRGM No. 4650-1). The new material from the Ufa Amphitheatre carries the collection number GIT 820+ specimen number. In the course of digitising the data, the reused agnathan specimens were assigned new numbers (GIT 297+, GIT 409+; Table 1).

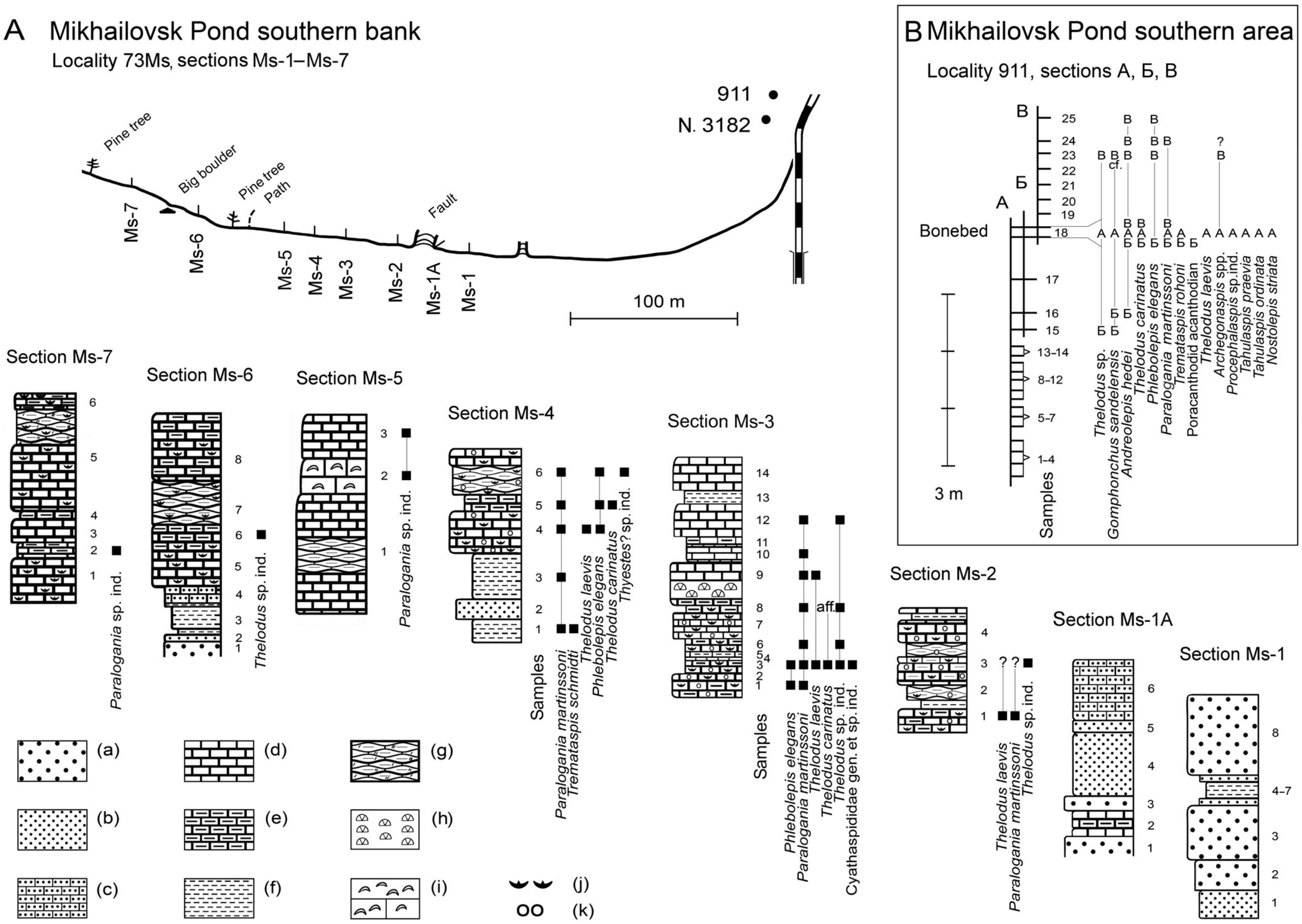

Fig. 2. Distribution of microvertebrate remains in the Mikhailovsk Pond area. **A** – locality 73Ms, sections 73Ms-1 to 73Ms-7 along the southern bank of the pond (samples collected by the Tallinn research team in 1973). **B** – locality 911, sections A, Б, and B, Mikhailovsk Pond southern area, south of the dam, near the railway (samples collected by the Tallinn, St Petersburg and Moscow research teams in 1987). Lithological legend: quartz-sandstones (a), siltstones (b), silty limestones (c), limestones in general (d), argillaceous limestones (e), calcareous mudstones (f), nodular limestones (g), argillaceous limestone with the tabulate coral *Laceripora cribrosa* Eichwald prevailing (h), *Conchidium* limestone (i), shells of unidentified variable small brachiopods (j), ostracods (k). Abbreviation: aff. – marking for a species somewhat similar to *Thelodus carinatus* in the Vesiku Beds of the Rootsiküla Stage and the Soeginina Beds of the Paadla Stage. The lithological columns are based on the original field descriptions and drawings made by E. Kurik and T. Märss during fieldwork in 1973 and can be found at https://geoloogia.info/en/locality/14061/attachments.

Table 1. New collection numbers assigned to the re-used specimens

Publication	Previous number	New number
Thelodonti (in Märss 1997): *Turinia pagei*	Pi 7243 Pi 7245 Pi 7270	GIT 297-48 GIT 297-49 GIT 297-50
Talivalia (= *Nikolivia*) *elongata*	Pi 7253 Pi 7254 Pi 7255 Pi 7269	GIT 297-52 GIT 297-53 GIT 297-51 GIT 297-54
Heterostraci, ‘*Traquairaspis*’ sp. (in Märss 1997)	Pi 7276	GIT 297-55
Anaspida (in Blom et al. 2001)	GI Pi 7225 GI Pi 7724 GI Pi 7717	GIT 409-20 GIT 409-43 GIT 409-44

Results

Distribution, age and correlations

The southern bank of Mikhailovsk Pond (locality 73Ms) (Fig. 2A)

Sections 73Ms-1 and 73Ms-1A on the southern bank exposed terrigenous rocks, with mottled, coarse-grained, weakly cemented sandstones in section 73Ms-1 and fine-grained sandstones higher up in 73Ms-1A. These sandstones did not yield any fish remains. These two sections correspond to locality N. 3183 by Patrunov and Shurygina (2002, fig. 2 on p. 99; with incorrect locality number 3133 in their fig. 1), which the authors interpreted as the lowest Kuba Beds, Ludlow.

Scarce scales in section 73Ms-2, sample 1 (shortly 73Ms-2/1) belong to *Thelodus laevis* and *Paralogania martinssoni*.

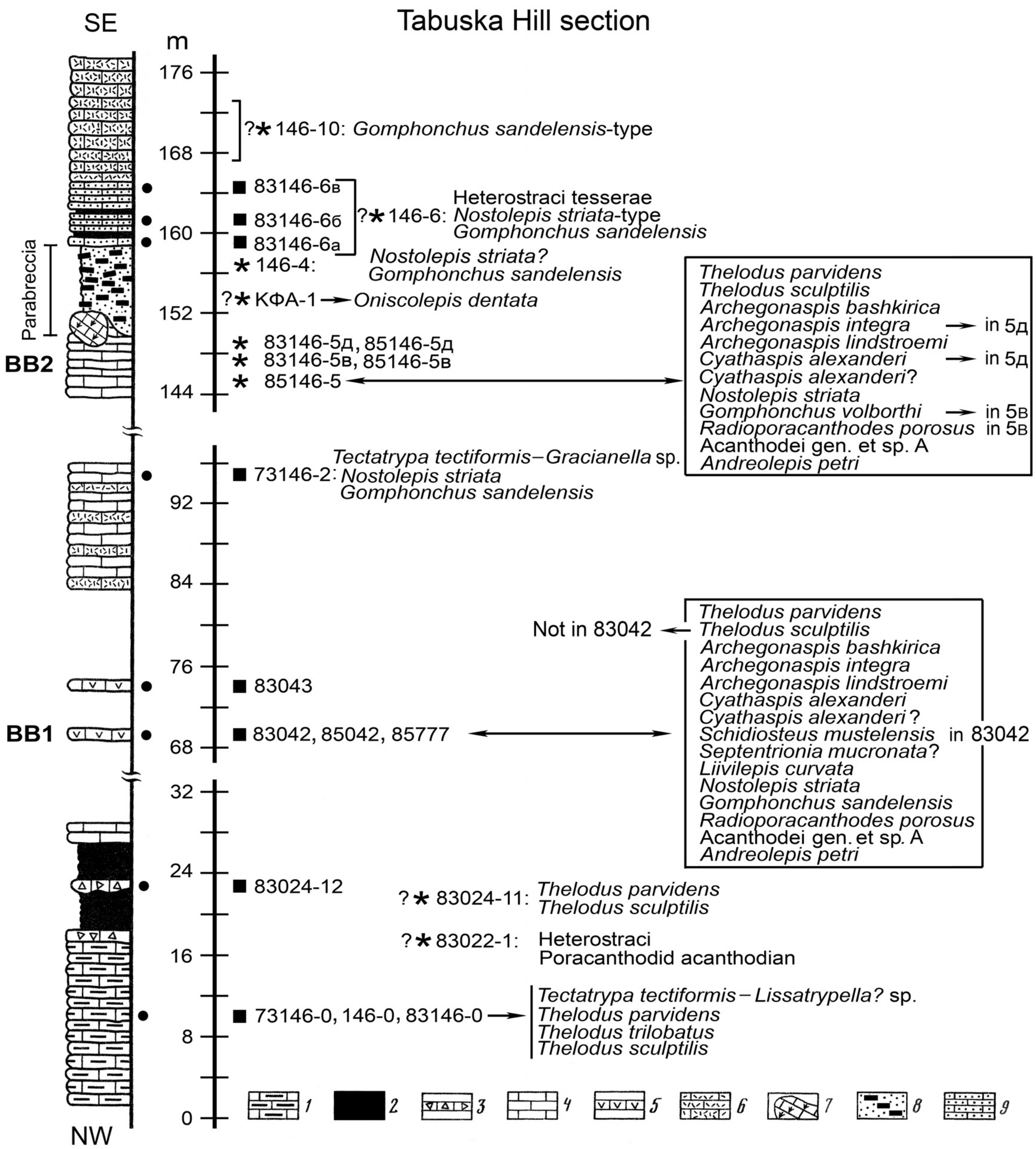

Fig. 3. Distribution of vertebrate remains in the Tabuska Hill section, on the right bank of the River Ufa, downstream of the mouth of the River Tabuska. This section represents the stratotype of the Tabuska Beds, upper Silurian. The measured lithological column, legend, and levels of outcrops and collected samples (black dots), as well as some conodont and brachiopod data, are from Zhivkovich and Chekhovich (1985, pp. 72–73, fig. 20). Asterisks and black squares denote recently specified sampling levels (P. Checkhovich, pers. comm., 26.11.2023), while asterisks with a question mark indicate approximate sampling levels. BB1 and BB2 point to the bonebed layers that contain very abundant vertebrate skeletal particles. Lithological legend: argillaceous limestones with cephalopod remains (1), pelites (2), biorudites (3), argillaceous limestones with scattered brachiopod *Clorinda* shells (4), brachiopod-crinoidal-vertebrate biorudites (bonebeds) with admixture of volcanoclastic material (5), brachiopod-crinoidal biosparites (6), biohermal limestones (7), intraclastic parabreccias (8), crinoidal biosparites (9).

Both taxa may possibly also be present in 73Ms-2/3. If found alone, these taxa refer to the impoverished Viita to Vesiku Beds of the Rootsiküla Stage, upper Homerian, Wenlock, lower Silurian in the East Baltic sections (Märss 1986, table on pp. 79–81).

Section 73Ms-3, sample 1 begins with *Paralogania martinssoni* and *Phlebolepis elegans*, while in 73Ms-3/3, *Thelodus laevis*, *Thelodus carinatus*, *Thelodus* sp. ind., and Cyathaspididae gen. et sp. ind. appear alongside them. Higher up in this section, two thelodonts alone, *Paralogania martinssoni* and *Thelodus* sp. ind., continue from 73Ms-3/6 to 73Ms-3/12, with *Thelodus laevis* reappearing in 73Ms-3/9, giving these beds a distinctly Wenlock appearance. In the lower part of this section, *Phlebolepis elegans* points to and is correlative with the Himmiste Beds of the Paadla Stage, upper Gorstian, Ludlow. Its co-presence with *Thelodus carinatus* supports this proposition, as this taxon is more common in the Ludlow than in the Wenlock, although it does occur in both. While *Phlebolepis elegans* and *Thelodus carinatus* may extend into the Uduvere Beds of the Paadla Stage, the absence of *Andreolepis hedei*, *Thelodus parvidens*, and poracanthodid acanthodians in the treated samples makes this unlikely.

In section 73Ms-4, *Paralogania martinssoni* is present in most samples except for the sandstone layer 73Ms-4/2. It occurs alongside the osteostracan *Tremataspis schmidti* in the lowest sample, 73Ms-4/1. Higher in the section, *Thelodus* *laevis* and *Phlebolepis elegans* join *Paralogania martinssoni* in 73Ms-4/4, while *Phlebolepis elegans* continues into 73Ms-4/6, occurring here together with osteostracan *Thyestes*? sp. ind. *Thelodus carinatus* is recorded only in 73Ms-4/5. With minor aberrancies, the lower part of this section (*Trematapsis schmidti* + *Thelodus laevis*) has the Upper Wenlock appearance, whereas its upper part with *Phlebolepis elegans* has the mid-Ludlow appearance, similar to the East Baltic vertebrate succession. In short, sections 73Ms-3 and 73Ms-4 contain the Wenlock and Ludlow interval, but the sequence of taxa in 73Ms-3 raises questions. It is possible that the succession in this section (Fig. 2A) is reversed (for further details, see the section 'On some peculiarities in the distribution of Silurian vertebrates in the Ufa Amphitheatre, the Central Urals'). Sections 73Ms-3 and 73Ms-4 correspond to outcrops 3184 and 3185 in Patrunov and Shurygina (2002, figs 1 and 2 on p. 99) and are dated to the Kuba Beds, Ludlow.

Sections 73Ms-5–73Ms-7 each contain only a single taxon, either *Paralogania* sp. ind. or *Thelodus* sp. ind. Their identification at species level was not possible, and biostratigraphic details are therefore unavailable. No vertebrates indicative of a Přidoli age were found in the examined sections.

Mikhailovsk Pond area south of the dam, near the railway (Fig. 2A, B)

The bedrocks of three sections within locality 911 (911A, 911Б, and 911B) (Figs 1B1, 2B) were excavated in an attempt to open the Ludlow–Přidoli boundary beds in 1987. These sections were only a few metres apart. The composition and abundance of vertebrate remains varied between layers, but a conspicuous bonebed, 911-18, extends throughout the locality, reaching a maximum thickness of about 10–20 cm (Fig. 2B).

The lowest vertebrate findings in section 911Б originate from layer 15 (911Б-15) and include the thelodont *Thelodus* sp. and acanthodian *Gomphonchus sandelensis* (Pander). These are followed by the actinopterygian *Andreolepis hedei* higher in 911Б-16. Further up in this section, *Andreolepis hedei*, thelodonts *Thelodus carinatus*, *Phlebolepis elegans*, *Paralogania martinssoni*, osteostracan *Trematapsis rohoni*, and a poracanthodid acanthodian occurred in bonebed 911Б-18. It is worth noting that the scales of *Paralogania martinssoni* from this locality are approximately three times larger than those found on the southern bank (sections 73Ms-2–73Ms-4), though they have the features of *Paralogania martinssoni* (in Fig. 5, separated by a fine line).

The samples from section 911A are barren with one exception, bonebed 911A-18. The taxonomic content of vertebrate microremains in this particular bonebed is the most variable for the southern vicinity of Mikhailovsk Pond, including thelodonts (*Thelodus carinatus*, *Thelodus* sp., *Paralogania martinssoni*), heterostracans (*Archegonaspis* spp.), osteostracans (*Trematapsis rohoni*, *Procephalaspis* sp. ind., *Tahulaspis praevia*, *Tahulaspis ordinata*), acanthodians (*Nostolepis striata*, *Gomphonchus sandelensis*), and the actinopterygian *Andreolepis hedei.*

Section 911B starts with bonebed 911B-18, which includes *Andreolepis hedei*, *Thelodus carinatus*, and *Paralogania martinssoni*. Higher in the section, layer 911B-23 contains *Thelodus* sp., *Gomphonchus sandelensis*, *Andreolepis hedei*, *Phlebolepis elegans*, and *Archegonaspis* spp. However, only two to three taxa continue higher into layers 911B-24 and 911B-25.

