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The Upper Famennian Ketleri Formation of Latvia: new data on the fauna and flora from tide-dominated delta deposits in a seasonal climate

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ABSTRACT

Combined sedimentological and palaeontological studies of the vertebrate fossil-bearing deposits of the Upper Devonian, Upper Famennian Ketleri Formation have provided new data on the sedimentary environment of the deposits, as well as on taxonomic and taphonomic peculiarities of the fossil assemblage. Data from numerical modelling of the Baltic Devonian Basin demonstrate that the sandy deposits of the Pavāri and Varkaļi members form a fan-shaped area resembling a wide delta developed in shallow-marine settings. Fluvial channels and bars with strong tidal influence were identified in a sedimentological study of the Pavāri site, suggesting a tide-influenced fluvial environment. Taphonomic studies indicate that the sedimentary concentrations of well-preserved vertebrate remains were formed under the influence of fluvial and strong tidal processes in a shallow-water environment, most likely in tide-influenced deltaic settings. Trace fossils recognised in the Ketleri and Pavāri-1 sites suggest a brackish-water or marine environment, and thus support the hypothesis. The analysis of rhizocretes from the Varkaļi Member suggests the strong influence of a seasonal climate. Well-preserved plant macroremains have been discovered for the first time during this study in the Ketleri Formation.

Introduction and geological setting

The Ketleri Formation (Fm) is a stratigraphic unit corresponding to the upper part of the Devonian Famennian Stage. Based on its position above the Sniķere, Švete, and Žagare formations, which yield conodonts of the *postera* Zone (from the Švete Fm), the Ketleri Fm was preliminarily correlated with the Upper *postera* or probably *expansa* conodont zone (CZ; Lukševičs 2001; Lukševičs and Stinkulis 2018). However, this formation has sometimes been correlated with the *expansa* CZ (Esin et al. 2000). A precise dating of the Ketleri Fm is difficult due to the lack of conodonts or stratigraphically important spores. This formation was first named by P. Liepiņš (1951), who replaced the index ‘h$_5$’ used by previous authors (e.g. Delle 1937; index ‘h’ in Gross 1942) for the sandy deposits of the uppermost Upper Devonian strata in Latvia.

The Famennian deposits of Latvia have been known for vertebrate palaeontology for almost a hundred years; e.g. the Ketleri locality has been known for almost a century for its fossil fishes (Gross 1933), and is particularly well known because the Ketleri Fm yields the remains of one of the best-preserved and most reconstructible Devonian tetrapods, *Ventastega curonica* Ahlberg, Lukševičs et Lebedev, 1994.

The deposits of the Ketleri Fm are distributed in southwestern Latvia and northwestern Lithuania (Fig. 1). In the northern and eastern parts of the area, the Ketleri Fm forms the bedrock surface in a 3–17 km wide band; outcrops occur on the banks of the rivers Venta, Mālupe, and Ciecere and their tributaries, e.g. the River Paksīte. Liepiņš (1964) chose the Ketleri outcrop on the right bank of the River Venta, near the abandoned Ketleri farmhouse, as the stratotype of the formation. However, since only about 15 m of the upper part of the formation crops out in this locality, later the 109.5–148.5 m interval of the Priekule-27 borehole was assumed to represent the typical section of the Ketleri Fm (Savvaitova 1995). The Ketleri outcrop is now

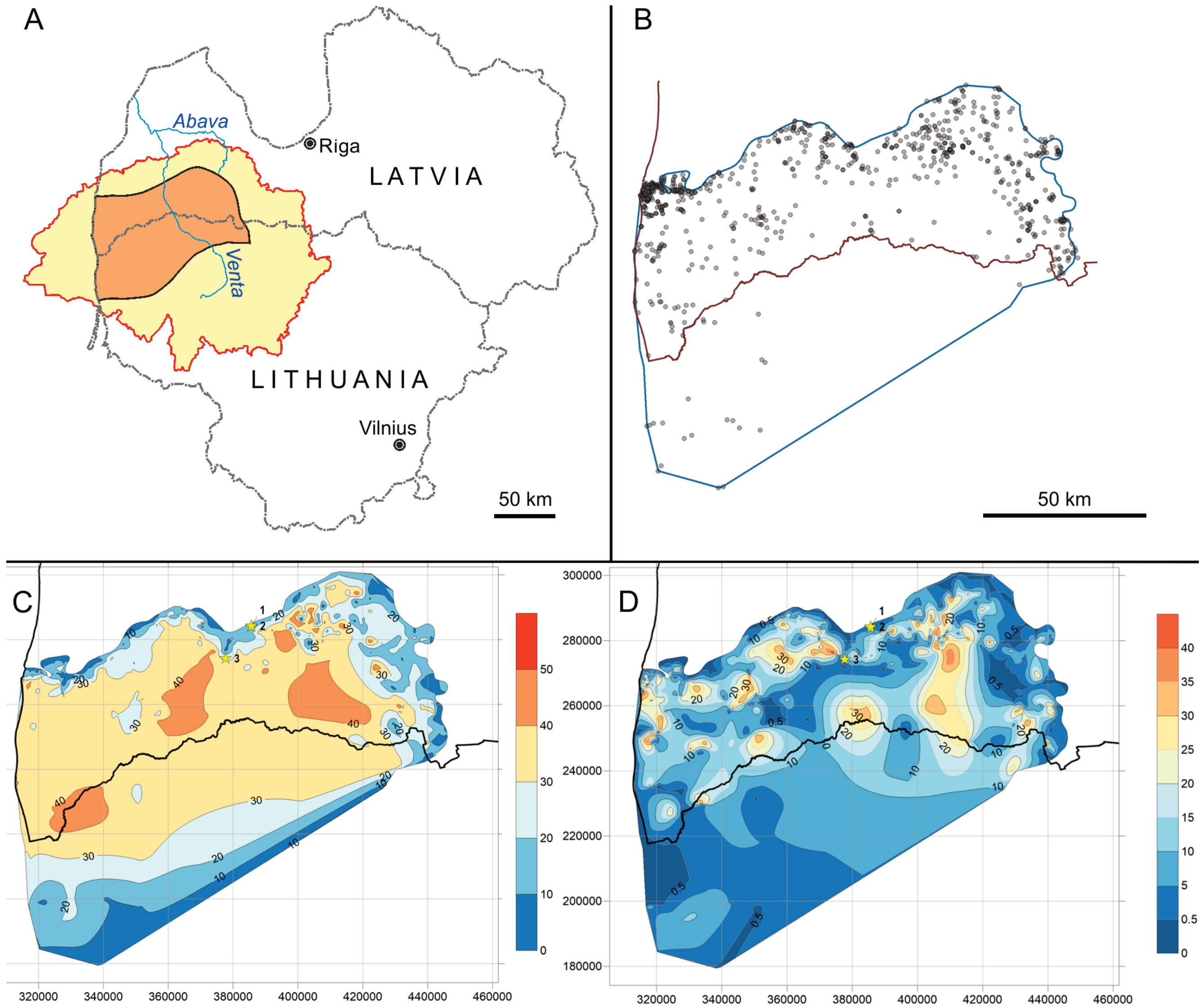

Fig. 1. **A** – distribution of deposits of the Famennian Stage (yellow) and Ketleri Formation (orange) in Latvia and Lithuania; **B** – location of the 907 boreholes used for the models; **C** – thickness model of the Ketleri Formation (m); **D** – thickness model of sandstone deposits of the Ketleri Formation (m). Coordinates used in graphs C and D are in the LKS-92 system. Yellow stars designate the studied localities: 1 – Pavāri-1; 2 – Pavāri-2; 3 – Ketleri outcrops.

treated as the stratotype of the uppermost part of the formation, the Varkaļi Member (Mb; Gailīte et al. 2000).