The presence of *Andreolepis hedei* suggests correlations with the Uduvere Beds of the Paadla Stage, Lower Ludfordian in northern East Baltic (for further details, see the section 'On some peculiarities in the distribution of Silurian vertebrates in the Ufa Amphitheatre, the Central Urals').

The historical sample N. 3182, the first sample from the Mikhailovsk Pond region, which yielded the first Silurian fish scales, originates from an area close to locality 911. It contains only *Phlebolepis elegans* scales. The limestones with interbeds of sandstone belong to the Kuba Beds, Ludlow, upper Silurian (Patrunov and Shurygina 2002, pp. 100, 104, figs 1 and 2 on p. 99).

The northern bank of Mikhailovsk Pond (locality 73Mn)

In 1973, the section was systematically sampled in the Přidoli part, upper Silurian, and the collecting continued a few metres into the Lower Devonian part (Märss 1997, fig. 8). The section contained scanty vertebrate remains, with mostly acanthodian scales preserved. This situation changed at the Silurian–Devonian boundary. The base of the Lochkovian, Lower Devonian, was marked by the appearance of thelodont *Turinia pagei* and heterostracan '*Traquairaspis*' sp. (sample 34), common in the British Isles but also in Latvia (Ventspils core in Märss 1986, fig. 43). There were some other thelodonts of the Lower Devonian age, such as *Talivalia elongata* and *Boreania minima* in sample 3. The acanthodian scales were very common, the scales of elasmobranchs less frequent, and only a few placoderm fragments were found in samples 45–48 (Märss 1997, fig. 8). Noteworthy are the acanthodian *Zemlyacanthus menneri* scales in samples 3, 34, and 48. This taxon was originally described by Valiukevičius (1992) under the name *Poracanthodes menneri*, on October Revolution Island, Severnaya Zemlya Archipelago, in the upper part of the Severnaya Zemlya Formation, Lochkovian, Lower Devonian. It enables correlations between the sections of the western slope of the Central Urals and the remote Severnaya Zemlya.

The Tabuska Hill section, right bank of the River Ufa, downstream of the mouth of the River Tabuska (Fig. 1B)

Scattered outcrops on a gentle slope have been studied by many geologists. In this work, the monograph by Zhivkovich and Chekhovich (1985, p. 72, fig. 20, and P. Chekhovich, pers. comm., 26.11.2023) has been used to determine the position of the samples and fish finds collected over several years from the section.

This is the stratotype of the Tabuska Beds, extending from the Upper Ludfordian, Ludlow, through the Přidoli, upper Silurian, into the Lower Devonian. The section is over 175 m long (Zhivkovich and Chekhovich 1985, p. 72, fig. 20). In its northwestern part (i.e. the lowest beds shown in Fig. 3), at about 10–23 m, in samples 73146-0, 146-0, and 83146-0, two to three thelodont species – *Thelodus parvidens*, *Thelodus sculptilis*, and *Thelodus trilobatus* – were found. Additionally, sample 83024-11 contains a few scales of *Thelodus parvidens* and *Thelodus sculptilis*, while sample 83022-1 includes unspecified heterostracan fragments and poracanthodid acanthodian scales, reminiscent of *Radioporacanthodes* sp. Sample 83024-12 was barren. In Estonia, the range of the species *Thelodus sculptilis* extends from the Tahula Beds of the Kuressaare Stage, Upper Ludfordian, Ludlow, up to the lower Äigu Beds of the Kaugatuma Stage, Přidoli. Its lower part is missing here due to a hiatus between the Paadla and Kuressaare stages (see the species ranges in Märss 1986; biozones and correlations in Märss and Männik 2013). The range of a particular taxon, designated as *Radioporacanthodes porosus* (Brotzen), spans the Tahula Beds of the Kuressaare Stage, Upper Ludfordian, and the lower Lõo Beds of the Kaugatuma Stage, Přidoli, in Estonia.

At about 69 m in the section, the biorudites with abundant skeletal remains of vertebrates, bonebed BB1, characterised by samples 83042, 85042, and 85777, contain 15 taxa, which is the highest number for this interval found in the Ufa Amphitheatre to date (Fig. 3). The list of taxa below (with the stratigraphic occurrence of each taxon elsewhere given in parentheses) includes thelodonts *Thelodus parvidens* and *Thelodus sculptilis* (as given above). All cyathaspidid heterostracans listed here are characteristic of the Ludlow: *Archegonaspis bashkirica* (River Belaya, Southern Urals), *Archegonaspis integra* (Lower Ludlow; Beyrichienkalk, Germany), *Archegonaspis lindstroemi* (Hemse Beds, Lower Ludlow; Gotland), *Cyathaspis alexanderi* and *Cyathaspis alexanderi*? (both described from the Tabuska Beds in the Tabuska Hill section). Anaspids in the Tabuska Beds are represented by *Schidiosteus mustelensis*, occurring in Estonia in the Viita and Vesiku Beds of the Rootsiküla Stage, Homerian, Wenlock, and in the Himmiste Beds of the Paadla Stage, Gorstian, Lower Ludlow (for further details of this species, see the section 'On some peculiarities in the distribution of Silurian vertebrates in the Ufa Amphitheatre, the Central Urals'); *Septentrionia mucronata*? (originally described from the Tabuska Beds in the Tabuska Hill section by Blom et al. 2001, p. 312); and *Liivilepis curvata* (the holotype originates from the Ohesaare Stage, Přidoli, in Estonia, but may also occur below this level; see Fig. 4 and Blom et al. 2001, p. 272). Acanthodians *Nostolepis striata* and *Gomphonchus sandelensis*

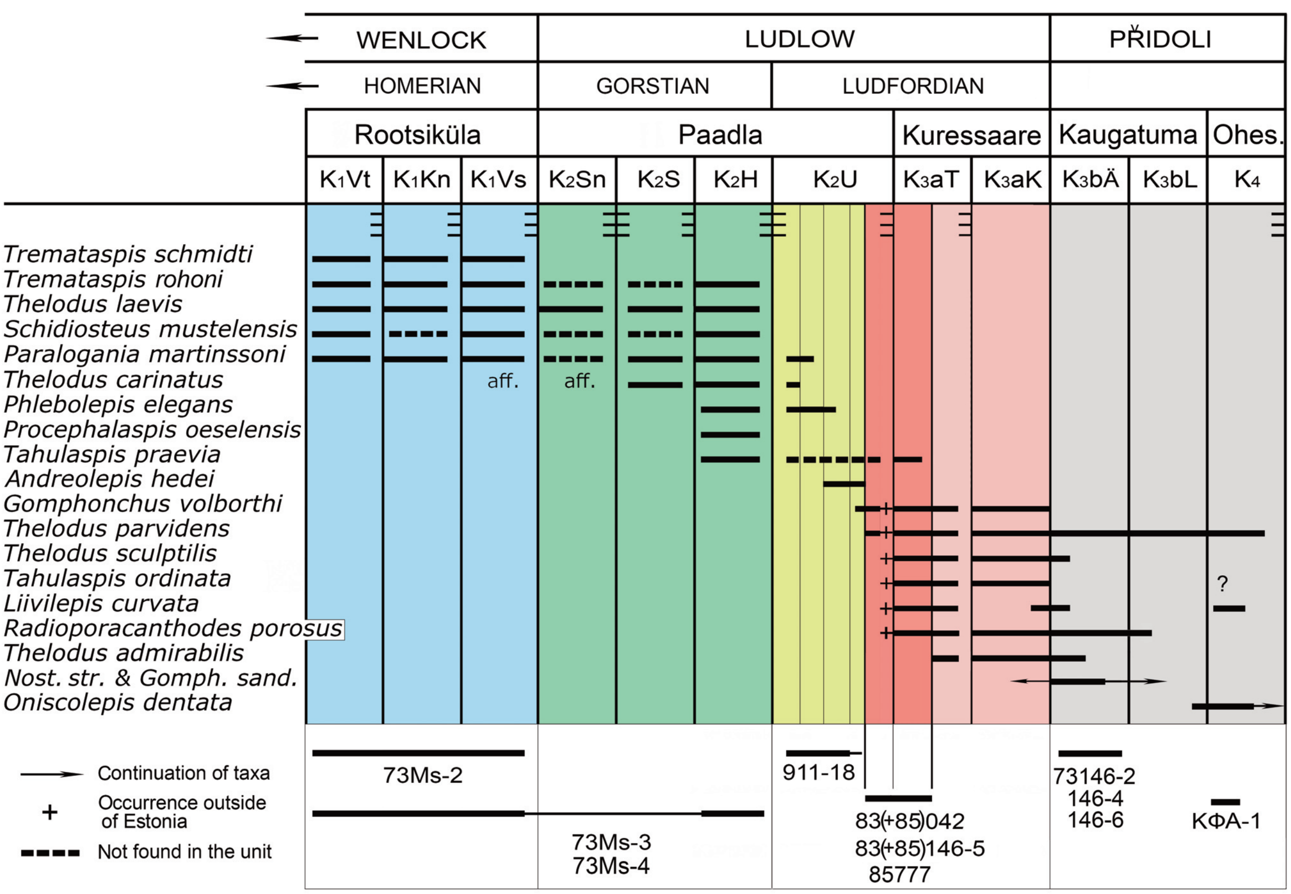

Fig. 4. Position of selected sections traced from the Ufa Amphitheatre to the East Baltic, plotted on the stratigraphic scheme of the Silurian. The distribution of selected species is indicated by a continuous line, while short dashes mark gaps in the records. Dark pink strip between the last occurrence of *Andreolepis hedei* and the first *Thelodus admirabilis* indicates the interval where BB1 and BB2 could be positioned. The sections outside the coloured area include 73Ms-2, 73Ms-3, and 73Ms-4 on the southern bank of Mikhailovsk Pond; 911-18 in the southern area of Mikhailovsk Pond, south of the dam; samples 83042, 85042, and 85777; samples with the main number 146-, namely, 83146-5, 85146-5, 73146-2, 146-4, 146-6; and sample KΦA-1 from the Tabuska Hill section. The anaspid *Schidiosteus mustelensis* from the Ufa Amphitheatre is not taken into account. The position of the Soeginina Beds in the lower Paadla Stage is drawn after Kaljo et al. (2022, fig. 3). Abbreviations: Ohes. – Ohesaare Stage, aff. – marking for a species somewhat similar to *Thelodus carinatus* in the Vesiku Beds of the Rootsiküla Stage and the Soeginina Beds of the Paadla Stage. Used northern East Baltic stratigraphic units: K_1Vt – Viita Beds, K_1Kn – Kuusnõmme Beds, K_1Vs – Vesiku Beds of the Rootsiküla Stage, K_2Sn – Soeginina Beds, K_2S – Sauvere Beds, K_2H – Himmiste Beds, K_2U – Uduvere Beds of the Paadla Stage, K_3aT – Tahula Beds, K_3aK – Kudjape Beds of the Kuressaare Stage, K_3bÄ – Äigu Beds, K_3bL – Lõo Beds of the Kaugatuma Stage, K_4 – Ohesaare Stage.

are widespread taxa, but these two alone are especially characteristic of the lower Äigu Beds of the Kaugatuma Stage; two additional acanthodians to list are *Radioporacanthodes porosus* (its range is given in the section above) and Acanthodei? gen. et sp. A., characterised by huge scales, which are absent in the Silurian of Estonia. Actinopterygian *Andreolepis petri* was identified in the Tabuska Beds, replacing here *Andreolepis hedei*, which has been known from the older strata in the Mikhailovsk Pond southern area (locality 911).

At about 95 m, sample 73146-2 contains a pair of acanthodians, *Nostolepis striata* and *Gomphonchus sandelensis*. These two acanthodians are also documented in samples 146-4, 146-6, and 146-10, although in a couple of levels, the *Nostolepis striata* scales are identified with some doubt. As mentioned, such a simple association is most common for the acanthodian interval in the lower Äigu Beds of the Kaugatuma Stage, Přidoli of Estonia and Latvia, before *Nostolepis gracilis* joins them higher up in the upper Äigu Beds, Přidoli (Märss 1986; Märss and Miller 2004; Märss and Männik 2013). *Nostolepis gracilis* has not been found in the Ufa Amphitheatre (Märss 1997, fig. 8). The Přidoli level of the same sample, 73146-2, is also confirmed by brachiopods *Tectatrypa tectiformis – Gracianella* sp. and conodonts *Ozarkodina remscheidensis eosteinhornensis* (Walliser) and *Delotaxis elegans* (Walliser) (Zhivkovich and Chekhovich 1985, pp. 72–73).

The interval between 144 and 150 m with five samples – 83146-5в, 83146-5д, 85146-5, 85146-5в, and 85146-5д – represents bonebed BB2 layers in the section. With some variations in the composition of species (small arrows indicate the exact sample (or layer) from which each species originates), these five samples share a very rich content of vertebrates. Compared with bonebed BB1 outcrops 83042, 85042, and 85777, the biggest difference is the absence of anaspids in BB2 and a somewhat different assemblage of acanthodians (including *Gomphonchus volborthi*, which is also present here). Sample 85146-5д contains exclusively heterostracans, as a result of selective collecting focused on obtaining the cyathaspidid heterostracans.

Sample КФА-1 contains the heterostracan *Oniscolepis dentata* tessera and comes from the parabreccia interval in the Tabuska Hill section; its more exact level in the section is not known (P. Chekhovich, pers. comm., 26.11.2023). Elsewhere, *Oniscolepis dentata* occurs in the upper part of the Kaugatuma and Ohesaare stages, Přidoli, and in the lowermost Tilžė Stage, Lower Devonian, in the East Baltic, as well as in the Eptarma Formation, Přidoli, on the River Velikaya, North Timan.

The River Kuba, right bank (Fig. 1B)

Outcrop 67, in its upper course downstream of the railway bridge, yielded the following samples: sample 67-II, which contained *Gomphonchus*-type acanthodians (possibly lower Přidoli, upper Silurian); sample 67-V, which had heterostracan fragments (no vacuoles visible), *Gomphonchus*-type, and poracanthodid acanthodians (possibly upper Přidoli, upper Silurian); and sample 67-VI, which contained *Gomphonchoporus hoppei* (Gross), *Radioporacanthodes biblicus* (Lehman), and *Lophosteus uralensis* Schultze et Märss (a few fragments showing similarities with *Lophosteus superbus* Pander) at an upper Přidoli, upper Silurian, or Lower Devonian level.

The River Serga, outcrops along the right bank (Fig. 1B)

Outcrop 52, in Nizhniye Sergi town on Chapaev Street, contained *Machaeracanthus*-type acanthodian scales in samples 52-г and 52-2e (Lochkovian or Pragian, Lower Devonian).

Outcrop 60, about 500 m downstream of the Katnikov Cave, yielded *Nostolepis striata* Pander and *Gomphonchus sandelensis* (Pander) (with one scale resembling *Gomphonchoporus hoppei* (Gross)) in sample 60-c (Přidoli, upper Silurian).

Outcrop 109, close to the previous one, about 500 m downstream of the Katnikov Cave, contained *Gomphonchus*-type scales in sample 109-4 (Přidoli, upper Silurian).

Outcrop 130, about 400 m upstream of the railway bridge near the village of Arakaevo, had rocks comprising *Thelodus* sp. and *Paralogania* sp. scales (Silurian).

Other localities

Fish scales found in some other riverbank rock samples are few and insufficient for the current analysis, but their value may increase with future discoveries. Mostly, acanthodian scales have been found and identified (for example, from outcrops 106 and 104 in the River Serga basin).

On some peculiarities in the distribution of Silurian vertebrates in the Ufa Amphitheatre, the Central Urals

Mikhailovsk Pond area

Biostratigraphic analysis revealed that the content of taxa on the southern bank of the Mikhailovsk Pond section 73Ms-2 (sample 73Ms-2/1) has a Wenlock composition (Fig. 2A), similar to the lower part of section 73Ms-4 (samples 73Ms-4/1–4/3), characterised by *Paralogania martinssoni* – either alone or together with osteostracan *Tremataspis schmidti* –, which are well known from the Rootsiküla Stage of Estonia. The lower part (samples 73Ms-3/1–3/3) and the upper part (73Ms-4/4–4/6), both containing *Phlebolepis elegans*, certainly belong to the Gorstian, Lower Ludlow, and are correlated with the Himmiste Beds of the Paadla Stage in the East Baltic. The succession of taxa in section 73Ms-3 is unusual, as *Phlebolepis elegans*, *Thelodus carinatus*, and Cyathaspididae gen. et sp. occur below *Paralogania martinssoni* and *Thelodus laevis*, whereas in section 73Ms-4, a typical succession occurs with the *Paralogania martinssoni* Zone below and the *Phlebolepis elegans* Zone above. In section 73Ms-3, this succession is reversed. *Andreolepis hedei* Gross is absent in all studied 73Ms sections. Such disruption of the fossil sequence in the rock layers suggests tectonic activity in the region, a matter discussed earlier by Patrunov and Shurygina (2002, p. 106). The possible position of sections 73Ms-2, 3, and 4 is shown in Fig. 4 (marked in blue and green strips) in the stratigraphic scheme of the East Baltic.