The Ketleri Fm consists mainly of sandstone, clay, siltstone, and dolomitic marl. In Latvia, it was divided into three parts, at that time called 'subformations', by Lyarskaya and Savvaitova (1974). Savvaitova (1977) named these three parts as the Nīgrande, Airītes, and Varkaļi 'sedimentary rhythms', which later were transferred into the Nīgrande, Pavāri, and Varkaļi members (Gailīte et al. 2000; Stinkulis 2003; Fig. 2). These three units are used in the stratigraphic chart of the Devonian deposits of Lithuania as 'subformations' (Sidaravičienė et al. 1999). The lower part of the section (Nīgrande Mb) consists of clay, clayey siltstone, and dolomitic marl, the middle part (Pavāri Mb) of dolomitic marl, siltstone, clay, and sandstone with conglomerate interbeds, and the upper part (Varkaļi Mb) of similar sedimentary rocks but without conglomerates (Lukševičs and Stinkulis 2018).

All three members are characterised by various vertebrate taxa, but the most significant and well-preserved fish and tetrapod fossils have been reported from the Pavāri and Varkaļi members (e.g. Lukševičs and Zupiņš 2004; Lebedev and Lukševičs 2017, 2018). The Pavāri Mb crops out in several places along the rivers Ciecere and Paksīte; the Pavāri-1 locality on the left bank of the River Ciecere, opposite the vanished Pavāri farmhouse, has been studied since the early 1970s, and the sedimentary environment, taphonomy, and composition of the vertebrate assemblage were reported in detail (e.g. Lukševičs and Zupiņš 2004).

The Varkaļi Mb is best exposed in the Ketleri locality, situated on the right bank of the River Venta close to the former Ketleri farm. The geological section of the Varkaļi Mb and the composition of the vertebrate assemblage have also been recently reported (Lebedev and Lukševičs 2017). However, regular field collecting in the fossiliferous sites of the Pavāri and Varkaļi members during the last decade has resulted in the discoveries of other fossil groups, e.g. trace fossils, rhizocretes, and plant macroremains. These finds were reported at conferences (e.g. Lukševičs et al. 2015, 2017; Meškis and Lukševičs 2018; Lukševičs and Stinkulis 2024), but, except for the rhizocretes (Lukševičs 2023), have never been published before. The sedimentological, environmental, and taphonomic context of the Pavāri site (Lukševičs and Zupiņš 2004) was significantly enhanced during the field seasons of 2011 and 2013. A new study concerning the same context of the Ketleri site was carried out in 2014 and 2016, when trace fossils and, for the first time, rhizocretes were recognised there (Lukševičs et al. 2015; Lukševičs 2023). A new fossiliferous locality on the left bank of the River Ciecere, close to its confluence with the River Paksīte, was discovered in 2019 (Lukševičs et al. 2022) and excavated annually during the 2019–2025 field seasons, providing extensive vertebrate material, including new taxa, and the first plant macroremains from the Ketleri Fm.

The main aim of this article is to describe the geological section of the newly discovered fossil site Pavāri-2 and to provide an interpretation of the sedimentary environment of the deposits of the Pavāri and Varkaļi members based on the combined sedimentological, taphonomic, and palaeontological analysis of the deposits and fossils from all three fossiliferous sites where the Ketleri Fm crops out. New palaeontological material obtained at the Ketleri site in 2014 and 2016 (trace fossils and rhizocretes) and at the Pavāri sites during the 2013 and 2019–2025 field seasons (trace fossils and vertebrates) is briefly described here.

Material and methods

Detailed logging of the Pavāri Mb succession was carried out for the outcrop at the Pavāri-2 locality, situated on the left bank of the River Ciecere, about 100 m upstream from the mouth of the River Paksīte, by Ģ. Stinkulis in 2022 and 2023 (Figs 2 and 3). Facies analysis was performed by Ģ. Stinkulis. Vertebrate remains were gathered by the team of participants of the summer schools in field palaeontology, led by E. Lukševičs in 2019 and 2022, and by V. Alksnītis in 2021, 2024, and 2025. Plant macroremains were discovered for the first time in 2023 during a joint expedition with the participation of P. E. Ahlberg (Uppsala University, Sweden) and R. Gess (Makhanda, South Africa). Taphonomic data on the spatial distribution, sorting, and azimuthal orientation of skeletal elements of vertebrates from the Pavāri-2 locality were collected in 2019, 2021, and 2022. A total of 86 measurements of the azimuth dip of elongated skeletal elements were taken.

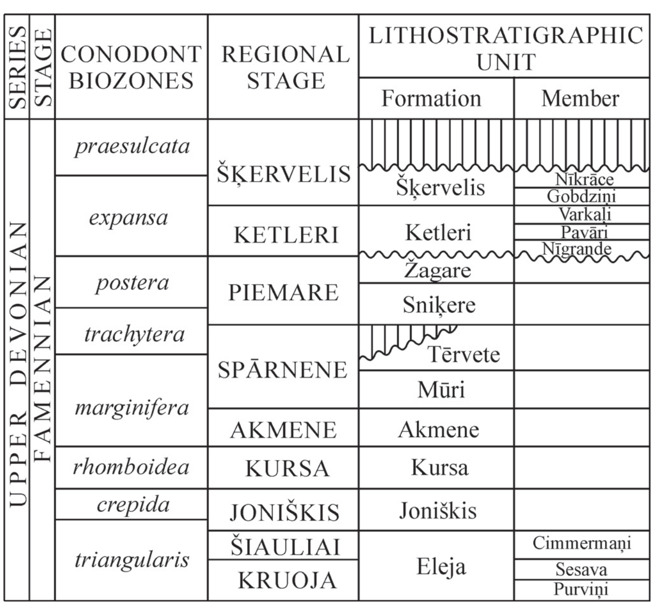

Fig. 2. Famennian stratigraphy of Latvia. Based on Lukševičs and Stinkulis (2018).

Data on 907 boreholes from the well database maintained by the Latvian Environment, Geology and Meteorology Agency, and similar records kept by the Lithuanian Geological Survey, have been used for the maps of distribution of the Ketleri Fm. Models were produced by J. Lukševičs using Golden Software Surfer v.26, LKS-92 coordinate system, and LAS-2000.5 height system.

A complex sedimentological and palaeontological study of the deposits of the Varkali Mb was carried out in 2016 in the framework of the summer school in field palaeontology. During the fieldwork, outcrop No. 5, containing rhizocretes, was described by E. Lukševičs. The 5 m-long sandstone wall was cleared along the shore, about 5 m above the River Venta water level, to study the rhizocretes. The rhizocretes were photographed, and their length, diameter, as well as the angle and azimuth of dip, were measured. Some samples were collected for further studies in the Mineralogical and Palaeontological Laboratory (MinPal) of the University of Latvia.

All collected vertebrate specimens were prepared mechanically by V. Alksnītis, E. Lukševičs, and T. Visotina under an optical microscope (ZEISS KL 1500 LCD) using a steel needle and a brush in the MinPal. Rhizocretes were mechanically prepared by E. Lukševičs. One sample was sawn cross-sectionally and mapped for chemical element distribution using a Phenom ProX tabletop electron microscope with an X-ray energy dispersive analyser (EDX) belonging to Hydrox Ltd. Five carbonate samples were analysed for carbon and oxygen stable isotopes composition at the Department of Geology, University of Tartu, Estonia. A stable isotope mass spectrometer, Thermo Delta V Advantage, coupled with GasBench II universal gas preparation and injection system, was used. The samples were dissolved in 99% orthophosphoric acid (H_3PO_4) for at least 8 hours at 70 °C. The results of the analyses are presented in δ notation relative to the Vienna Pee Dee Belemnite standard.

Results

Facies analysis and interpretation of sedimentary environments

As a result of sedimentological logging of the three studied sections, six facies (F1 to F6) and two facies associations (FA1 and FA2) were distinguished. Data on their lithology, structures, geometry, and interpretations are summarised in Table 1. Logged geological sections with data on facies, facies associations, and current directions are shown in Fig. 3.

The oldest deposits documented are very fine- to fine-grained sandstones (with a large cross-bed) in section 1 (Fig. 3). They probably belong to a bar without obvious tidal influence and can be conditionally included in facies 2 (F2).

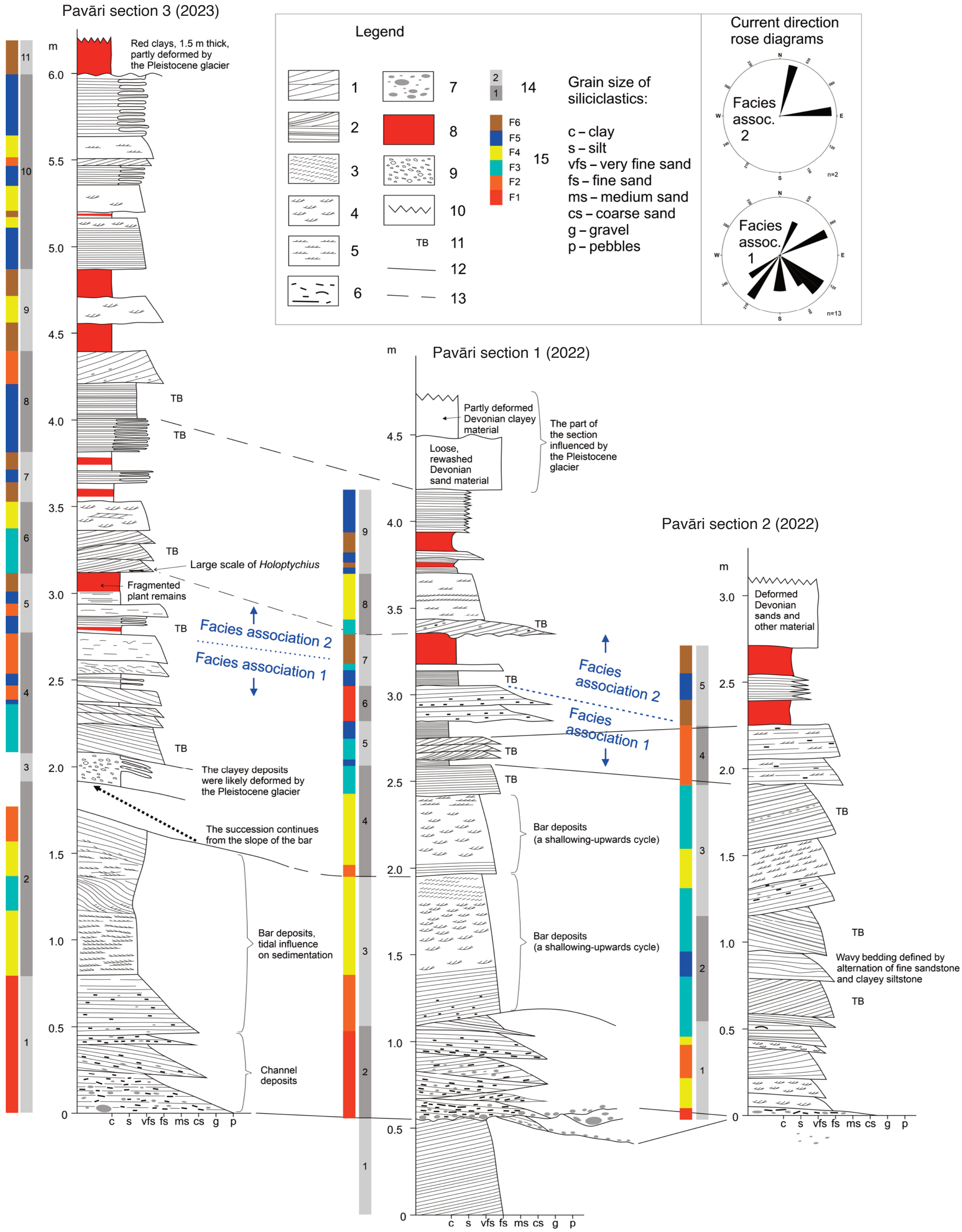

Fig. 3. Geological sections of the Ketleri Formation on the left bank of the River Ciecere near the mouth of the River Paksīte in the Pavāri-2 fossil vertebrate and plant locality. Numbers of the sections correspond to those in Fig. 4. 1 – cross-bedding and other structures; 2 – mud and mica drapes (tidal features); 3 – climbing ripple-lamination; 4 – trough-current ripple-lamination; 5 – parallel-current ripple-lamination; 6 – vertebrate fossils in deposits; 7 – clay clasts; 8 – homogeneous clayey deposits; 9 – fragmented clayey deposits, probably due to Pleistocene glacial activity; 10 – upper boundary of the sections affected by glacial erosion and landslides; 11 – tidal bundles; 12 – clay laminae; 13 – silt laminae; 14 – bed numbers; 15 – facies and their numbers.

Table 1. Facies identified in the Ketleri Formation, Pavāri-2 site

Facies (F)	Bed (cross-set) thickness, lithology, and fossils	Structures	Geometry, bounding surfaces	Interpretation
F1: Clay and vertebrate fossil conglomerate	Beds and cross-sets 0.05–0.25 m thick, clay clasts (up to 8 cm long) and vertebrate bones in silty to sandy matrix. In one case (0.35 m-thick bed), F1 grades upward to F2.	Low-angle cross-stratification, rarer poorly sorted material.	Scoured, in some cases irregular base. In some cases, no visible evidence of erosion.	Channel lag deposits (Pontén and Plink-Björklund 2007; Nichols 2009). Vertebrate bones transported and accumulated in rapid currents.
F2: Trough cross-stratified sandstone	Cross-sets 0.05–0.2 m thick. Very fine-grained to fine-grained, rarer medium-grained sandstone. Vertebrate bone debris and clay clasts are present in some cases.	Trough cross-stratification.	Scoured bases, lateral thinning and thickening of cross-beds.	Accumulation of sand, vertebrate bone debris, and clay clasts in linguoid or lunate subaqueous dunes, which migrated in water currents (Allen 1968; Ashley 1990).
F3: Trough cross-stratified sandstone with tidal bundles	Cross-sets 0.03–0.33 m thick. Very fine-grained to fine-grained sandstone, in some cases clay clasts up to gravel-size.	Trough cross-stratification with mud/mica drapes and tidal bundles.	Scoured bases, lateral thinning and thickening of cross-beds.	Migrating linguoid or lunate subaqueous dunes (Allen 1968; Ashley 1990). Influence of tidal processes on sedimentation (Davis 2012).
F4: Sandstone with current ripple-lamination	Beds 0.07–0.55 m thick. Very fine-grained sandstone, rarer silty sandstone and fine-grained sandstone. The thickest beds are fining-upwards.	Current ripple-lamination, in some cases combined with cross-stratification. In places, the ripples are slightly climbing, in one case with rhythmic changes of climbing angle.	Non-erosive bases. In some cases, gradual transformation to cross-beds in lateral and vertical direction.	Accumulation of sand in low-energy water currents (Reineck and Singh 1980). Gradual transition to cross-beds indicates the change of energy with no erosion. This and the changes of ripple climb angle point to tidal processes.
F5: Laminated sandstones to clays	Beds 0.03–0.37 m thick. Usually clayey-silty material alternates with very fine-grained sand. In some cases, only sandy or clayey material is present.	Fine, rhythmic lamination. Thickness of the laminae is some mm, often < 1 mm. Tidal bundles are present in 30% of the beds.	Non-erosive, usually sharp bed boundaries. In some cases, gradational boundaries with F6.	Rhythmic variation from low to rather high-energy environment due to tidal processes, probably also seasonal changes.
F6: Homogeneous clayey deposits	Beds 0.10–0.18 m thick. In the uppermost part of the section in 2023, the clays are 1.5 m thick, but deformed and mixed by glacial and landslide processes. From clayey siltstone to clay.	Homogeneous structure.	Non-erosive, usually distinct bed boundaries. In some cases, gradational boundaries with F5.	Low-energy environment.