Three sections, 911A, 911Б, and 911В, in the Mikhailovsk Pond area south of the dam, somewhat overlap (Fig. 2B), with some variation in the composition of vertebrate taxa and the number of specimens, with bonebed 911-18 being the richest. *Andreolepis hedei* is present in all three sections, and based on this, these sedimentary rocks belong to the *Andreolepis hedei* Zone, upper Kuba Beds (Modzalevskaya and Märss 1991) in the Ufa Amphitheatre, and correlate with the Uduvere Beds of the Paadla Stage, Lower Ludfordian, Ludlow of the East Baltic (Fig. 4, yellow strip). *Thelodus sculptilis*, *Thelodus parvidens*, and *Gomphonchus volborthi* have not yet appeared, confirming the age of this part of the section as Lower Ludfordian. The osteostracan *Tahulaspis praevia* occurs in Estonia (Fig. 4, green, yellow, and pink strips) both below and above the Uduvere Beds and may theoretically be present also in the layers in between. The presence of another *Tahulaspis* species, *Tahulaspis ordinata*, in section 911A, together with *Andreolepis hedei*, also warrants attention. In Estonia, *Tahulaspis ordinata* appears above the *Andreolepis hedei* species range, in the *Thelodus sculptilis* Zone (Fig. 4, pink strip). On Gotland, at the Uddvide 1 locality in the Burgsvik Sandstones, *Andreolepis hedei* and *Zenaspis*? sp. (now *Tahulaspis* sp.) occur together but without *Thelodus sculptilis* (Märss 1992). Possibly, the first appearance datum (FAD) of *Tahulaspis ordinata* was somewhat earlier than previously known.

The Uduvere Beds of the Paadla Stage, Lower Ludfordian, form an interesting stratigraphic unit because of two bioevents – an extinction event and an innovation event (discussed in detail by Märss 1992, fig. 2). First, taxa that occurred below the Uduvere Beds and in its lower part became extinct at this level. Second, new taxa that appeared higher in the Uduvere Beds continued into the Tahula Beds of the Kuressaare Stage and beyond. This interval of change was called the *Andreolepis hedei* Event (Märss 1992, fig. 2). The same distribution pattern of taxa is obvious in the Ufa Amphitheatre (Fig. 4).

Tabuska Hill section

To date, the richest collection of early vertebrate remains from the Central Urals originates from the Tabuska Beds in the Tabuska Hill section. This stratigraphic unit has been interpreted in various ways: as lower Přidoli (Shujskij 1981; Shurygina et al. 1981), upper Ludlow (e.g. Modzalevskaya and Märss 1991), or left undetermined, suggesting it could belong to either the Upper Ludlow or lower Přidoli (Märss 2001). It has been noted that ‘the level with fishes in the Tabuska Beds in the Tabuska Hill section may be stratigraphically rather high in the Ludlow, as *Andreolepis hedei* is replaced here by another species, *Andreolepis petri*, co-occurring with the zonal taxon *Thelodus sculptilis* in these rocks’ (Märss and Männik 2013; Märss 2019, p. 115).

Zhivkovich and Chekhovich (1985, pp. 72–73, fig. 20) established two distinctly dated levels in the Tabuska Hill section. The first level, 73146-0 at the base (NW) of the section, was defined by brachiopods *Tectatrypa tectiformis* – *Lissatrypella*? sp. and thelodonts *Thelodus sculptilis* – *Thelodus parvidens*. This assemblage was correlated with the base of the Kuressaare Stage, Upper Ludfordian, Upper Ludlow of Estonia. The second level, 73146-2, situated in the SE part of the section, contained brachiopods *Tectatrypa tectiformis* – *Gracianella* sp., along with the conodonts *Ozarkodina remscheidensis eosteinhornensis* (Walliser) and *Delotaxis elegans* (Walliser), which the authors correlated with the beginning of the Přidoli (ibid.). The presence of only two acanthodians and the absence of thelodonts in 73146-2 further support the lower Přidoli age of this bed. (The Silurian fish data in Zhivkovich and Chekhovich 1985 originate from the author of this paper.)

Several samples from the Tabuska Hill section (Fig. 3) contain *Thelodus sculptilis* scales (Fig. 8). However, these scales are consistently present in small numbers and are dated to the mid-late Ludfordian, Late Ludlow. The scale drawings, ordered by outcrops according to Zhivkovich and Chekhovich (1985, fig. 20) – from sample 146-0 up to 83146-5в and 83146-5д, and 85146-5в and 85146-5д – show that the morphological characteristics of the scales remain almost unchanged throughout their whole range in the Tabuska Beds.

A different situation is observed in the Kuressaare drill core (Saaremaa, Estonia), where the entire range of two *Thelodus* species is confined to a short interval of about 11 metres (Märss 2011, fig. 3). Here, the section begins with simple, small scales, and continues upwards with larger and more complex sculptured scales. Higher in the section, a new sculpture pattern emerges, marking the FAD of a new species, *Thelodus admirabilis*. *Thelodus admirabilis* is absent in the Central Urals. Simple scales of *Thelodus sculptilis* from the Tabuska Hill section correspond to those from the beginning of the species’ range in Estonian sections.

The vertebrate assemblages, broadly similar in composition (Fig. 3), are exposed in outcrops 83042, 85042, and 85777, and in 83146-5в, 83146-5д, 85146-5, 85146-5в, and 85146-5д – corresponding to bonebeds BB1 and BB2, respectively. The thelodonts *Thelodus sculptilis* and *Thelodus parvidens* are present in both assemblages (except *Thelodus sculptilis* in 83042). The range of *Thelodus parvidens* starts in the upper Uduvere Beds of the Paadla Stage, while *Thelodus sculptilis* begins in the lowest Tahula Beds of the Kuressaare Stage, mid-Ludfordian, in Estonia, continuing into higher beds in the Kuressaare Stage, Upper Ludfordian (see Fig. 4). Findings of cyathaspidid heterostracans were discovered in both sets of outcrops – 83042, 85042, 85777 and 85146-5, 85146-5в, 83146-5д, 85146-5д – with five similar taxa in both. Osteostracans were completely absent in the Tabuska Hill section, and anaspid fossils were exceptionally rare, both taxonomically and in the number of specimens.

Three taxa, *Schidiosteus mustelensis*, *Septentrionia mucronata*?, and *Liivilepis curvata*, were present in the bonebed BB1 but were absent in the bonebed BB2 (Fig. 3). *Schidiosteus mustelensis* complicates age determination because it co-occurs with *Thelodus parvidens* in outcrop 85042, which is correlated with two other samples, 83042 and 85777, in the Tabuska Hill area. *Thelodus sculptilis* scales were not found in sample 83042 but were present in the other two samples, 85042 and 85777. Placing the Estonian distribution interval of *Shidiosteus mustelensis* into the stratigraphic scheme shows that here it spans from the Viita Beds of Rootsiküla Stage, upper Homerian, to the Himmiste Beds of the Paadla

Stage, Gorstian (Fig. 4, blue and green strips). In the Ufa Amphitheatre, it would even extend through the faunal renewal event in the Lower Ludfordian (Fig. 4, yellow strip), correlating with the Uduvere Beds of the Paadla Stage in Estonia. However, this seems unlikely. The reason for such occurrence remains unclear – whether undocumented original Wenlock–Lower Ludlow strata are still present in the section, whether redeposition of such sediments took place, or whether a human error occurred during collecting or treating the samples. For now, we retain it in the list as a potential taxon of the Ufa Amphitheatre, pending further investigation.

Considering the other two anaspid taxa, *Septentrionia mucronata*? and *Liivilepis curvata*, the first taxon occurs only in the Tabuska Beds of the Central Urals, while the confirmed *Septentrionia mucronata* is also described from the Burgsvik/Hamra Beds, Upper Ludfordian, Upper Ludlow of Gotland Island. The range of the second taxon, *Liivilepis curvata*, is rather wide; its holotype was described from the Ruhnu core (depth 172.6 m) in the Ohesaare Stage, Přidoli. Other specimens of *Liivilepis curvata* are known from the Kuressaare Stage of Estonia. The species also occurs in the Burgsvik and Hamra Beds of Gotland (correlative with the Uduvere Beds of the Paadla Stage and the Tahula Beds of the Kuressaare Stage in Estonia), and the Öved Sandstone Formation, Upper Ludfordian of Skåne, Sweden (Blom et al. 2001, table on p. 272). If we set aside the findings of *Schidiosteus mustelensis*, the species *Septentrionia mucronata* itself would well support the mid-Ludfordian (upper Uduvere Beds of the Paadla Stage and Tahula Beds of the Kuressaare Stage in Estonia) level of the bonebed BB1 (Fig. 4, dark pink strip).

Samples sharing the main number (146-) (Fig. 3), including 73146-2, 146-4, 146-6, and 146-10, almost always yield two acanthodian taxa (Fig. 4, grey strip), which are characteristic of the lower Äigu Beds, Kaugatuma Stage, Přidoli, below the *Nostolepis gracilis* Zone in the East Baltic. The locations of samples 85146-5, 83146-5в, 83146-5д, 85146-5в, and 83146-5д were positioned below the intraclastic parabreccias. The sample with the short marking 146-4 originated from the intraclastic parabreccia below sample 83146-6a. Sample КФА-1 contains a tessera of the tessellated heterostracan *Oniscolepis dentata*, a species typically found in the Ohesaare Stage and crossing the Silurian–Devonian boundary, but rarely also present rather low, at the top of the Kaugatuma Stage, Přidoli (Fig. 4, grey strip). The position of the sample in the lithological column was given by P. Chekhovich (pers. comm. 26.11.2023).

Systematic palaeontology

The systematics of the agnathans treated here are based on the most recent publications: Anaspida (Blom et al. 2001); Thelodonti (Märss et al. 2007); Osteostraci (Märss et al. 2014); Cyathaspididae, Heterostraci (Märss 2019). These publications include the synonymics and data on types and type localities for each taxon, which are not repeated here. We mostly limit biostratigraphic relationships to the East Baltic region, although the taxa may be more widespread. When describing the agnathan fossils, such as thelodont scales or fragmentary shields, plates, and scales of heterostracans, osteostracans, and anaspids, the sculptural elements and surface patterns are decisive in species identification. In thelodonts, the postpectoral and precaudal scales exhibit the most distinct species-specific characteristics. These scales are also the most numerous, covering the largest area on their body (Karatajūtė-Talimaa 1978; Turner 1984; Märss 1986; Märss and Ritchie 1997; Märss et al. 2007), while other types of scales are spread on smaller areas, such as on the anteriormost head and fins.

Class AGNATHA Cope, 1889
Subclass THELODONTI Jaekel, 1911
Order SHIELIIFORMES Märss, Wilson and Thorsteinsson, 2002
Family SHIELIIDAE Märss, Wilson and Thorsteinsson, 2002
Genus *Paralogania* Karatajūtė-Talimaa, 1997
Paralogania martinssoni (Gross, 1967)
Figure 5

Material. Over 2500 scales were collected, with numerous scales of varying preservation remaining in the acetic acid residues. Southern bank of Mikhailovsk Pond, locality 73Ms: samples 73Ms-2/1, 3?; 73Ms-3/1, 3, 6, 8–10, 12; 73Ms-4/1, 3–6; *Paralogania martinssoni* and *Phlebolepis elegans* zones; Homerian, Upper Wenlock, and Gorstian, Lower Ludlow; Mikhailovsk Pond area south of the dam, samples 911A-18, 911Б-18, 911B-18, and 911B-24; Kuba Beds; *Andreolepis hedei* Zone, Lower Ludfordian, Ludlow.

Species range. The vertical range of the species *Paralogania martinssoni* in Estonia extends from the Viita Beds of the Rootsiküla Stage, Homerian, Upper Wenlock, up to the lower Uduvere Beds of the Paadla Stage, Lower Ludfordian, Ludlow (Märss and Männik 2013, fig. 2B).

Description. The diagnostic features of *Paralogania martinssoni* scales include their rhomboidal crown configuration and up to four pairs of spines posterolaterally of the crown. The crown may have a smooth and flat plate, or, depending on its placement on the body, the whole crown surface may be ridged. An unpaired spine beneath the posterior apex of the crown plate is characteristic of its trunk scales. The neck forms a shallow groove. The base may be swollen in anterior body scales, with a spur-like projection in more posterior trunk and fin scales (Märss 2003, p. 101).

Figure 5 illustrates the scales of *Paralogania martinssoni* from two localities in the Mikhailovsk Pond area, with images separated by a line: (1) locality 73Ms (Fig. 5A–G), and (2) locality 911, south of the dam (Fig. 5H–P). The morphological features (general shape) and sculpture details of the scales from both localities remain within the limits of the diagnosis of species, but the size of the scales differs two- to three-fold, being larger in bonebed 911A-18. Typically, the scales increase in size at stratigraphically higher levels (Märss 2003, fig. 2), which is also the case here. The higher stratigraphic position of locality 911 (A, Б, B) is confirmed by the presence of *Andreolepis hedei* scales in the samples, which are absent in sections 73Ms-2 to 73Ms-7.

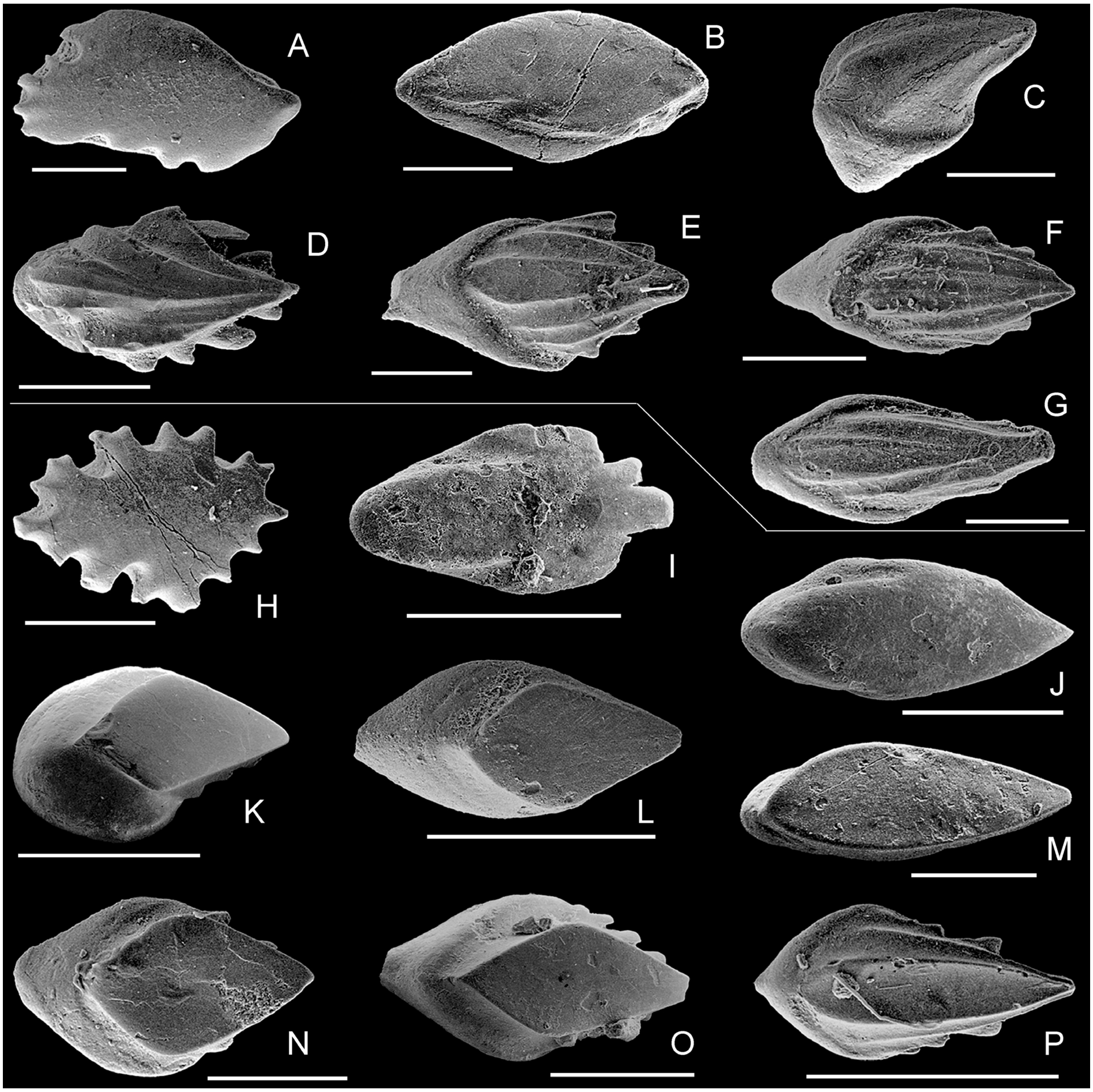

Fig. 5. *Paralogania martinssoni* (Gross). Scales from two different localities (separated by a fine line) and different parts of squamation. **A, B, I, J** – cephalo-pectoral scales. **C, M** – scales with a stout vertical base anteriorly, possibly from the fins. **D–G, P** – precaudal scales. **H** – rostral scale. **K, L, N, O** – possibly postpectoral scales. Localities: 73Ms-3/8, the southern bank of Mikhailovsk Pond, Kuba Beds, *Paralogania martinssoni* Zone, upper Homerian, Wenlock (A–G); excavation 911A-18, Mikhailovsk Pond area south of the dam, *Andreolepis hedei* Zone, Lower Ludfordian, Ludlow, upper Silurian (H–P). Specimens: GIT 820-38 (A), GIT 820-44 (B), GIT 820-43 (C), GIT 820-39 (D), GIT 820-42 (E), GIT 820-40 (F), GIT 820-41 (G), GIT 820-32 (H), GIT 820-30 (I), GIT 820-26 (J), GIT 820-29 (K), GIT 820-35 (L), GIT 820-27 (M), GIT 820-34 (N), GIT 820-28 (O), GIT 820-36 (P). Scale bars: 200 μm (A–H, K), 500 μm (I, J, L–P).

The scales exhibit transitional features between different types. The head (rostral) scales are roundish to oval, with a smooth medial crown surface and notched margins around the scale (Fig. 5H). The transitional (cephalo-pectoral) scales have a pair or multiple notches anterolaterally along the crown margins; medially, the crowns are smooth and slightly convex (Fig. 5A, B, I, J). The trunk (postpectoral) scales (Fig. 5K, L, N, O), which are the most common in squamation, show two variations: one has a smooth crown surface (plate) with 2–4 spines posterolaterally (Fig. 5K, N, O), while the other lacks spines but has smooth margins (Fig. 5L). The scales, thick and compact anteriorly (Fig. 5K), become narrower towards the posterior of the body, while the strong spur-like projection anteriorly of the base (Fig. 5L, N, O) obtains a more horizontal, longer, and narrower shape in the more posterior scales. The next type, the precaudal scales (Fig. 5D–G, P), has features of longitudinal ridges on the crown surface and posterolateral spines with a rather long anterior spur at the base (Fig. 5E, F). The scales covering the leading edges of the fins are stocky, with a smooth crown

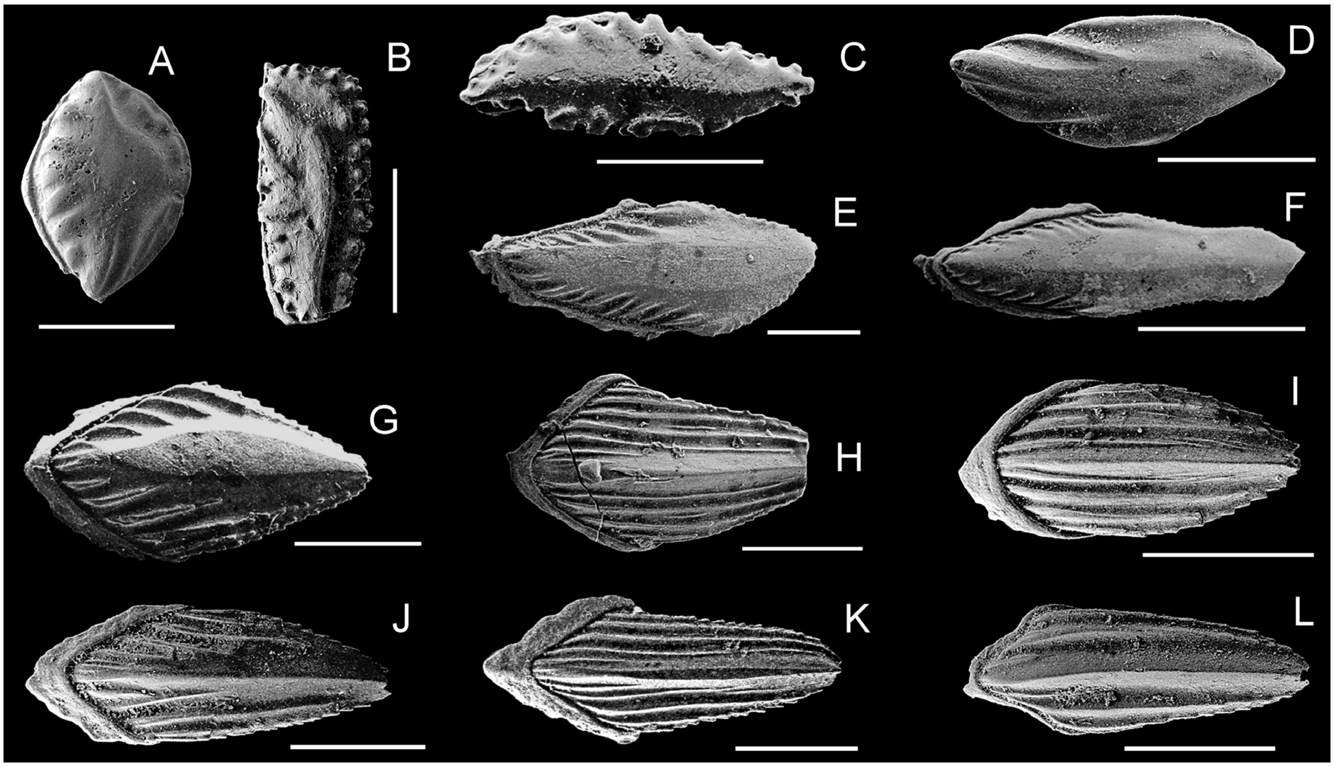

Fig. 6. *Phlebolepis elegans* Pander. **A–C** – rostral scales. **D** – scale from the leading edge of a lateral? fin. **E–G** – cephalo-pectoral scales. **H–K** – postpectoral scales. **L** – precaudal scale. Localities: sample 73Ms-3/3 (A, C); sample 73Ms-4/4 (B, D, E–G, L), southern bank of Mikhailovsk Pond; sample N. 3182 (H–K), Mikhailovsk Pond area, south of the dam, Kuba Beds, *Phlebolepis elegans* Zone, Gorstian, Ludlow. Specimens: GIT 820-1 (A), GIT 820-3 (B), GIT 820-2 (C), GIT 820-4 (D), GIT 820-8 (E), GIT 820-11 (F), GIT 820-9 (G), GIT 820-10 (H), GIT 820-6 (I), GIT 820-7 (J), GIT 820-12 (K), GIT 820-5 (L). Scale bars: 500 μm (all except F, which is 1 mm).

surface and a vertical base anteriorly (Fig. 5C); the crowns are narrow throughout their length (Fig. 5M).

Order PHLEBOLEPIDIFORMES Berg, 1937
Family PHLEBOLEPIDIDAE Berg, 1940
Genus *Phlebolepis* Pander, 1856
Phlebolepis elegans Pander, 1856
Figure 6

Material. About 100 scales of different preservation were collected from the southern bank of Mikhailovsk Pond, including samples 73Ms-3/1 and 73Ms-3/3, as well as samples 73Ms-4/4–73Ms-4/6 (Kuba Beds, *Phlebolepis elegans* Zone, upper Gorstian, Lower Ludlow). Additional samples were taken from the area south of the dam, locality 911, including samples 911Б-18 and 911B-23–911B-25 (containing *Andreolepis hedei*), and a sample from locality N. 3182, including *Phlebolepis elegans*, only (Kuba Beds, upper Gorstian and Lower Ludfordian, Ludlow).

Species range. The species ranges from the Himmiste Beds into the lower part of the Uduvere Beds of the Paadla Stage in the East Baltic. The southern section of Mikhailovsk Pond, which contains *Phlebolepis elegans*, correlates with the upper Gerd'ju Stage in the northern regions of the Urals and Novaya Zemlya (Modzalevskaya and Märss 1991). Other important findings originate from the upper Gorstian and Lower Ludfordian of the Welsh Borderland, Great Britain; Hemse Beds, Ludlow, Gotland; Upper Mielnik Stage, Ludlow of Poland; the middle part of the Ust'-Spokojnaya Formation, Ludlow, on the River Matusevich, and the lower part of the same formation on the River Spokojnaya, October Revolution Island, Severnaya Zemlya (for further data, see Märss and Männik 2013, p. 187).

Description. The scale varieties on the body are well known, owing to findings of articulated specimens found in the Himmiste quarry, Saaremaa, Estonia. All morphological varieties (except wedge-shaped pinnal scales) have been recognised: rostral, cephalo-pectoral, postpectoral, precaudal, and scales from the leading edges of fins (Märss 1986). The features of the scales in the current samples are fully comparable to those previously diagnosed. The most characteristic feature is the flattened shape of rather large scales (up to 2.4 mm in length), with mainly ridged crowns. The rostral scales (Fig. 6A–C) are rhomboidal in shape, with relatively high and short sculpture, and many scales on the rostral area have transverse crest(s). Cephalo-pectoral scales (Fig. 6E–G) are relatively large compared with other scale types of this species, elongate, with the sculpture of short ridges occurring only anterolaterally on the crown. In postpectoral scales (Fig. 6H–K), the shape is rhomboidal, with crowns covered over the entire surface with numerous relatively low longitudinal ridges. The precaudal scales (Fig. 6L) posteriorly on the body become narrow and relatively high, carrying a few relatively high ridges. The leading edges of fins are covered with more robust (stocky) scales (Fig. 6D), while the scales on the trailing edges become shorter and narrower, sculptured with fine ridges. These scales are fragile and very rare in the acetic acid residues. The posterolateral crown margins are serrate; the neck forms a shallow groove; and the base is narrow anterolaterally, slightly exceeding the crown. In the collection, there are scales with pores of lateral line canals.

Order THELODONTIFORMES Kiaer, 1932
Family COELOLEPIDIDA Pander, 1856
Genus *Thelodus* Agassiz, 1838
Thelodus carinatus (Pander, 1856)
Figure 7A–K

Material. Southern bank of Mikhailovsk Pond, locality 73Ms: samples 73Ms-3/3 and 73Ms-4/5, where *Thelodus carinatus* occurs together with *Phlebolepis elegans*, and the Mikhailovsk Pond area south of the dam, near the railway, locality 911: samples 911Б-18 with *Phlebolepis elegans*, and 911A-18, 911Б-18, and 911B-18 with *Andreolepis hedei* (Kuba Beds, upper Gorstian to Lower Ludfordian, Ludlow).

Species range. Vesiku Beds of the Rootsiküla Stage?, upper Homerian, Wenlock, and Soeginina Beds? (stage and beds questioned); Sauvere to Uduvere Beds of the Paadla Stage, upper Gorstian to Lower Ludfordian, Ludlow of Estonia; Hemse Beds, Ludlow of Gotland.

Description. This species has relatively big scales, up to 1.65 mm long. According to the diagnosis (e.g. Märss et al. 2007, p. 90), the scales have simple rectangular crown, a raised medial area, and downstepped marginal areas with a carina and fine riblets between them (Fig. 7A–K). The scales have transitional features from one variety to another. Rostral scales (Fig. 7A) are roundish, with convex crown surface and notches anteriorly or anterolaterally. Anterior body scales (cephalo-pectoral; Fig. 7B, C) have rhomboidal crown configuration and slightly convex surface; the raised triangular medial area is large, and lateral lowered rims sometimes may be rather wide; short low riblets occur anteriorly and in the middle of the triangular area of the crown; the base may have a spur-like process anteriorly (Fig. 7C). In the posterior body scales (postpectoral in Fig. 7D–I, and precaudal in Fig. 7J), the short ridges in anteriorly positioned scales become gradually longer in more posteriorly positioned scales; the lowered lateral rim is still relatively wide. The ridges on the crown surface are low and may appear as short ridgelets (Fig. 7D–F, H). Figure 7K shows the scale that may originate from any fin (long ridges reach the posterior point of the crown surface of narrow scales). Comparison of the *Thelodus carinatus* scales from the Mikhailovsk Pond area with the East Baltic ones shows that the scales from the Mikhailovsk Pond southern sections have more distinct ridges and ridgelets on the crown surface than those from the East Baltic, where they are lower.

Thelodus laevis (Pander, 1856)
Figure 7L

Material. The number of obtained scales is small, fewer than 20 specimens, mostly broken. Southern bank of Mikhailovsk Pond, locality 73Ms: samples 73Ms-2/1 and 3?; 73Ms-3/3 and 73Ms-3/9; 73Ms-4/4 (upper Homerian, Upper Wenlock, up to upper Gorstian, Lower Ludlow); Mikhailovsk Pond area south of the dam, locality 911: sample 911A-18 (Kuba Beds).

Species range. The Rootsiküla Stage, upper Homerian, Upper Wenlock, to the Paadla Stage, Ludfordian of the East Baltic; Upper Wenlock of Ringerike, Norway; Wenlock, Homerian, Halla, and Mulde Beds of Gotland, Sweden; Ludlow of Lithuania; Ludlow, Middle Elton Beds of Welsh Borderland, Great Britain.

Description. The scales placed anteriorly on the body have a rhomboidal configuration with a slightly convex, smooth crown surface and a lowered anterior edge. The base may have a vertical thickening anteriorly. Such scale was found in 73Ms-3/3 together with *Paralogania martinssoni*, *Thelodus carinatus*, and *Phlebolepis elegans*. The more posteriorly placed scales have a very distinct groove-ridge alternation on the crown (Fig. 7L). Important features for differentiation of *Thelodus laevis* from *Thelodus carinatus* are that the first taxon has the crowns with relatively strong and high ridges with a square cross-section, while in *Thelodus carinatus*, they are much lower, gentle, and triangular in cross-section.

Thelodus aff. *Thelodus carinatus*
Figure 7R

One scale (Fig. 7R) was found in sample 73Ms-3/8, on the southern bank of Mikhailovsk Pond, while *Thelodus carinatus* s. str. occurs below (in 73Ms-3/3) and *Thelodus laevis* both below and above sample 73Ms-3/8. The scale is tiny, with four parallel distinct but delicate longitudinal ridges and a short ridgelet on both sides of the crown margins. The scale base is broken anteriorly. Small scales such as this one, but with only two parallel ridges, are occasionally found together with *Thelodus parvidens* and identified as *Thelodus bicostatus*. In rare cases, they have occurred together with other *Thelodus* species, such as *Thelodus carinatus* and *Thelodus laevis*. In the scale herein (Fig. 7R), the crown is covered with several low ridges with a triangular cross-section.

Thelodus parvidens Agassiz, 1839
Figure 7M, N

Material. About 200 black, heavily pyritised scales from the following samples (Fig. 3): 146-0, 73146-0, 83146-0, 83024-11; BB1 83042, 85042, and 87777; 8547; BB2 85146-5; 83146-5в, 83146-5д; 85146-5в, 85146-5д. Tabuska Hill section, right bank of the River Ufa, downstream of the mouth of the River Tabuska; Tabuska Beds, mid-Ludfordian, Ludlow, upper Silurian.

Range. The species range embraces the Ludfordian (including the FAD, uppermost Uduvere Beds of the Paadla Stage), Ludlow, up to the upper Přidoli (except the uppermost beds), upper Silurian of Europe (East Baltic; Skåne, Sweden; Poland; Welsh Borderland, Great Britain).