FA1 – tidally-influenced channel

The lower part of the succession consists of facies F1, F2, F3, and F4, with also F5 present in the upper part. The lowermost part of the channel infill consists of conglomeratic to sandy deposits of F1, at least 0.8 m thick. The number and size of clay clasts and vertebrate debris decrease upwards. These deposits likely represent the basal part of channel infill, accumulated in rapid currents (Pontén and Plink-Björklund 2007).

The next part of the succession is represented by F2, F3, and F4: fine- to very fine-grained sandstones with cross-stratification (also sigmoid cross-stratification), current ripple-lamination, including climbing ripples. The sedimentary structures are well-preserved, with minimal influence of erosion. In section 1, this part of the succession is represented by two fining-upwards (also shallowing-upwards) cycles, each likely representing one bar. The total thickness of the bars in sections 1 and 3 is 1.2 m. The bar surface is smooth and gently inclined. In section 3, the bar is at least 8 m long (across the whole width of the exposure). The correlation of bars documented in 2022 (sections 1 and 2) and 2023 (section 3) is unclear.

Interpretation: the general structure and fining-upwards of the succession indicate that the deposits represent an infill of a channel (Allen 1968). The rather abundant tidal bundles, occasional climbing ripples on cross-beds, and variable current directions indicate the influence of tidal processes. The fining-upwards cycles in section 1 have well-preserved sedimentary structures and shallowing-upwards trends; therefore, their thickness could approximately correspond to a water depth of 0.4–0.8 m.

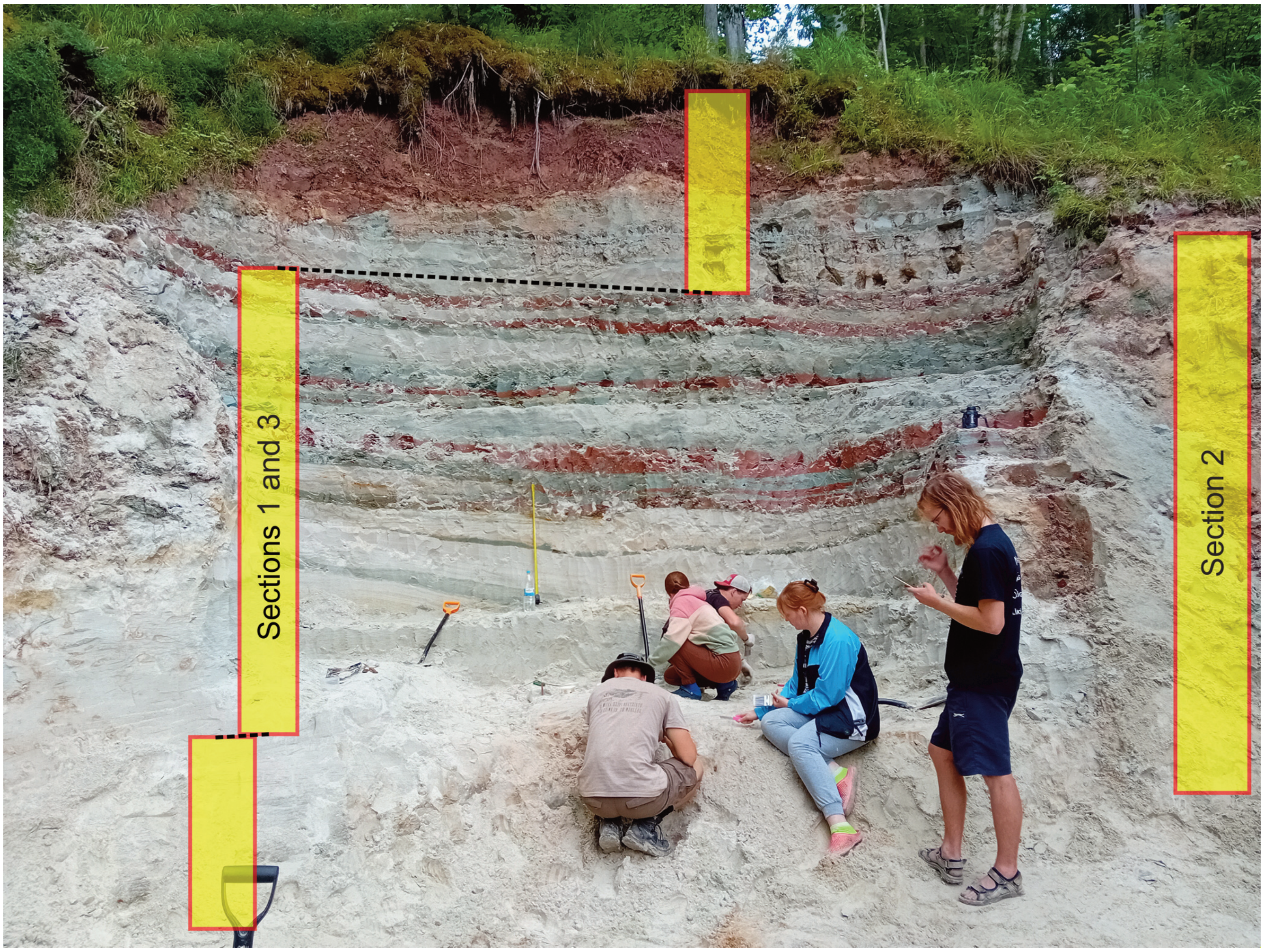

Fig. 4. Photo of the Pavāri-2 site (28 July 2023) showing the position of the documented sections. The position of sections 1 and 2 (documented in 2022) is approximate, because a large part of the deposits was removed by landslides and outcrop cleaning. Photo by Ģ. Stinkulis.

FA2 – small, tidally influenced, abandoned channels

The upper part of the succession (the dominant part) in all documented sections is represented by an alternation of fine- and very-fine-grained sandstones (F2, F3, and F4), laminated clays to very fine-grained sandstones (F5), and red clayey deposits (F6). The deposits form up to four units (section 3), 0.3–1.2 m thick, which cover each other slightly obliquely, in various directions. Each unit is usually composed of sandy deposits (F2, F3, and F4) in the lower part and sandy to clayey deposits (F5 and F6) in the upper part. The proportion of the clayey deposits gradually increases downdip, towards the axial parts of the channels. Obvious features of tidal influence on sedimentation are found in an up to 4.2 m-thick interval in section 3, but probably the laminated clays to very fine-grained sandstones (F5) in all cases are rhythmic tidal deposits.