Remarks. The crowns of scales have a very simple configuration; they are rhombic to rectangular, with smooth, flat, or slightly convex surface; the anterior margin of the crown

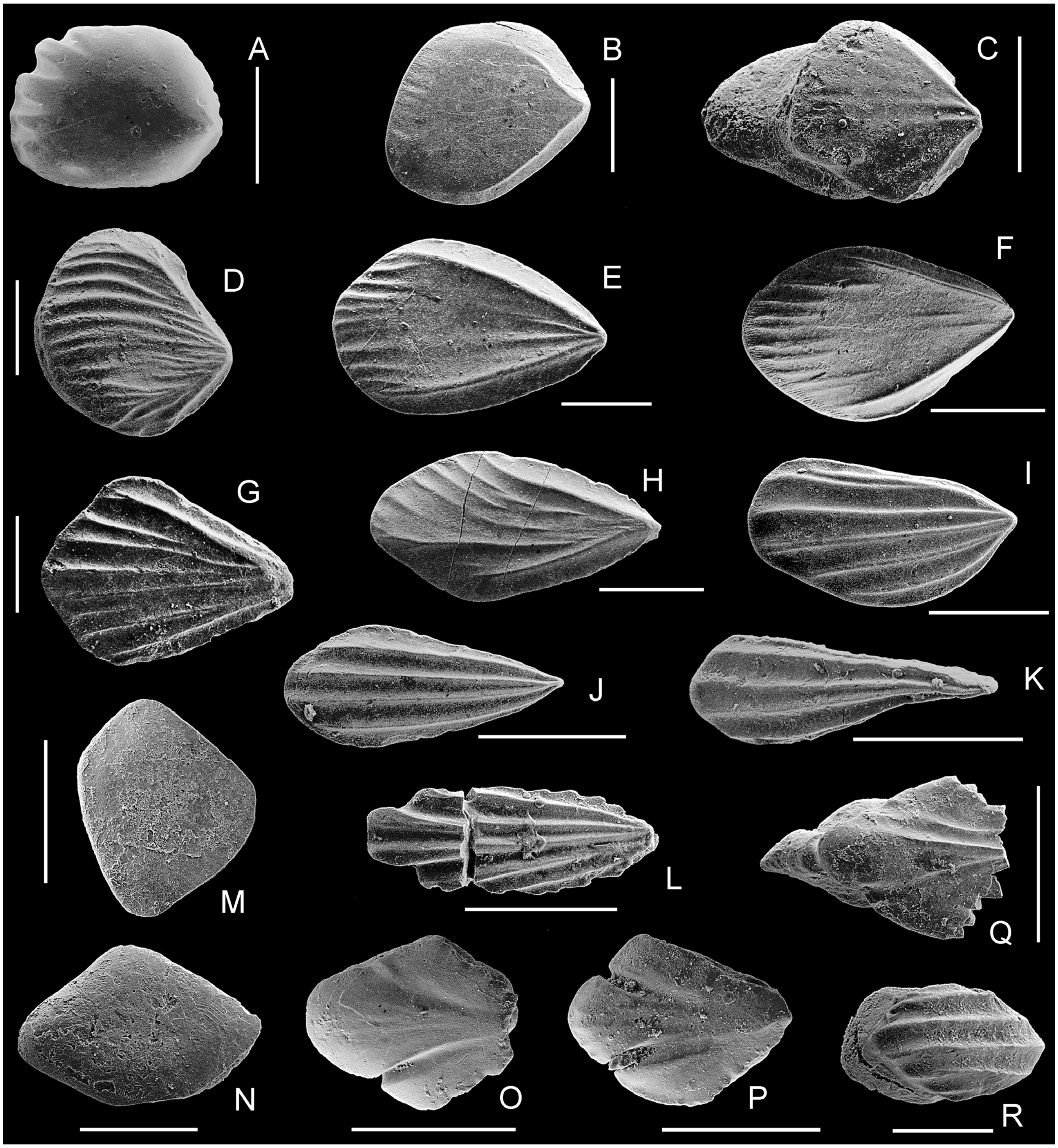

Fig. 7. Scales of various *Thelodus* species. *Thelodus carinatus* (Pander) (A–K): **A –** rostral scale, **B, C** – anterior body scales (cephalo-pectoral), **D–I** – postpectoral scales, **J** – precaudal scale, **K** – fin scale. **L** – *Thelodus laevis* (Pander), broken posterior body scale. **M, N** – *Thelodus parvidens* Agassiz. **O, P** – *Thelodus sculptilis* Gross. **Q** – *Thelodus trilobatus* (Hoppe). **R** – *Thelodus* aff. *carinatus*. Localities: sample 911A-18, Mikhailovsk Pond area, south of the dam, near the railway, Kuba Beds, Ludlow, upper Silurian (A–L); outcrops 85042 (M, N, Q) and 85146-5 (O, P), Tabuska Hill section, downstream of the mouth of the River Tabuska, right bank of the River Ufa, Tabuska Beds, mid-Ludfordian, Ludlow, upper Silurian; sample 73Ms-3/8 (R), southern bank of Mikhailovsk Pond, possibly from the Wenlock. Specimens: GIT 820-13 (A), GIT 820-15 (B), GIT 820-22 (C), GIT 820-16 (D), GIT 820-17 (E), GIT 820-18 (F), GIT 820-20 (G), GIT 820-19 (H), GIT 820-21 (I), GIT 820-23 (J), GIT 820-25 (K), GIT 820-24 (L), GIT 820-53 (M), GIT 820-57 (N), GIT 820-54 (O), GIT 820-55 (P), GIT 820-56 (Q), GIT 820-45 (R). Scale bars: 500 µm (all except L, which is 200 µm).

is turned downwards; the distinct neck is constricted and carries small vertical ridgelets on its posterolateral surface (Fig. 7M, N).

Thelodus sculptilis Gross, 1967
Figures 7O, P; 8

Material. Thelodus sculptilis scales are not common in the rocks of the Ufa Amphitheatre. The samples from the Tabuska Hill section on the right bank of the River Ufa, downstream of the mouth of the River Tabuska, yielded some dozens of specimens together with *Thelodus parvidens* in 73146-0, 146-0, 83146-0, 83024-11; BB1 85042, 85777; 8547; BB2 85146-5; 83146-5в, 83146-5д; 85146-5в, 85146-5д. Tabuska Beds, mid-Ludfordian, Upper Ludlow; *Thelodus sculptilis* Zone.

Species range. Uppermost Uduvere Beds of the Paadla Stage, the whole Kuressaare Stage up to basal Äigu Beds of the Kaugatuma Stage, Upper Ludlow to lower Přidoli of Estonia and Latvia; Öved-Ramsåsa Beds, Skåne, and Burgsvik Sandstone of Gotland, Sweden; Greben' Stage, Ludlow, Novaya Zemlya Archipelago, Russia.

Description. As diagnosed (Gross 1967; Märss 1986, p. 87), *Thelodus sculptilis* has scale crowns with a central longitudinal division ending with a pointed, peg-like posterior projection and separated from lateral ones by furrows; the furrows are deeper and steeper anteriorly than posteriorly of the crown (Figs 7O, P; 8). These three divisions of the crown (one central and two lateral ones) are in turn subdivided into more complicated sculptures by several additional narrow ridges and furrows, but the main tripartite division is still retained. The scale crowns are smoother in anterior cephalo-pectoral body scales (Figs 7O, P; 8, area I), while the postero-medial projection is not distinct or may even be absent. Postpectoral and more posterior scales (Fig. 8, area II) have a tripartite division, multiple longitudinal ridges, and a postero-medial projection of the crown, which is separated from the main crown by a cleft on both sides. The posterior-most trunk and fin scales become very small.

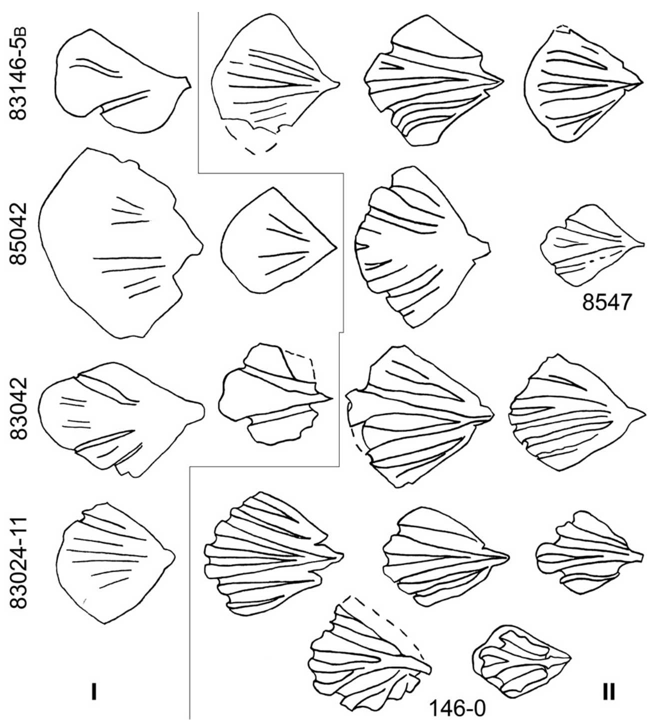

Fig. 8. *Thelodus sculptilis* Gross. The scales are arranged by outcrops (numbers on the figure), starting from the NW part of the section (146-0) and moving towards its SE part (83146-5в) (outcrop numbers from Zhivkovich and Chekhovich 1985, fig. 20). The smoother crowns (area I) originate from the anterior part of the body, while the ridged scales (area II) come from the more posterior parts. Note the relatively similar scale sculpture within each type throughout the section. Locality: Tabuska Hill section, downstream of the mouth of the River Tabuska, right bank of the River Ufa, Tabuska Beds, mid-Ludfordian, Ludlow, upper Silurian. Specimens: GIT 820-58–GIT 820-75. Magnification: ×50 for all scales.

Thelodus trilobatus (Hoppe, 1931)
Figure 7Q

Material. A few scales from the Tabuska Hill sections, samples 146-0, 73146-0, 83146-0, 85042; Tabuska Beds, mid-Ludfordian, Upper Ludlow.

Species range. Upper Ludlow to Přidoli (except its highest beds) of the East Baltic; Skåne, Sweden; Whitcliffe Group, Upper Ludlow of Welsh Borderland, Great Britain.

Remarks. A few trilobatiform scales were found, their crowns divided into three to five parts, with a roundish anterior margin and spines (still often broken) posteriorly extending over the posterior end of the base; the base often has a spur-like process anteriorly (Fig. 7Q). There have been discussions regarding the validity of this taxon, with some authors equating it with *Thelodus parvidens* as a variation of scales in squamation, while others consider it a separate species (Märss and Miller 2004; synonymy in Märss et al. 2007, p. 92, and discussion on p. 94). The number of scales from the Tabuska Hill section is small and does not contribute any new information for solving this problem. In this paper, the *Handbook on Thelodonti* is followed, where *Thelodus trilobatus* (Hoppe) is considered a distinct, valid species (Märss et al. 2007, p. 92, fig. 103).

Family TURINIIDAE Obruchev, 1964
Genus *Turinia* Traquair, 1894
Turinia pagei (Powrie, 1870)
Figure 9A–F

Material. A few tens of scales of *Turinia pagei* originate from samples 73Mn-34, 73Mn-45, and 73Mn-48 from the northern bank of Mikhailovsk Pond. These samples also contained *Talivalia elongata* (Karatajūtė-Talimaa), '*Traquairaspis*' sp., and *Zemlyacanthus* (*Poracanthodes*) *menneri*?. Later, in 1987, the expedition to the same location enriched the scale collection with the discovery of *Turinia pagei* in samples 87510-7, 87510-12–87510-14, and 87510-25, while in most cases, it occurred together with '*Traquairaspis*' sp. in the Mikhailovsk Beds, Lochkovian, Lower Devonian (Märss 1997; Fig. 9).

Species range. Lochkovian to Pragian, Lower Devonian. The species *Turinia pagei* is an important taxon for determining

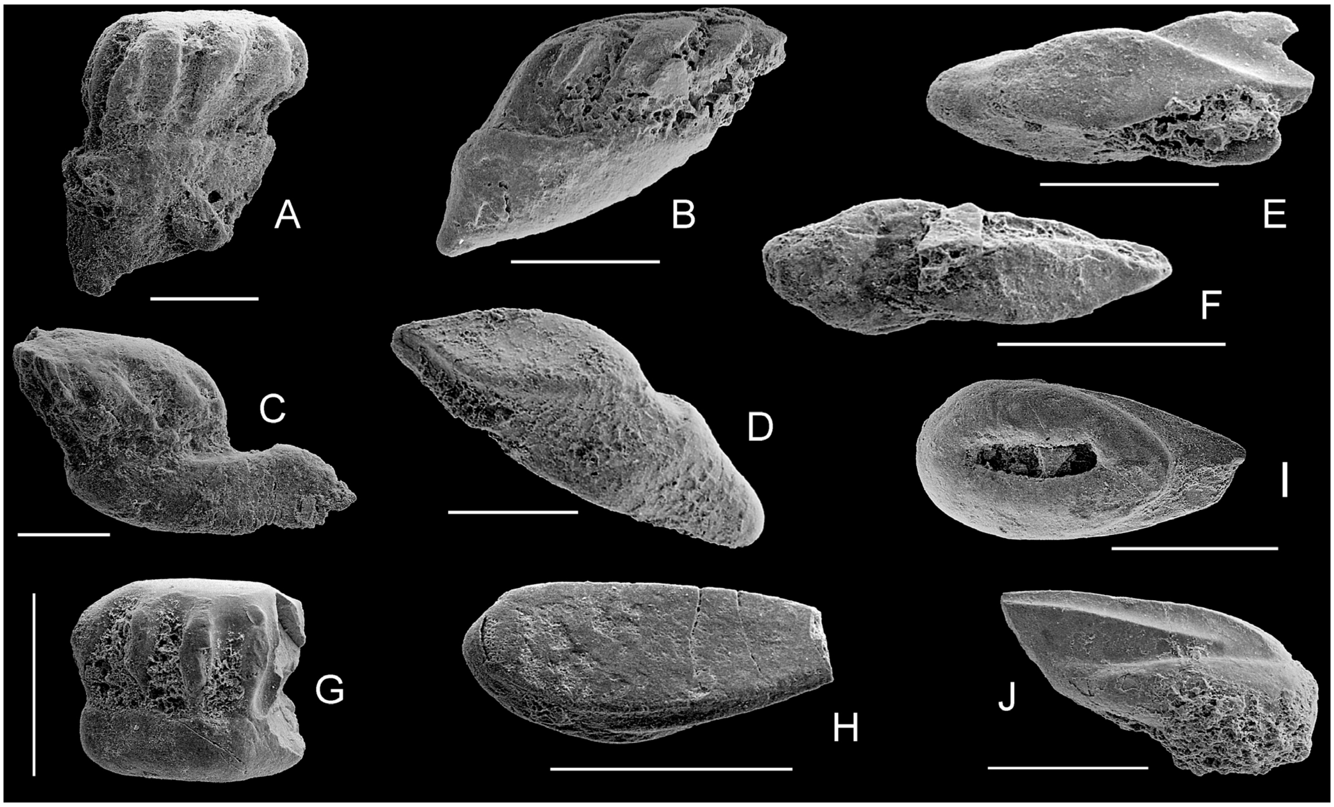

Fig. 9. Scales of two Devonian thelodonts. *Turinia pagei* (Powrie) (A–F): **A** – costatiform rostral scale, **B, C** – transitional scales, **D** – trunk scale, **E** – trilobatiform, possibly a lateral fin scale, **F** – cuneiform caudal fin scale. *Talivalia elongata* (Karatajūtė-Talimaa) (G–J): **G** – rostral scale, **H–J** – trunk scales, including a scale with a lateral longitudinal ridge on the crown side (J). Views: scales in lateral view (A–C, G, J), scale in anterolateral view (D), scales in crown view (E, F, H), scale in base view (I). Localities: sample 73Mn-34 (A–F), sample 73Mn-3 (G–J), northern bank of Mikhailovsk Pond, Ufa Amphitheatre, Mikhailovsk Beds, Lochkovian, Lower Devonian. Specimens: GIT 297-48 (A), GIT 297-49 (B), GIT 297-92 (C), GIT 297-90 (D), GIT 297-50 (E), GIT 297-93 (F), GIT 297-51 (G), GIT 297-54 (H), GIT 297-53 (I), GIT 297-52 (J). Scale bars: 500 μm (all except G, which is 400 μm).

the Silurian–Devonian boundary, both in carbonate and terrigenous sedimentary rocks. It has been found in many outcrops of both western and eastern Europe; in the eastern regions, it occurs in Lithuania, Latvia, the Brest District in Belarus, Volhynia and Podolia of Ukraine, the Northern and Central Urals, Timan-Pechora region, Spitsbergen, and further away on Figurnyi and October Revolution islands of the Severnaya Zemlya Archipelago, Russia (Karatajūtė-Talimaa 1978, 1985; Märss 1986, 1997; Märss et al. 2007, p. 104).

Remarks. Karatajūtė-Talimaa (1978, pp. 116–117) described the scattered scales of *Turinia pagei*, using the material from many localities in Europe, and presented an extended diagnosis of the species. Märss and Ritchie (1998) described the scale varieties on the intact holotype from the Turin Hill quarry, Scotland, and found that the variety was not as high as was shown by Karatajūtė-Talimaa (1978).