Interpretation: the deposits of FA2 likely formed in small channels, which is indicated by their small-thickness, shallowing-upwards successions, and oblique contacts. At some stage of their development, the channels became separated from active distributaries and were filled by suspended clayey material (F6), probably transported there by high-tide currents. The rhythmites (F5) likely indicate the transition from active to abandoned stages of the channels. It is also possible that the deposits of FA2 are crevasse-splay or tidal-gully deposits (Pontén and Plink-Björklund 2007).

Interpretation of sedimentary environments

Analysis of sedimentary environments has limits due to the small size of the studied outcrop (Fig. 4), as well as problems in precisely correlating the sections documented in 2022 and 2023. The deposits were accumulated under a high- to low-energy current regime. Tidal processes considerably influenced the development of sandy deposits of FA1 and the lower part of sandy to clayey deposits of FA2. Their role in the development of the upper part of FA2 is not clear. Larger, higher-energy channels (FA1) transitioned into smaller, lower-energy, abandoned channels (FA2). The vertebrate fossils were transported and accumulated in the channel thalweg (Pontén and Plink-Björklund 2007) and in bar deposits of FA1, whereas plant remains accumulated in the suspended clay infill of abandoned channels (FA2). The variable current directions (Fig. 3) could point to rapid channel migration, as well as to the opposite directions of fluvial and tidal currents. The analysis of the studied succession aligns well with the interpretation of a tidally-influenced delta environment.

Fossil vertebrates

Excavations in 2014 and 2016 provided more than 7000 specimens of fossil fishes and primitive tetrapods from the Ketleri site, as well as several samples of trace fossils and rhizocretes (Fig. 5I–N). The list of identified fossil taxa from the Ketleri site includes at least 19 vertebrates and two trace fossil ichnogenera, as well as rhizocretes, evidencing the existence of plants (Table 2). The list of vertebrate taxa from the Ketleri site is the longest. The assemblage from this site is dominated by the remains of *Holoptychius*, followed by the scales of *Ventalepis* and *Glyptopomus*, contrary to the Pavāri-1 and Pavāri-2 sites, which are dominated by *Bothriolepis*. Most of the remains are fragmented, and almost each specimen shows traces of wear, sometimes to a very high degree. Almost all vertebrate remains from the Ketleri site are represented by fully disarticulated plates of antiarchs, separate teeth, scales, or rarely bones of sarcopterygian fishes and tetrapods, with only occasional articulated portions of the head or lower jaw of sarcopterygian fishes.

Vertebrate remains from the Pavāri-1 and Pavāri-2 localities are usually represented by fully disarticulated skeletons (Fig. 5C–H), but articulated portions of placoderm head shields (Fig. 5B), trunk and pectoral fin armour, complete lower jaws, or portions of skulls of sarcopterygians and tetrapods (Fig. 5A) have also been often found. The list of identified vertebrate taxa is almost identical for both localities (see Table 2); however, '*Dipterus*' cf. *expressus* Krupina (Lukševičs et al. 2022) and a possible new species of tetrapod (Lukševičs et al. 2024) were found for the first time in the Pavāri-2 locality within the deposits of the Ketleri Fm.

The Pavāri-2 outcrop yields most of the well-preserved vertebrate fossils in poorly consolidated sandstones and silty clayey deposits (facies F1). Most of the articulated specimens belong to the placoderm *Bothriolepis*, the porolepiform *Holoptychius*, and the tetrapod *Ventastega*. Acanthodian spines are relatively rare elements; however, microscopic acanthodian scales were found in some samples in great quantities, reaching 10 scales per 1 gram of sandstone. The degree of preservation varies from small fragments representing only 10% of the whole bone to skeletal elements such as whole skull shields, many anterior ventral lateral bones connected to pectoral fin armour, and even a whole ventral wall of the trunk armour of *Bothriolepis*, the mandible of *Cryptolepis*, the mandibles and the interconnected cleithrum and scapulocoracoid of *Ventastega*, and others.

Broken bones constitute about 17% of all 564 measured specimens at the Pavāri-2 site, but only a few show traces of wear. Separate bones or articulated elements are frequently cracked and deformed. Fossil azimuth measurements of elongated small bones (Fig. 6C) and slightly elongated convex bones (e.g. anterior median dorsal and posterior median dorsal plates of *Bothriolepis*; Fig. 5A) show a relatively well-defined orientation in the NNE–SSW direction. The orientation of trunk shield bones consisting of two laminae (e.g. posterior ventro-lateral bone of *Bothriolepis*) is almost perpendicular, in the SE direction (Fig. 6B).

Specimens with pathologies are often found among vertebrate fossils. Pathologies include predator bite marks both on placoderm bone plates (Fig. 5E, F) and sarcopterygian scales (Fig. 5H), as well as possible parasite attachment traces on the bones (Fig. 5G). A few skeletal elements of *Ventastega* with healed injuries have been found at the Pavāri-2 locality for the first time in the Ketleri Fm.

Trace fossils

Trace fossils, represented by two ichnotaxa, *Planolites* Nicholson isp. and *Palaeophycus* Hall isp., are distributed sporadically in a thin interval within the fish-fossiliferous sandstone bed from the Ketleri site (Lukševičs et al. 2015). Burrow systems are filled with fine-grained sandstone with mica, strongly cemented by fine- to medium-crystalline dolomite. Occasionally, burrows contain small vertebrate remains, such as scales of *Glyptopomus* or acanthodian spines. *Palaeophycus* burrows are about 12 mm in diameter, sometimes bifurcate, forming a horizontal net (see Fig. 5J, K). In places, these large burrows occur together with systems of meandering burrows of smaller diameter (3–5 mm), oriented horizontally or inclined against the bed surface, which have been determined as *Planolites* isp. (Fig. 5L–N).

Vertical cylindrical burrows of *Skolithos* isp., 1–2 cm in diameter and up to 35 cm long, were traced in clayey-silty deposits at the Pavāri-1 site for the first time in 2013 (Mešķis and Lukševičs 2018). In places, the burrows are completely filled with fine sand. A structure of both horizontally and vertically arranged passages, interconnected like a grid, was found between the deep burrows of *Skolithos*. These can be interpreted as three-dimensional living caves (domichnia). The three-dimensional network of feeding burrows and passages consists of both simple tunnel-like traces and more complex passage structures resulting from combined sediment feeding and movement. This is also evidenced by the presence of knots at the junctions of the passages, which exceed the average diameter of the burrows; it is likely that the animal lingered in such places, either to form a temporary living chamber or to perform a turning manoeuvre.

Plant remains and rhizocretes

Sandstone about 5 m above the main fish fossil-bearing bed of the Ketleri locality is heavily cemented by dolomite and represents a dolocrete. Subvertical tubes of dolomitic crusts, altogether 16 specimens, were found in four thin beds (Nos 8–11) just below the dolocrete and were interpreted as rhizocretes (Lukševičs 2023; Fig. 5I). Most of the samples showed areas of downward branching, probably in whorls. The diameter of the primary axes (4–12 cm) and branches (0.8–1.2 cm) differs significantly, clearly supporting their interpretation as rhizocretes. The diameter of the primary axes and secondary branches decreases distally.