Description. The scales of the holotype are relatively big (up to 1.9 mm in length); the crown of all scale types, except the rostral ones, rises posteriorwards. Elongate diamond-shape body scales have a central area with a smooth, flat, or slightly concave surface; the lateral areas are narrow. More posterior scales have a short oblique rib on the posterolateral walls of the crown. The anterior part of the base can extend forward as a spur-like process, which may be rather long; the rear end of the crown protrudes back beyond the base (specified by Karatajūtė-Talimaa 1978 and Märss and Ritchie 1998). The scales from the Mikhailovsk Pond northern section 73Mn illustrate the rostral (also called costatiform, Fig. 9A), transitional (Fig. 9B, C), trunk (Fig. 9D), possibly lateral fin (trilobatiform, Fig. 9E), and possibly caudal fin (cuneiform, Fig. 9F) scales.

Genus *Boreania* Karatajūtė-Talimaa, 1985
Boreania minima Karatajūtė-Talimaa, 1985

Remarks. Very small scales (length 0.2–0.8 mm, according to Karatajūtė-Talimaa 1985) were found in sample 73Mn-3 in the Mikhailovsk Beds, Lower Lochkovian, in the Mikhailovsk Pond northern section (Märss 1997, distribution in fig. 8). The scale crowns are elongate, the neck is low, the base is small and circular, and may have a small process anteriorly. The species occurs in sample 73Mn-3 together with thelodont *Talivalia elongata*, heterostracans, acanthodians, including *Zemlyacanthus menneri*, but also with placoderm and osteichthyan fragments.

Species range. Uppermost Přidoli, upper Silurian, up to mid-Lochkovian, Lower Devonian of Eurasia. The Silurian scale findings are very rare, whereby they were found together with *Trimerolepis timanica* and *Trimerolepis lithuanica* in the uppermost Silurian of the Timan-Pechora region. The scales of the findings are common in the Lower and middle Lochkovian of Lithuania, Brest District, Podolia, Kaliningrad District, Timan-Pechora region, Spitsbergen, Subpolar Urals, and the Severnaya Zemlya Archipelago, Russia (Karatajūtė-Talimaa 1985, Märss et al. 2007, p. 110).

Family TALIVALIIDAE Märss, Wilson et Thorsteinsson, 2002
Genus *Talivalia* Märss, Wilson et Thorsteinsson, 2002
Talivalia elongata (Karatajūtė-Talimaa, 1978)
Figure 9G–J

Material. Some dozens of specimens were found in samples 73Mn-3, 73Mn-45, 73Mn-48, and 87510-25 on the northern bank of Mikhailovsk Pond; Mikhailovsk Beds, Lower Lochkovian, Lower Devonian.

Species range. Northern Hemisphere (Eurasia, northern and Arctic Canada), uppermost Přidoli, upper Silurian, to Lochkovian, Lower Devonian (Karatajūtė-Talimaa 1978, p. 155; Märss et al. 2007, p. 116).

Remarks. Figure 9 demonstrates three varieties of *Talivalia elongata* scales: a costatiform rostral scale with serrated margins (Fig. 9G), a cephalo-pectoral trunk scale with smooth medial and lowered lateral areas (Fig. 9H) and the same type of trunk scale in basal view with a very characteristic thick oval wall around the rather narrow elongate pulp opening (Fig. 9I). A possible postpectoral scale in lateral view (Fig. 9J) has a lateral ridge of the crown rising backwards.

Subclass HETEROSTRACI Lankester, 1868
Order ERIPTYCHIIFORMES Ørvig, 1958
Family ONISCOLEPIDIDAE Märss et Karatajūtė-Talimaa, 2009
Genus *Oniscolepis* Pander, 1856
Oniscolepis dentata Pander, 1856
Figure 10A

Material. One broken tessera originates from sample КФА-1, taken from the parabreccia interval in the Tabuska Hill section, on the right bank of the River Ufa, downstream of the mouth of the River Tabuska; Tabuska Beds. The presence of the taxon indicates that the corresponding level is of Přidoli, upper Silurian age.

Species range. Uppermost part of the Kaugatuma Stage and Ohesaare Stage, Přidoli, upper Silurian of Estonia and Latvia, and the Tilže Stage, Lower Lochkovian, Lower Devonian of Latvia; upper part of the Jūra Stage, Lithuania; Eptarma Beds, North Timan, upper Silurian, Russia (Märss and Karatajūtė-Talimaa 2009).

Remarks. The exoskeleton of this species is covered with tesserae and scales, which in turn are overlain with dentine ridges forming a concentric pattern on the tesserae and a longitudinal pattern on the scales; different head platelets are covered by complicated ridge patterns. The ridges have crenulated margins, are flat-topped, or have a longitudinal crest. The surface of the basal part of the elements can be very uneven, with holes and canals (adapted from Märss and Karatajūtė-Talimaa 2009). The specimen from sample КФА-1 from the Tabuska Hill section (Fig. 10A) is identified as *Oniscolepis dentata* based on characteristics such as the flat ridge surface, with some ridges displaying a very delicate longitudinal crest. In this particular specimen, the edges of the ridges are weakly serrated, and the ridges are anteriorly either curved or angled, similar to those found in tesserae. The ridges are attached to the uneven surface of the basal plate.

Order TRAQUAIRASPIDIFORMES Tarlo, 1962
‘*Traquairaspis*’ sp.

Remarks. Some ‘*Traquairaspis*’ sp. specimens were found in samples 34 and 45 from the northern bank of Mikhailovsk Pond, locality 73Mn (Märss 1997, text-fig. 8; in that paper identified as ‘*Traquairaspis*’ spp.). They occurred together with two other biostratigraphically important taxa: the thelodont *Turinia pagei* and the acanthodian *Zemlyacanthus menneri*. The ‘*Traquairaspis*’ sp. exoskeletal fragments were covered with characteristic high zigzag sculpture ribs (ibid., pl. 5, fig. 8).

Order CYATHASPIDIFORMES Berg, 1937
Family CYATHASPIDIDAE Kiaer, 1932
Subfamily ARCHEGONASPIDINAE Märss, 2019
Genus *Archegonaspis* Jaekel, 1927
Archegonaspis bashkirica Märss, 2019
Figure 10B, D

Material. Head shield fragments in samples 83042, 85777 and 85146-5, and 85146-5д from both bonebeds in the Tabuska Hill section on the right bank of the River Ufa, downstream of the mouth of the River Tabuska; Tabuska Beds, mid-Ludfordian, Ludlow, upper Silurian.

Species range. Ludlow, upper Silurian, the Southern and Central Urals.

Remarks. Obruchev (1938) presented the first description and pictures of the specimens, which were later named *Archegonaspis bashkirica* (Fig. 10B, a detail, reversed image). They were found in the Ludlow beds on the right bank of the River Siren-gupan, the Southern Urals. At the time of publishing the name (Märss 2019), it had not been recognised in the Central Urals. The specimens of this species were noted during the re-examination of the acetic acid residues (Fig. 10D). By diagnosis, the taxon has long dentine ridges of two widths, with three narrower ones placed between two relatively coarser/wider ridges, forming the sets 1:3:1 (Fig. 10B). The sets of ridges and furrows occur in an anteroposterior direction over most of the head shield, with the pattern consisting of longitudinal, straight, nearly parallel dentine ridges. On the recently found fragments, the ridges are arranged according to the formula 1:5:1 (Fig. 10D).

Archegonaspis integra (Kunth, 1872)
Figure 10C, E

Material. Head shield fragments in samples 85042, 85777 and 85146-5, and 85146-5д from both bonebeds, collected in the Tabuska Hill section, on the right bank of the River Ufa, downstream of the mouth of the River Tabuska; Tabuska Beds, mid-Ludfordian, Ludlow.

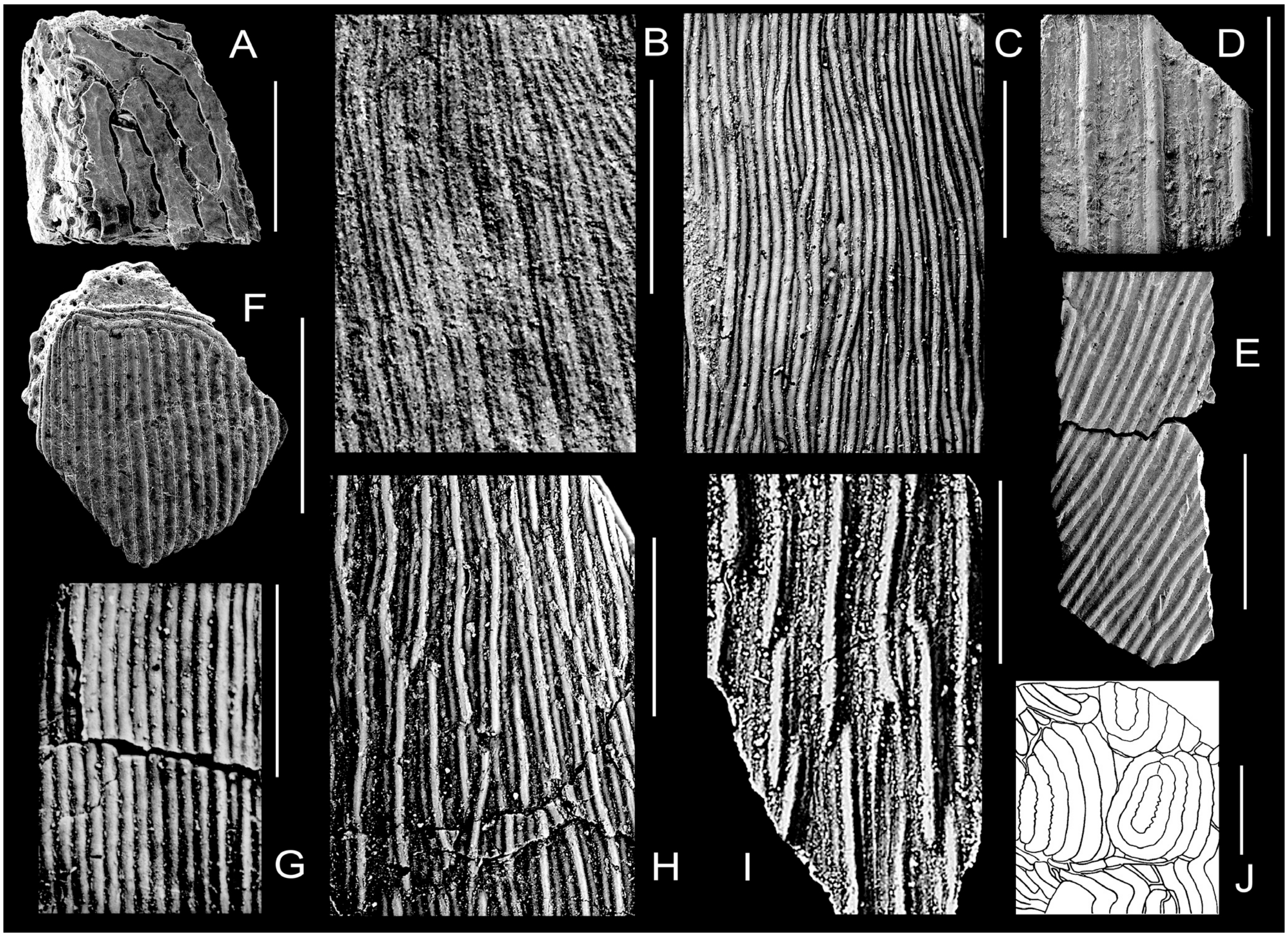

Fig. 10. Dentine ridge patterns on the exoskeleton of heterostracans from the Ural Mountains. **A** – eriptychiiform *Oniscolepis dentata* Pander, a broken tessera. **B, D** – *Archegonaspis bashkirica* Märss, including a part of the holotype No. 4650-1, with the photograph turned over (B), and a shield fragment picked up from the acetic acid residues (D). **C, E** – *Archegonaspis integra* (Kunth). **F, G** – *Archegonaspis lindstroemi* Kiaer, including a scale (F) and a possibly branchial plate fragment (G). **H, I** – *Cyathaspis alexanderi* Märss. **J** – *Cyathaspis alexanderi*? Märss. Localities: sample КФА-1 (A) from a parabreccia layer in the Tabuska Hill section; locality 2769 (B), 15 km upstream of the mouth of the River Siren-gupan, locality on its right bank, River Belaya basin, the Southern Urals, with the age determined as Ludlow by Obruchev (1938, pp. 37–38); sample 85146-5д (C); sample 85042 (D, E); sample 85146-5 (F); sample 85042 (G–I); sample 85146-5д (J), Tabuska Hill section, right bank of the River Ufa, downstream of the mouth of the River Tabuska, Tabuska Beds, mid-Ludfordian, Upper Ludlow, upper Silurian. Specimens: GIT 408-57 (A), CSRGM 4650-1 (B), GIT 408-5 (C), GIT 408-51 (D), GIT 408-54 (E), GIT 408-48 (F), GIT 408-12 (G), GIT 408-14 (H), GIT 408-16 (I), GIT 408-45 (J). Scale bars: 500 µm (A), 3 mm (B, C, H), 2 mm (D–G, I), 1 mm (J).

Species range. Upper Ludfordian, Ludlow of the Ufa Amphitheatre, the Central Urals, and the East Baltic; Lower Ludlow, glacial erratics of northern Germany.

Remarks. According to the diagnosis (Märss 2019, p. 127), the dentine ridges on the central epitegum are medium long to long and gently meandering. On the lateral epitega, the ridges are long and of the same width and height. Figure 10C (refigured from Märss 2019, fig. 5F) shows the diagnosed pattern of part of the dorsal shield. The ridges tend to be double-ridged, with the higher ridge sometimes crossing the lower one; in certain areas, the double-ridge appearance is particularly distinct (Fig. 10E). The meandering and double ridges are characteristic features of the *Archegonaspis integra* ridge pattern.

Archegonaspis lindstroemi Kiaer, 1932
Figure 10F, G

Material. A scale in sample 85146-5, and head shield fragments in samples 83-042, 85-042, 85777, 8547, 85146-5, and 85146-5д, collected from both bonebeds in the Tabuska Hill section, on the right bank of the River Ufa, downstream of the mouth of the River Tabuska; Tabuska Beds, mid-Ludfordian, Upper Ludlow (Modzalevskaya and Märss 1991).

Species range. Ludfordian, Upper Ludlow of the Ufa Amphitheatre and Baltic Sea region. The holotype comes from the Lau Canal, Gotland Island, Sweden; Hemse Beds, Ludlow.

Remarks. As diagnosed, the ridges on the central and lateral epitega are longitudinal, long, flattened, uniform, and of the same width (Lindström 1895, pp. 3–8, with the main focus on the sculpture in Märss 2019). The scale (Fig. 10F) and a possible fragment of a branchial part (Fig. 10G, refigured from Märss 2019, fig. 3F) both exhibit a highly regular dentine ridge pattern, with parallel ridges that are somewhat flattened and of uniform width.

Cyathaspis alexanderi Märss, 2019
Figure 10H, I

Material. Head shield fragments in samples 85042, 85777, and 85146-5д, collected from both bonebeds in the Tabuska Hill section, on the right bank of the River Ufa, downstream of the mouth of the River Tabuska; Tabuska Beds, mid-Ludfordian, Ludlow, upper Silurian.

Range. Ludfordian, Ludlow, upper Silurian of the Ufa Amphitheatre.

Remarks. This taxon is not widely distributed, having been found in only three samples. Its head shield fragments are covered with 'long, weakly expressed tesserae-like units having a straight or gently meandering prominent medial ridge accompanied by 2–3 lower ridges on both sides; the endings and beginnings of prominent medial ridges do not follow one another directly but slightly pass each other' (Märss 2019, p.132, fig. 8A, C) (Fig. 10H, I).

Cyathaspis alexanderi? Märss, 2019
Figure 10J

Material. Head shield fragments in samples 83042, 85042 and 85146-5, 85146-5в, and 85146-5д, collected from both bonebeds in the Tabuska Hill section, on the right bank of the River Ufa, downstream of the mouth of the River Tabuska; mid-Ludfordian, Ludlow, upper Silurian.

Remarks. This taxon is not well understood. The ridge pattern of the tesserae-like units is somewhat similar to both *Tolypelepis undulata* and *Cyathaspis* sp. However, in *Tolypelepis*, the tesserae-like units are more complex and flattened, with each unit consisting of several pairs of ridges located along the sides of the tesserae. In *Cyathaspis alexanderi*?, the ridges typically form closed rings, with one ring partially resting on the ring below, forming rather high 'towers' (Fig. 10J). Considering the possible location of these tesserae on the head shield, for example, near the pineal macula (Märss 2019), it was decided to integrate these high tesserae-like elements with *Cyathaspis alexanderi*?.

Subclass OSTEOSTRACI Lankester, 1868–1870
Order TREMATASPIDIFORMES Berg, 1937
Family TREMATASPIDIDAE Woodward, 1891
Genus *Tremataspis* Schmidt, 1866
Tremataspis schmidti Rohon, 1892
Figure 11A

Material. A few fragments of the head shield and an anal plate from the southern bank of Mikhailovsk Pond, sample 73Ms-4/1, upper Homerian, Wenlock.

Species range. The stratigraphic interval for *Tremataspis schmidti* in the Baltic Sea region extends from the Viita to the Vesiku Beds of the Rootsiküla Stage, Saaremaa Island, and the Halla Beds, Gotland Island, upper Homerian, Wenlock.

Remarks. The anal plate has a triangular configuration, with a convex upper surface and two shallow transverse furrows anteriorly. It is up to 8.5 mm wide and 8.0 mm long. According to the diagnosis of the species, *Tremataspis schmidti* has a pore density of 100 pores per mm^2 on the medial part of the head shield (Märss et al. 2014, p. 86). Based on this characteristic – 100 pores per mm^2 on the anal plate – it should belong to this species.

Tremataspis rohoni Robertson, 1938
Figure 11B

Material. A few scale fragments from locality 911, samples BB 911A-18 and BB 911Б-18, Mikhailovsk Pond area south of the dam (Fig. 2A, B); Kuba Beds. The interval from 911Б-16 up to 911B-25 corresponds to the *Andreolepis hedei* Zone, Lower Ludfordian, Ludlow, upper Silurian.

Species range. Tremataspis rohoni occurs from the Rootsiküla Stage, upper Homerian, to the Himmiste Beds of the Paadla Stage, upper Gorstian, Lower Ludlow of the East Baltic. It is a relatively rare taxon.

Remarks. The fragment of a high and short scale (Fig. 11B) has a smooth surface pierced by small pores. The pores are more densely spaced than in *Tremataspis mammillata* (approx. 15 pores per mm^2), but more widely spaced than in *Tremataspis schmidti* (approx. 100 pores per mm^2) or *Tremataspis milleri* (approx. 200 pores per mm^2). The estimated pore density of approximately 66 pores per mm^2 suggests an identification of *Tremataspis rohoni*, based on comparison with Denison (1947, p. 347).

Family THYESTIDAE Rohon, 1892
Thyestes? sp. ind.
Figure 11C

Material. A few small fragments from the southern bank of Mikhailovsk Pond, sample 73Ms-4/6, which co-occur with *Paralogania martinssoni* and *Phlebolepis elegans* scales, confirming the level of this bed as upper Gorstian, Lower Ludlow.

Species range. The range of the distinct species *Thyestes verrucosus* Eichwald in the East Baltic extends from the Rootsiküla Stage, upper Homerian, Wenlock, to the Paadla Stage, upper Gorstian, Lower Ludlow. This supports the age assigned to the finds, here referred to as *Thyestes*? sp. ind.

Remarks. The dentine ridges of the depicted specimen form a pattern resembling a chessboard. The ridges are smooth, relatively high, narrow, and short, and of the same width. The ridgelets along the sides of the ridges, common for the species *Thyestes verrucosus*, are absent; small pores occur on the base between the ridges. In *Thyestes verrucosus*, the pores around the ridges become elongated and appear to 'climb' towards the top of the ridges, whereas in the specimen from the Urals, the pores remain confined to the base between the ridges.

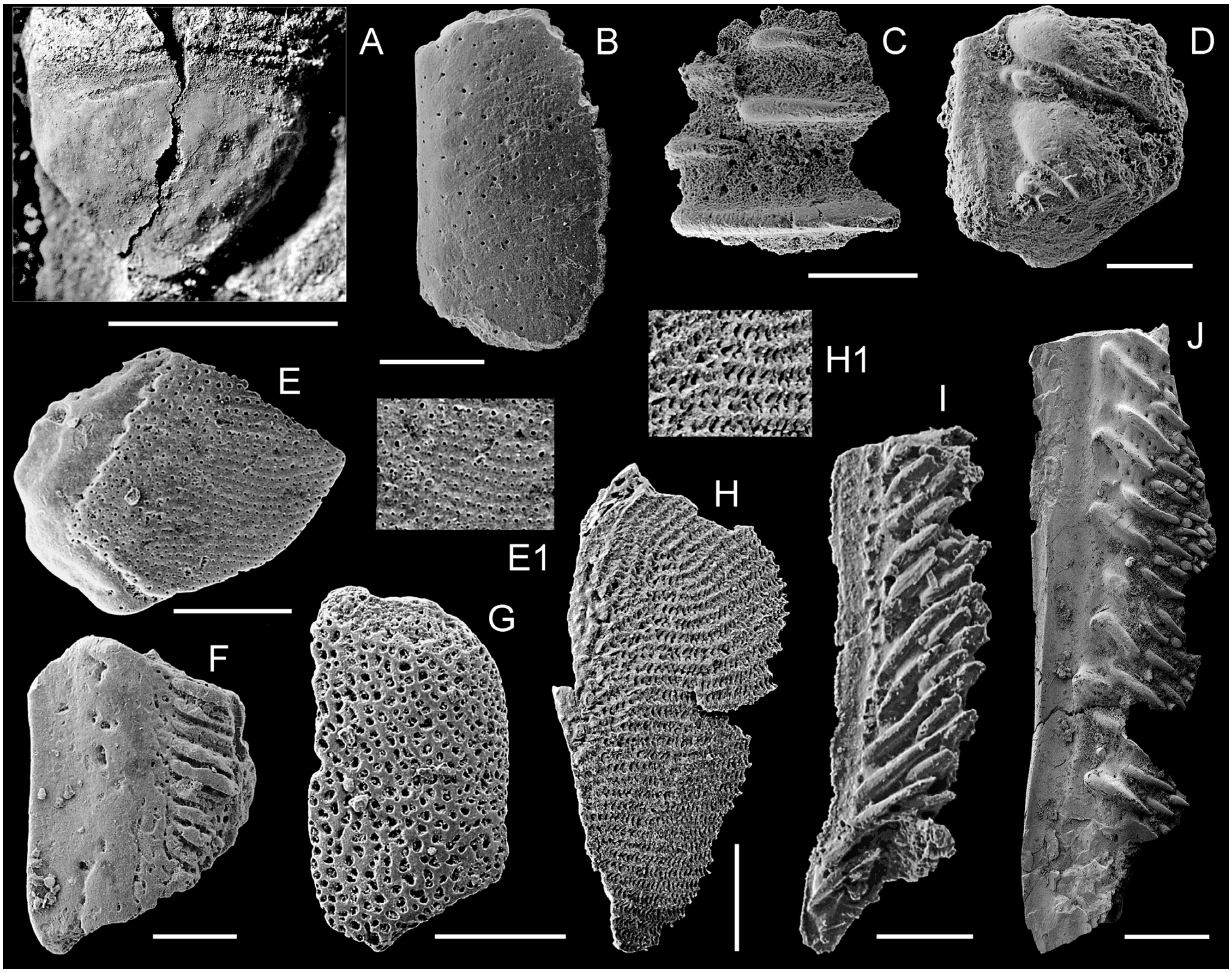

Fig. 11. Osteostracans and anaspids from the Silurian of the Ufa Amphitheatre. Osteostracans: **A** – *Tremataspis schmidti* Rohon, an anal plate in external view, **B** – *Tremataspis rohoni* Robertson, an incomplete scale, **C** – *Thyestes*? sp. ind., a fragment, **D** – *Procephalaspis* sp. ind., a tessera from the head?, **E, E1** – *Tahulaspis ordinata* Märss et al., a well-preserved scale, **F** – *Tahulaspis* sp. cf. *ordinata* Märss et al., an incomplete scale, **G** – *Tahulaspis praevia* Märss et al., an incomplete scale. Anaspids: **H, H1** – *Schidiosteus mustelensis* Pander, a scale (from Blom et al. 2001, fig. 30I), **I** – *Septentrionia mucronata*? Blom et al., a high and short, almost intact scale (from Blom et al. 2001, fig. 45J), **J** – *Liivilepis curvata* Blom et al., a high and short, almost intact scale (from Blom et al. 2001, fig. 48E). Localities: sample 73Ms-4/1 (A); sample 73Ms-4/6 (C), southern bank of Mikhailovsk Pond; sample 911A-18 (B, D–G), Mikhailovsk Pond area south of the dam, near the railway, Kuba Beds, Ludlow; sample 85042 (H = H1, I–J), the Tabuska Hill section, right bank of the River Ufa, downstream of the mouth of the River Tabuska, Tabuska Beds, mid-Ludlow, upper Silurian. Specimens: GIT 820-52 (A), GIT 820-47 (B), GIT 820-51 (C), GIT 820-50 (D), GIT 820-48 (E = E1, close up), GIT 820-46 (F), GIT 820-49 (G), GIT 409-20 (H = H1, close up), GIT 409-43 (I), GIT 409-44 (J). Scale bars: 500 μm (all except A, which is 7 cm, and C, which is 250 μm).

Family PROCEPHALASPIDIDAE Stensiö, 1958
Procephalaspis sp. ind.
Figure 11D

Material. A few specimens, including a tessera from the head, were found in the Mikhailovsk Pond area south of the dam, locality 911, sample BB 911A-18; Kuba Beds, Lower Ludfordian, upper Silurian.

Genus range. The genus *Procephalaspis*, represented by the single species *Procephalaspis oeselensis* (Robertson), comes from the Himmiste Beds of the Paadla Stage, upper Gorstian, Lower Ludlow of Estonia, the *Phlebolepis elegans* Zone. The stratigraphic level for the specimen from the Ufa Amphitheatre is higher because it originates from the *Andreolepis hedei* Zone.

Remarks. The sample also contained specimens with robust sculptural elements, which most likely belong to *Procephalaspis*; however, the material is too scanty to definitely identify them as the known *Procephalaspis oeselensis*. A tessera originates from the anterior part of the body (Fig. 11D); it has a pentagonal outline, strengthened edges, and four sculptural ridges and tubercles on the surface. The ridges are thicker anteriorly (compare Fig. 11D with Märss et al. 2014, fig. 33O, T) and narrower posteriorly, with fine tubercles between the ridges.

Family TAHULASPIDIDAE fam. nov.

Type genus. Tahulaspis Märss, Afanassieva et Blom, 2014.

Diagnosis. As for the type genus (Märss et al. 2014, p. 129).

Content. Tahulaspis Märss, Afanassieva et Blom, 2014.

Stratigraphic range. Upper Gorstian to Upper Ludfordian (questionably up to upper Přidoli), upper Silurian, Baltic Sea region (including Skåne, Sweden), and the Ufa Amphitheatre.

Genus *Tahulaspis* Märss, Afanassieva et Blom, 2014
2014 *Tahulaspis* Märss, Afanassieva et Blom, 2014, p. 129

Type species. Tahulaspis ordinata Märss, Afanassieva et Blom, 2014, from Reo-927 core, depth 9.7 m, Saaremaa Island, Estonia; Tahula Beds of the Kuressaare Stage, Upper Ludfordian, Ludlow.

Species content. Tahulaspis ordinata Märss, Afanassieva et Blom; *Tahulaspis praevia* Märss, Afanassieva et Blom; possibly one more taxon in Přidoli.

Diagnosis. 'Exoskeleton thin and covered with ridges in early stages of development; inter-ridge grooves covered with a porous layer in later stages of development; superficial layer pierced by pores, either in regular rows or distributed unevenly' (Märss et al. 2014, p. 129).

Occurrence. Ludlow and lower Přidoli (questionably up to upper Přidoli), upper Silurian, Baltic Sea region (including Skåne, Sweden) and the Ufa Amphitheatre.

Tahulaspis ordinata Märss, Afanassieva et Blom, 2014
Figure 11E, E1

Material. A well-preserved scale from locality 911, BB 911A-18, in the Mikhailovsk Pond area south of the dam. The specimen was found together with *Andreolepis hedei*; Kuba Beds, Lower Ludfordian, Upper Ludlow.

Species range. In the East Baltic, *Tahulaspis ordinata* appears at the base of the Tahula Beds of the Kuressaare Stage, Upper Ludfordian, Ludlow, within the *Thelodus sculptilis* Zone; its occurrence in the Ohesaare Stage, Přidoli, was questioned (Märss et al. 2014, p. 78, fig. 3).

Remarks. A characteristic feature of the species is the presence of fine rows of pores running parallel on the scale surface, following the course of the inter-ridge grooves. This is also characteristic of the scale from 911A-18 (Fig. 11E, E1). This specimen is in the mature stage of development of the scale because the inter-ridge grooves are already covered with a porous superficial layer, and the fine pores run in parallel rows.

Tahulaspis sp. aff. *ordinata* Märss, Afanassieva et Blom, 2014
Figure 11F

Material. A few fragments come from sample 911A-18 from the Mikhailovsk Pond area south of the dam; Kuba Beds, Lower Ludfordian, Upper Ludlow.

Range. As for *Tahulaspis ordinata*.

Remarks. Märss et al. (2014, fig. 37) depicted somewhat similar scales, with a surface that was partially covered by parallel ridges and partially by a layer perforated with pores, identifying it as *Tahulaspis* sp. aff. *ordinata*. The specimen with a similar sculpture is depicted herein (Fig. 11F).

Tahulaspis praevia Märss, Afanassieva et Blom, 2014
Figure 11G

Material. A few fragments were found from bonebed 911A-18 in the Mikhailovsk Pond area south of the dam; Kuba Beds, Lower Ludfordian, Upper Ludlow.

Species range. Himmiste Beds of the Paadla Stage, upper Gorstian, and Tahula Beds of the Kuressaare Stage, Upper Ludfordian, Ludlow of the East Baltic.

Remarks. The species was diagnosed as 'exoskeleton covered with short straight or longer curved fine ridges in early stages of development and with a porous superficial layer in later stages; pores vary in diameter and in outline and are distributed irregularly' (Märss et al. 2014, p. 133, fig. 38). The scale surface of the specimens from BB 911A-18 displays a pattern of pores with highly irregular sizes and shapes, while the rows of pores are only faintly visible (Fig. 11G). These rows run diagonally from top left to bottom right in the figure and may result from short ridges situated beneath the porous layer, positioned between the indistinct pore rows.

Subclass ANASPIDA Traquair
Order BIRKENIIFORMES Berg, 1937
Family BIRKENIIDAE Traquair, 1899
Genus *Schidiosteus* Pander, 1856
Schidiosteus mustelensis Pander, 1856
Figure 11H, H1

Material. One scale from bonebed BB1 85042 in the Tabuska Hill section, on the right bank of the River Ufa, downstream of the mouth of the River Tabuska. (For the age, see the section 'On some peculiarities in the distribution of Silurian vertebrates in the Ufa Amphitheatre, the Central Urals'.)

Species range. The Viita and Vesiku Beds of the Rootsiküla Stage, upper Homerian, Upper Wenlock, and the Himmiste Beds of the Paadla Stage, upper Gorstian, Lower Ludlow of Estonia; Upper Wenlock–Lower Ludlow of Gotland, Sweden; and Ludlow, Severnaya Zemlya, Russia.

Remarks. The sculpture pattern on the scale found from the Tabuska Hill section (Fig. 11H, H1) is similar to those from the East Baltic (compare specimens in Blom et al. 2001, fig. 30A, C–I, K–M), as 'the sculpture of scales and plates is fine; short, wide triangular or heart-shaped sculptural elements in closely spaced or overlapping regular rows' (ibid., pp. 295 and 297). According to data from the Baltic Sea region (Saaremaa and Gotland islands), the range of *Schidiosteus mustelensis* remains well below *Thelodus sculptilis* and never occurs together with or higher than the *Thelodus sculptilis* range. The finding of *Schidiosteus mustelensis* scale at such a high stratigraphic level as in the Tabuska Beds is highly questionable and requires further studies.

Family SEPTENTRIONIIDAE Blom, Märss et Miller, 2002
Genus *Septentrionia* Blom, Märss et Miller, 2002
Septentrionia mucronata? Blom, Märss et Miller, 2002
Figure 11I

Material. A scale and a few scale fragments originate from bonebed BB1 83042 and 85042 in the Tabuska Hill section, on the right bank of the River Ufa, downstream of the mouth of the River Tabuska; Tabuska Beds, mid-Ludfordian, Ludlow. In BB1 83042, *Thelodus sculptilis* is absent, but in BB1 85042, it is present.

Species range. The species *Septentrionia mucronata* occurs in the Burgsvik and Hamra Beds, Upper Ludfordian, Upper Ludlow of Gotland, Sweden.

Remarks. The diagnosis of the species *Septentrionia mucronata* emphasises that 'the ridges of main area of the scale are smooth, elongate and sharply pointed posteriorly, and the ridges extend to the area between following ridges, and the inter-ridge area is with elongate pores' (Blom et al. 2001, p. 309). Our high but short scale resembles *Septentrionia mucronata* in its ridge arrangement; however, unlike *Septentrionia mucronata*, the ridges on our specimen are rounded in cross-section and exhibit longitudinal striae on their surfaces. Due to these differences, the identification of the species remains uncertain.