Two morphotypes were distinguished: elongated unbranched rhizocretes (morphotype A) and branched rhizocretes (morphotype B). The length of the rhizocretes varies greatly, ranging from 3.5 to 22.0 cm. The length–width (diameter) index varies from 3 to 11 for morphotype A and from 1.6 to 2.7 for morphotype B. The concentric structure of the axial part and the branches in cross-section is well-expressed visually in all sawn samples. It is also identified in

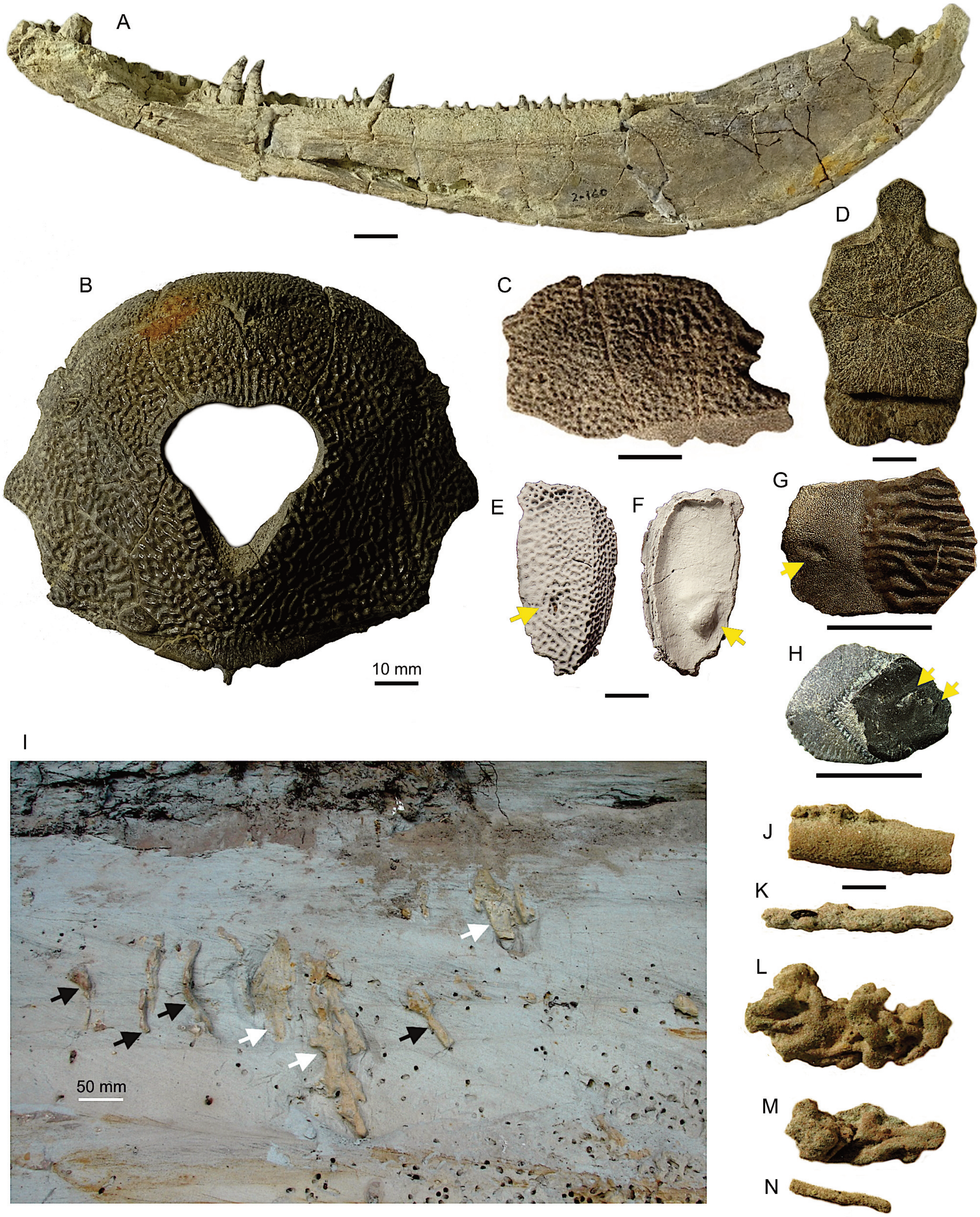

Fig. 5. Fossils from the Ketleri Formation. A–H – variously preserved vertebrate fossils from the Pavāri-2 locality on the left bank of the River Ciecere close to its confluence with the River Paksīte. **A** – complete lower jaw of the tetrapod *Ventastega curonica* MP 2-160 in lingual view; **B** – almost complete head shield of the placoderm *Bothriolepis ciecere* MP 2-1; **C** – disarticulated lacrimal bone of the porolepiform sarcopterygian *Holoptychius*; **D** – disarticulated B bone of an undetermined lungfish; **E–H** – fish fossils with pathologies (yellow arrows): fragmentary anterior dorso-lateral bone of *B. ciecere* MP 2-55 (E–F), fragmentary scale of *Holoptychius* MP 2-280 with parasite attachment pits (G), scale of the osteolepiform sarcopterygian *Cryptolepis grossi* MP 2-281 (H). **I** – Ketleri outcrop No. 5, right bank of the River Venta, 200 m downstream from the Ketleri outcrop No. 1, showing rhizocretes of two morphotypes: black arrows point to morphotype A (unbranched) and white arrows to morphotype B (branched). J–N – trace fossils from the Ketleri outcrop No. 1, right bank of the River Venta close to the abandoned Ketleri farm: **J–K** – *Palaeophycus* isp., with small scales of sarcopterygian fish (K); **L–N** – *Planolites* isp.: network of passages around the *Palaeophycus* burrow (L), network of burrows (M), individual burrow (N). All scale bars equal 10 mm, except for I (50 mm). Photos by V. Alksnītis and E. Lukševičs.

Table 2. Distribution of fossils and rhizocretes in the three localities of deposits of the Ketleri Formation

		Ketleri*	Pavāri-1**	Pavāri-2
Placodermi	*Bothriolepis ciecere* Lyarskaya	+	+	+
Acanthodii	'*Devononchus*' *tenuispinus* Gross	+	+	+
	'*D.*' *ketleriensis* Gross	+	+	+
	Haplacanthus? sp.	+		
	'*Cheiracanthus*' sp.	+		
	'*Acanthodes*' sp.	+		
Actinopterygii	Actinopterygii gen. et sp. indet.	+	+	
Struniiformes	*Strunius* sp.	+		
Porolepiformes	*Holoptychius* ex gr. *nobilissimus* Agassiz	+	+	+
	?*Glyptolepis dellei* (Gross)	+	+	+
	Ventalepis ketleriensis Schultze	+	+	+
Dipnoi	*Orlovichthys* cf. *limnatis* Krupina	+	+	
	'*Dipterus*' *arcanus* Krupina	+		
	'*D.*' cf. *expressus* Krupina			+
	Dipnoi gen. et sp. indet.	+		+
Osteolepiformes	*Cryptolepis grossi* Vorobyeva	+	+	+
	Glyptopomus bystrowi (Gross)	+	+	+
	Tristichopteridae gen. et sp. indet.	+		+
Tetrapoda	*Ventastega curonica* Ahlberg et al.	+	+	+
	Tetrapoda gen. et sp. indet. 1	+		
	Tetrapoda gen. et sp. indet. 2			+
Trace fossils	*Planolites* isp.	+		
	Palaeophycus isp.	+		
	Skolithos isp.		+	
Rhizocretes		+		
Plant macroremains				+

* Data from Lukševičs et al. (2015), Lebedev and Lukševičs (2017), and Lukševičs (2023).
** Data from Lukševičs and Zupiņš (2004) and Mešķis and Lukševičs (2018).