Genus *Liivilepis* Blom, Märss et Miller, 2001
Liivilepis curvata Blom, Märss et Miller, 2001
Figure 11J

Material. An intact scale and a few scale fragments originate from the outcrops BB1 83042 and 85042 in the Tabuska Hill section, right bank of the River Ufa, downstream of the mouth of the River Tabuska; Tabuska Beds, mid-Ludfordian, Upper Ludlow, upper Silurian.

Species range. Tahula Beds of the Kuressaare Stage, Upper Ludfordian, Ludlow, up to the Ohesaare Stage, Přidoli, upper Silurian, Saaremaa, Estonia; Hoburgen 3, Hamra Beds, Upper Ludlow, Gotland, and Öved Sandstone Formation, lower Přidoli of Skåne, Sweden.

Remarks. The scale in Fig. 11J was previously depicted (Blom et al. 2001, fig. 48E, H). The diagnosis, emended from Blom et al. (2001, p. 314), characterises the scale as follows: 'The ridges on the scales are straight or slightly curved in a side direction. Sculptural elements do not form regular antero-posterior rows but extend posteriorly between the more anterior ridges; the scale surface around the ridges has short (as long as are the ridges) but distinct pore rows.'

Conclusion

The taxonomy and biostratigraphy of the Silurian and lowermost Devonian vertebrates of the Ufa Amphitheatre, the Central Urals, have been studied. This research focused on the agnathan groups: Thelodonti, Heterostraci, Osteostraci, and Anaspida, while the most important gnathostomes, such as the zonal forms, were listed where necessary.

The described taxa clearly show that the seas of East and West Baltica were connected and inhabited by nearly the same early vertebrate taxa. The thelodont taxa presented include *Paralogania martinssoni* (Gross), *Phlebolepis elegans* Pander, *Thelodus laevis* (Pander), *Thelodus carinatus* (Pander), *Thelodus parvidens* Agassiz, *Thelodus sculptilis* Gross, *Turinia pagei* (Powrie), *Boreania minima* Karatajūtė-Talimaa, and *Talivalia elongata* (Karatajūtė-Talimaa). Heterostracans are represented by the eriptychiid *Oniscolepis dentata* Pander, traquairaspid '*Traquairaspis*' sp., and a diverse group of cyathaspidids, including *Archegonaspis bashkirica* Märss, *Archegonaspis integra* (Kunth), *Archegonaspis lindstroemi* Kiaer, *Cyathaspis alexanderi* Märss, and *Cyathaspis alexanderi*? Märss. Osteostracans *Tremataspis schmidti* Rohon, *Tremataspis rohoni* Robertson, *Thyestes*? sp. ind., *Procephalaspis* sp. ind., *Tahulaspis praevia* Märss, Afanassieva et Blom and *Tahulaspis ordinata* Märss, Afanassieva et Blom have been described for the first time from the Central Urals.

A new family, Tahulaspididae fam. nov., with the type-genus *Tahulaspis* Märss, Afanassieva et Blom, 2014, was established in the order Tremataspidiformes Berg, 1937, in the present publication.

Birkeniid anaspids include a few specimens of *Septentrionia mucronata*? Blom, Märss et Miller, *Liivilepis curvata* Blom, Märss et Miller, and *Schidiosteus mustelensis* Pander. However, the presence of *Schidiosteus* in the bonebed BB1 layer, Tabuska Hill section, caused problems with age determination and requires further investigation.

Several Silurian vertebrate zones were recognised in the Ufa Amphitheatre: the *Paralogania martinssoni*, *Phlebolepis elegans*, *Andreolepis hedei*, and *Thelodus sculptilis* zones. The Silurian–Devonian boundary was previously established by the appearance of thelodont *Turinia pagei* and confirmed by the heterostracan '*Traquairaspis*' sp. on the northern bank of Mikhailovsk Pond (Märss 1997). Some zonal species, such as *Phlebolepis ornata* (in Lower Ludlow), *Thelodus admirabilis* (Upper Ludlow and lower Přidoli), and acanthodians *Nostolepis gracilis* and *Poracanthodes punctatus* (in Přidoli), were not found in the Ufa Amphitheatre.

Detailed distribution data of vertebrates were crucial in determining the age of the strata and in discovering the reversed succession of vertebrates in section 73Ms-3 on the southern bank of Mikhailovsk Pond. Equally important was the discovery of a recurrence of vertebrate bonebed layers with almost identical taxonomic content in the Tabuska Hill section. Both occurrences are attributed to past tectonic activities in the region.

Data availability statement

The data are contained within the article, and the original materials are housed in the Department of Geology at Tallinn University of Technology.

Acknowledgements

The author is grateful to O. Hints, Director of the Department of Geology at Tallinn University of Technology, for providing research facilities and funding for the publication of this paper. Many years ago, V. A. Nasedkina (Sverdlovsk, now Yekaterinburg) provided us with the first thelodont scales from the Mikhailovsk Pond area, which laid the foundation for research on Silurian and lowermost Devonian fish in the western slope of the Central Urals. P. Chekhovich and A. Zhivkovich are thanked for their joint fieldwork in the Ufa Amphitheatre, their input on the Tabuska Hill lithological section in Fig. 3, and for providing part of the samples and fish specimens. P. Chekhovich is also acknowledged for specifying the fossil fish locations used in the schematic geographical maps in Fig. 1. SEM photographs were taken by U. Toom, and the figures were improved for publication by G. Baranov, both from the Department of Geology at Tallinn University of Technology. Special thanks to P. Männik, E. Lukševičs, and O. Tinn for their comments on the text and for improving the English in the manuscript. The publication costs of this article were partially covered by the Estonian Academy of Sciences.

References

Blom, H., Märss, T. and Miller, G. C. 2001. Silurian and earliest Devonian birkeniid anaspids from the Northern Hemisphere. *Earth and Environmental Transactions of the Royal Society of Edinburgh*, **92**(3), 263–323. https://doi.org/10.1017/S026359330 0000250

Chekhovich, P. A. 2007. *Карбонатные платформы в ордовикско-силурийских окраинных и эпиконтинентальных бассейнах Северной Евразии. Седиментологические и тектонические аспекты эволюции (Carbonate platforms in the Ordovician–Silurian marginal and epicontinental basins of northern Eurasia. Sedimentological and tectonic aspects of evolution)*. Summary of doctoral dissertation. M. V. Lomonosov Moscow State University, Moscow.

Chekhovich, P. A. and Zhivkovich, A. E. 2024. Ordovician–Silurian carbonate platforms on the western slope of the Urals: conventional model revised. *Paleontological Journal*, **58**(S4), S445–S464. http://dx.doi.org/10.1134/S0031030124601798

Chekhovich, P. A., Zhivkovich, A. E. and Medvedovskaya, N. I. 1994. Изотопно-углеродная летопись силура и нижнего девона в опорных разрезах на Среднем Урале (Carbon isotope record of the Silurian and Lower Devonian in reference sections in the Middle Urals). *Доклады Академии наук*, **338**, 514–516.

Denison, R. H. 1947. The exoskeleton of *Tremataspis*. *American Journal of Science*, **245(**6), 338–365.

Gross, W. 1967. Über Thelodontier-Schuppen. *Palaeontographica, Abteilung A*, **127**, 1–67.

Kaljo, D., Martma, T., Märss, T., Nestor, V.-K. and Viira, V. 2022. A bio- and chemostratigraphic search for the Mid-Ludfordian Carbon Isotope Excursion interval in the Ludlow of the Ohesaare core, Estonia. *Estonian Journal of Earth Sciences*, **71**(1), 44–60. https://doi.org/10.3176/earth.2022.04

Karatajūtė-Talimaa, V. 1978. *Силурийские и девонские телодонты СССР и Шпицбергена* (*Silurian and Devonian Thelodonts of the USSR and Spitsbergen*). Mokslas, Vilnius.

Karatajūtė-Talimaa, V. 1985. Телодонты подьемненской свиты (нижний девон, жедин) Северной Земли и их корреляционное значение (Thelodonts of the Podyomnaya Formation (Lower Devonian, Gedinnian) of Severnaya Zemlya and their correlative importance). *Geologija*, **6**, 50–60.

Lindström, G. 1895. On remains of a *Cyathaspis* from the Silurian strata of Gotland. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **21**, 1–15.

Märss, T. 1986. *Силурийские позвоночные Эстонии и Западной Латвии* (*Silurian Vertebrates of Estonia and West Latvia*). Valgus, Tallinn. http://www.digar.ee/id/nlib-digar:649668

Märss, T. 1989. Vertebrates. *National Museum of Wales. Geological Series*, **9**, 284−289.

Märss, T. 1992. Vertebrate history in the late Silurian. *Proceedings of the Estonian Academy of Sciences. Geology*, **41**(4), 205–214. https://doi.org/10.3176/geol.1992.4.05

Märss, T. 1997. Vertebrates of the Přidoli and Silurian–Devonian boundary beds in Europe. *Modern Geology*, **21**(1), 17–41.

Märss, T. 2001. *Andreolepis* (Actinopterygii) in the upper Silurian of northern Eurasia. *Proceedings of the Estonian Academy of Sciences. Geology*, **50**(3), 174–189. https://doi.org/10.3176/geol.2001.3.03

Märss, T. 2003. *Paralogania* from the Rootsiküla (Wenlock) and Paadla (Ludlow) stages of Estonia. *Proceedings of the Estonian Academy of Sciences. Geology*, **52**(2), 98–112. https://doi.org/10.3176/geol.2003.2.03

Märss, T. 2011. Siluri selgroogsed – ühe rühma arengulugu. (Silurian vertebrates – the evolutionary history of a group). In *Teadusmõte Eestis (VI). Elu- ja maateadused* (*Scientific Thought in Estonia (VI). Life and Earth Sciences*) (Parmasto, E., Laisk, A. and Kaljo, D., eds), Eesti Teaduste Akadeemia Kirjastus, Tallinn, 117–124.

Märss, T. 2019. Silurian cyathaspidid heterostracans of northern Eurasia. *Estonian Journal of Earth Sciences*, **68**(3), 113–146. https://doi.org/10.3176/earth.2019.11

Märss, T. and Karatajūtė-Talimaa, V. 2009. Late Silurian–Early Devonian tessellated heterostracan *Oniscolepis* Pander, 1856 from the East Baltic and North Timan. *Estonian Journal of Earth Sciences*, **58(**1), 43–62. http://dx.doi.org/10.3176/earth.2009.1.05

Märss, T. and Männik, P. 2013. Revision of Silurian vertebrate biozones and their correlation with the conodont succession. *Estonian Journal of Earth Sciences*, **62**(4), 181–204. https://doi.org/10.3176/earth.2013.15

Märss, T. and Miller, C. G. 2004. Thelodonts and distribution of associated conodonts from the Llandovery–lowermost Lochkovian of the Welsh Borderland. *Palaeontology*, **47**(5), 1211–1265. https://doi.org/10.1111/j.0031-0239.2004.00409.x

Märss, T. and Ritchie, A. 1997. Articulated thelodonts (Agnatha) of Scotland. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, **88**(3), 143−195. https://doi.org/10.1017/S026359330 000691X

Märss, T., Turner, S. and Karatajūte-Talimaa, V. 2007. *Handbook of Paleoichthyology: "Agnatha" II: Thelodonti, Vol. 1B*. Verlag Dr. Friedrich Pfeil, München.

Märss, T., Afanassieva, O. and Blom, H. 2014. Biodiversity of the Silurian osteostracans of the East Baltic. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, **105**(2), 73–148. https://doi.org/10.1017/S1755691014000218

Modzalevskaya, T. and Märss, T. 1991. О возрасте подошвы гребенского горизонта Урала (On the age of the lower boundary of the Greben Regional Stage of the Urals). *Proceedings of the Estonian Academy of Sciences. Geology*, **40**(3), 100–103. https://doi.org/10.3176/geol.1991.3.03

Patrunov, D. K. and Shurygina, M. V. 2002. Силур и ранний девон в Уфимском Амфитеатре (Silurian and Early Devonian in the Ufa Amphitheatre). *Litosfera*, **2**, 96–111.

Schultze, H.-P. and Märss, T. 2004. Revisiting *Lophosteus* Pander 1856, a primitive osteichthyan. In *The Gross Symposium 2: Advances in Palaeoichthyology* (Lukševičs, E., ed.). *Acta Universitatis Latviensis*, **679**, 57–78.

Shujskij, V. P. 1981. Фациально-литологические особенности верхнесилурийских и нижнедевонских рифов западного склона Среднего Урала (Facial-lithological peculiarities of the upper Silurian and Lower Devonian reefs on the western slope of the Central Urals). In *Биостратиграфия и фауна среднего палеозоя Урала* (*Biostratigraphy and Fauna of the Middle

Palaeozoic of the Urals) (Sapel′nikov, V. P. and Chuvashov, B. I., eds). Уральский научный центр Академии наук СССР, Свердловск, 96–110.

Shurygina, M. V., Breivel', M. G., Breivel', I. A., Zenkova, G. G., Militsina, V. S. and Yanet, F. E. 1981. Пржидольский ярус на Северном и Среднем Урале (The Přidoli Series in the Northern and the Central Urals). In *Биостратиграфия и фауна среднего палеозоя Урала* (*Biostratigraphy and Fauna of the Middle Palaeozoic of the Urals*) (Sapel'nikov, V. P. and Chuvashov, B. I., eds). Уральский научный центр Академии наук СССР, Свердловск, 55–73.

Turner, S. 1984. *Studies of Palaeozoic Thelodonti (Craniata: Agnatha)*. Unpublished PhD thesis. University of Newcastle upon Tyne, England.

Valiukevičius, J. 1992. First articulated *Poracanthodes* from the Lower Devonian of Severnaya Zemlya. In *Fossils as Living Animals* (Kurik, E., ed.). Academia, Tallinn, 193–213.

Viira, V. and Einasto, R. 2003. Wenlock–Ludlow boundary beds and conodonts of Saaremaa Island, Estonia. *Proceedings of the Estonian Academy of Sciences. Geology*, **52**(4), 213–238. http://dx.doi.org/10.3176/geol.2003.4.03

Zhivkovich, A. E. and Chekhovich, P. A. 1985. *Палеозойские формации и тектоника Уфимского амфитеатра* (*Palaeozoic Formations and Tectonics of the Ufa Amphitheatre*). Наука, Москва.

Zhivkovich, A. E. and Goreva, N. V. 1976. Стратиграфия пограничных отложений силура и девона западного склона Среднего Урала (Stratigraphy of the Silurian and Devonian boundary beds of western slope of the Central Urals). *Известия Академии наук СССР. Серия Геологическая*, **7**, 70–83.

Zhivkovich, A. E., Chekhovich, P. A. and Märss, T. 1990. Late Silurian and earliest Devonian vertebrate microfossils of the Ufimian circus on the western Urals. *Ichthyolith Issues: News and Views on Palaeozoic Vertebrate Microfossils*, **3**, 22.

Siluri ja Alam-Devoni selgroogsetest Ufa amfiteatris, Kesk-Uuralis, rõhuga lõuatutel ja korrelatsioonil Baltikumiga

Tiiu Märss

Uuriti selgroogsete mikrojäänuseid Wenlockist, alam-Silurist kuni Alam-Lochkovini, Alam-Devonis, Ufa amfiteatrist Kesk-Uurali läänenõlvalt. Selgroogsete taksonoomiat ja biostratigraafiat käsitletakse rõhuga lõuatutel rühmadest Thelodonti, Heterostraci, Osteostraci ja Anaspida. Esimest korda on Kesk-Uuralist kirjeldatud osteostraagid *Tremataspis schmidti* Rohon, *Tremataspis rohoni* Robertson, *Thyestes*? sp. ind. ja *Procephalaspis* sp. ind. ning püstitatud osteostraakide uus sugukond Tahulaspididae perekonnaga *Tahulaspis* Märss, Afanassieva et Blom. Sugukond sisaldab liike *Tahulaspis ordinata* Märss, Afanassieva et Blom ja *Tahulaspis praevia* Märss, Afanassieva et Blom. Töö sisaldab ka varem kirjeldatud tsüataspiidseid heterostraake ja anaspiide, mis on lisatud, et koondada kõik Kesk-Uurali läänenõlva lõuatud ühte publikatsiooni. Selgroogsete levikuandmeid on töös kasutatud kihtide vanuse määramiseks ja korrelatsiooniks Baltikumiga. Samuti olid need olulised selgroogsete taksonite ümberpööratud järgnevuse avastamisel Mihhailovski tiigi lõunakaldal asuvas 73Ms-3 läbilõikes ja ühe kihikompleksi (nn kondikiht) kordumise tõestamisel Tabuska mäe läbilõike Ludlow ülemises osas.