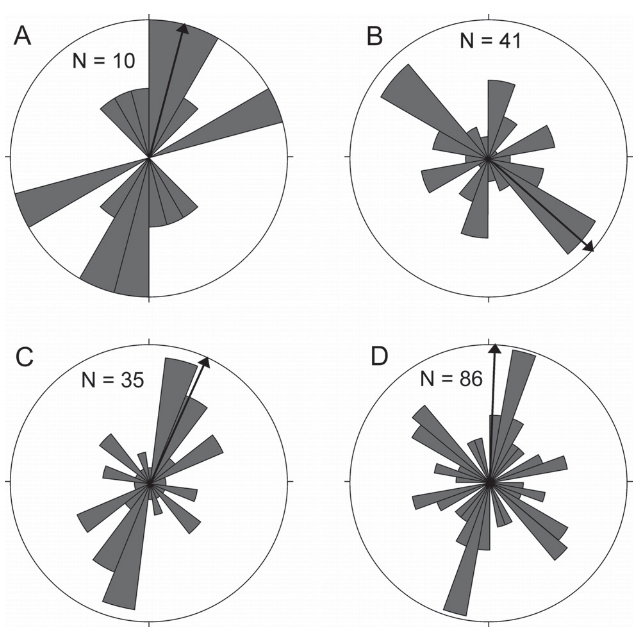

Fig. 6. Azimuthal orientation of vertebrate skeletal elements from the Pavāri-2 locality. **A** – rose diagram from measurements of slightly elongated convex bones; **B** – rose diagram from measurements of trunk bones of *Bothriolepis*, consisting of two laminae; **C** – rose diagram from measurements of elongated small bones; **D** – rose diagram from all measured specimens. Arrow shows the mean azimuth; N – number of measured specimens.

mineralogical and chemical analyses. In the middle of the rhizocrete is a void or a fill with poorly cemented sand grains; this probably corresponds entirely to the diameter of the dead root, reaching up to 5 mm. A relatively narrow, dolomite-rich ring surrounds the central part. The second ring consists of dark pink sandstone enriched in iron oxides and hydroxides, with a lower dolomite content of less than 30% of the rock. This outer ring is interpreted as a rhizohalo, and its transition to the surrounding sandstone mass is gradual, with no clear boundary, but it differs from the main sandstone mass in colour and greater mechanical strength. The rhizocrete-containing sandstone is dominated by quartz with an admixture of mica and clay minerals.

The stable isotope composition in the carbonate material of the rhizocretes shows values from –2.9 to –4.0 for $\delta^{13}C$ and from –0.34 to 1.39 for $\delta^{18}O$. Slightly negative carbon isotope values of the rhizocretes are indicative of weak soil processes in which the rhizocretes were formed. This could be caused both by enrichment in ^{12}C from plant decay products and by the influence of meteoric waters (Sharp 2017). The $\delta^{18}O$ values can be influenced by multiple factors, including seawater, evaporation, and diagenesis (Goldstein 1991; Melezhik et al. 2004; Sharp 2017), and are difficult to interpret.

Twelve of the 16 rhizocretes are oriented subvertically, one vertically, three obliquely (subhorizontally), and only one horizontally along the bedding plane. The dip angle of the oblique rhizocretes varies between 32° and 90°, and the azimuth between 192° and 282°.

Well-preserved plant macroremains, including branches, appendages, and possible fertile appendages, were discovered in 2023 during cleaning of the outcrop wall at the Pavāri-2 site. Plant remains are distributed in few centimetre-thick lenses within the red clay about 1–1.5 m above the main fish-fossiliferous bed (see Fig. 3). Preparation of these remains is in progress.

Discussion

The model of the distribution of sandy deposits of the Ketleri Fm (Fig. 1) shows shapes typical of deltas, as suggested for the Baltic Devonian Basin (e.g. Pontén and Plink-Björklund 2007). During the Ketleri time, sandy and clayey material dominated significantly in the northern part of the Baltic Devonian Basin, while the share of carbonate deposits increased to the south, in the central part of the basin. Borehole data demonstrate the maximum thickness of the Ketleri Fm reaching 55 m in Lithuania and about 45 m in Latvia. The thickness of the sandy deposits might reach more than 40 m; however, thick sandstone beds show a rather uneven distribution, forming two or three areas, which can be interpreted as the distributary channels of the delta.

The widely distributed signatures of tidal processes indicate a marine influence on the siliciclastic sedimentation. Sedimentary structures indicative of tidal processes have been found in various stratigraphic units in Latvia, Estonia, and northwestern Russia, from the Eifelian Pärnu Fm (Tovmasjana 2013) to the uppermost Famennian Ketleri Fm. The facies analysis at the Pavāri-2 site reveals the development of high- to low-energy channels with tidal influence, whereas the vertebrate remains are accumulated in the lower part of the tidally influenced channel infill, the channel thalweg, and bar deposits. The plant remains are associated with clayey infilling of an abandoned channel. The thickness of some well-preserved bar successions indicates shallow-water (<1 m) settings.

The extensive fossil material collected during the last two decades provides additional insights into the environment and biogeography of the Baltica part of Euramerica. Placoderms, diverse sarcopterygian fishes, tetrapods, and other vertebrates, as well as some invertebrates, judging by the trace fossils, inhabited the Ketleri basin. However, the deltaic environment was not favourable for the most typical marine invertebrates, such as corals, echinoderms, or rhynchonelliformean brachiopods.

Taphonomic studies of the Pavāri-1 and Pavāri-2 sites demonstrated that the vertebrate remains were dispersed by water transport in a low-concentration flow after short transportation of the remains before final burial, testifying that the oryctocoenosis was formed in relatively shallow-water conditions dominated by stream and weak wave influence. Initially, these conditions were interpreted as representing a low-tidal near-shore environment (Lukševičs and Zupiņš 2004), but more recently a deltaic depositional environment was suggested (Lebedev and Lukševičs 2016). Most likely, vertebrates from the Pavāri sites dwelled in a marine coastal environment, although at least some fishes probably lived in the lower reaches of rivers.

Rates of disarticulation and preservation of fossil skeletal elements are almost the same in the Pavāri-1 and Pavāri-2 sites; however, separate bones or articulated elements are more frequently cracked (e.g. Fig. 5A) and deformed at the Pavāri-2 locality. These differences may be explained by variations in rock composition, as the grain size of sandy-silty deposits at the Pavāri-2 locality is smaller on average. The analysis of azimuthal orientation of skeletal elements in both localities shows strong similarity: dominant NNE–SSW orientation of the whole set of measured skeletal elements from the Pavāri-1 site (Lukševičs and Zupiņš 2004, fig. 9D) and the same NNE–SSW orientation of elongated small bones and flat slightly elongated bones from the Pavāri-2 site (Fig. 6A, C, D). However, the orientation of trunk shield bones consisting of two laminae differs, showing almost the same NNE–SSW orientation at the Pavāri-1 site (Lukševičs and Zupiņš 2004, fig. 9A) and an almost perpendicular SE direction at the Pavāri-2 site (Fig. 6B). These differences may be explained by stronger currents at the Pavāri-2 site, which were able to reorient strongly convex bones before final burial.

The analysis of taphonomic peculiarities of the Ketleri site shows that the accumulation of vertebrate remains occurred in a tidally dominated deltaic or possibly estuarine environment influenced by weak currents. However, the final burial took place after relatively long transportation. Most probably, the initial vertebrate assemblage, characteristic of all three fossil sites of the Ketleri Fm, was the same. The differences between the Pavāri and Ketleri sites are mainly determined by the shorter distance of transportation at the Pavāri sites and possibly by more turbulent water in the tidal channel at the Ketleri site.

Palaeophycus burrows might be interpreted as combined domichnia and fodinichnia produced by deposit-feeding, filter-feeding, or predatory worm-like organisms similar to acorn worms (enteropneusts), modern marine hemichordates. Usually, traces of *Planolites* are interpreted as fodinichnia produced by worm-like detritophagous animals. Possibly the *Planolites* producers dwelled in the *Palaeophycus* burrows or around them (e.g. Fig. 5L), using the remains of food or excreted substances of an animal resembling the acorn worm. Vertically oriented tubular traces of *Skolithos*, usually much longer than wide, are often interpreted as traces of possible sestonophagous animals (Seilacher 1967; Frey and Pemberton 1984) or as escape burrows (fugichnia) formed during rapid sedimentation. Such traces are typical of intertidal conditions, as well as storm or active upwelling zones and submarine slope conditions (Frey et al. 1990). The palaeoichnological data support the hypothesis that the Ketleri sandstones were formed in a deltaic setting.

Rhizocretes found in the thin beds 8–11 of outcrop No. 5 of the Ketleri Fm, together with plant remains (work in progress), indicate the development of seasonal vegetation very close to the burial place, confirming the deltaic sedimentary environment of the Ketleri Fm. Judging by the rhizohalos, it is likely that the rhizocretes formed after the roots died (Klappa 1980). The ancient plants that inhabited the sandy substrate of the Ketleri Fm grew in very shallow water or very close to the water level on land, most likely on the edge of a channel in deltaic conditions with significant tidal influence. It is likely that the plants grew for a relatively short period, as indicated by the carbon stable isotope data, which confirm poorly developed soil processes (Alonso-Zarza 2003). The $\delta^{13}C$ values are much higher (less negative) compared with the rhizocretes from the Middle Devonian Aruküla and Burtnieki formations (Lagzdiņa and Stinkulis 2020), and the soil formations of the Šķervelis Fm (Pipira et al. 2023), which directly overlies the Ketleri Fm. This is most likely due to the relatively short time of formation of individual rhizocretes during the accumulation of Ketleri Fm sediments, when plants grew rapidly in the wet season and died in the dry season. These data thus support the hypothesis put forward earlier on the monsoon-related seasonality of climate in the Baltic area during the Famennian (Lukševičs 2017; Pipira et al. 2023). The $\delta^{18}O$ values obtained in this study are difficult to interpret because they range from slightly positive to slightly negative and can be influenced by several factors (Sharp 2017).

The morphological features of rhizocretes from the Ketleri Fm differ from the roots of Archaeopterydales (Progymnospermae), Pseudosporochnales, or lycopsid roots, or the roots of bushy and liana-shaped aneurophytes (Progymnosperms; Algeo and Scheckler 1998), but are similar to those of the rhizomes of horsetails. They were probably fast-growing hydrophilic plants. Judging by the size of the rhizocretes and the proportions of the root and stem (Mokany et al. 2006; Szrek et al. 2015), these plants could have been 1–2 m tall.

Conclusions

The sandy-clayey and dolomitic marl deposits of the Ketleri Formation were formed in a deltaic sedimentary environment under strong tidal influence. The main faunal components in the Ketleri basin were vertebrates and some burrowing invertebrates. Most probably, the vertebrates dwelled in the coastal area of the shallow epicontinental basin, or their remains originated from different environments and were mixed together in the delta. Rhizocretes and plant macrofossils indicate that the shallow water or low banks of the deltaic channels were seasonally (during wet seasons) populated by primitive sporophyte plants.

Data availability statement

The collections of fossil vertebrates, plant macroremains, and trace fossils referred to in this study are kept in the Mineralogical and Palaeontological Laboratory of the Department of Geology, University of Latvia, designated here as MP. Other data are contained within the article.

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References

Ahlberg, P. E., Lukševičs, E. and Lebedev, O. 1994. The first tetrapod finds from the Devonian (Upper Famennian) of Latvia. *Philosophical Transactions of the Royal Society B*, **343**(1305), 303–328. https://doi.org/10.1098/rstb.1994.0027

Algeo, T. J. and Scheckler, S. E. 1998. Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society B*, **353**(1365), 113–130. https://doi.org/10.1098/rstb.1998.0195

Allen, J. R. L. 1968. The nature and origin of bed-form hierarchies. *Sedimentology*, **10**(3), 161–182. https://doi.org/10.1111/j.1365-3091.1968.tb01110.x

Alonso-Zarza, A. M. 2003. Palaeoenvironmental significance of palustrine carbonates and calcretes in the geological record. *Earth Science Reviews*, **60**(3–4), 261–298. https://doi.org/10.1016/S0012-8252(02)00106-X

Ashley, G. M. 1990. Classification of large-scale subaqueous bedforms; a new look at an old problem. *Journal of Sedimentary Research*, **60**(1), 160–172. https://doi.org/10.2110/jsr.60.160

Davis, R. A., Jr. 2012. Tidal signatures and their preservation potential in stratigraphic sequences. In *Principles of Tidal Sedimentology* (Davis, R. A., Jr. and Dalymple, R. W., eds). Springer, 35–55.

Delle, N. 1937. Zemgales līdzenuma, Augšzemes un Lietuvas devona nogulumi (Devonian deposits of Zemgale plain, Augšzeme and Lithuania). *Acta Universitatis Latviensis*, **2**(5), 105–384.

Esin, D., Ginter, M., Ivanov, A., Lebedev, O., Lukševičs, E., Avkhimovich, V. et al. 2000. Vertebrate correlation of the Upper Devonian and Lower Carboniferous on the East European Platform. *Courier Forschungsinstitut Senckenberg*, **223**, 341–359.

Frey, R. W. and Pemberton, S. G. 1984. Trace fossil facies models. In *Facies Models*, 2nd ed. (Walker, R. G., ed.). American Association of Petroleum Geologists, Tulsa, 189–207.

Frey, R. W., Pemberton, S. G. and Saunders, T. D. A. 1990. Ichnofacies and bathymetry: a passive relationship. *Journal of Paleontology*, **64**(1), 155–158. https://www.jstor.org/stable/1305557

Gailīte, L. I., Kuršs, V., Lukševiča, L., Lukševičs, E., Pomeranceva, R., Savaitova, L. et al. 2000. *Latvijas pirmskvartāra nogulumu ģeoloģisko karšu apzīmējumi* (*Legends for Geological Maps of Latvian Bedrock*). State Geological Survey of Latvia, Riga.

Goldstein, R. H. 1991. Stable isotope signatures associated with palaeosols, Pennsylvanian Holder Formation, New Mexico. *Sedimentology*, **38**(1), 67–77. https://doi.org/10.1111/j.1365-3091.1991.tb01855.x

Gross, W. 1933. Die Fische des baltischen Devons. *Palaeontographica*, **79**(1–2), 1–74.

Gross, W. 1942. Die Fischfaunen des baltischen Devons und ihre biostratigraphische Bedeutung. *Korrespondenzblatt des Naturforscher – Vereins zu Riga*, **64**, 373–436.

Klappa, C. F. 1980. Rhizoliths in terrestrial carbonates: classification, recognition, genesis and significance. *Sedimentology*, **27**(6), 613–629. https://doi.org/10.1111/j.1365-3091.1980.tb01651.x

Lagzdiņa, G. and Stinkulis, Ģ. 2020. Augu darbības pazīmes vidējā devonā Latvijā (Traces of plant activity during the Middle Devonian in Latvia). In *78th Scientific Conference of the University of Latvia. Geography. Geology. Environmental Science. Abstracts*. University of Latvia, Riga, 124–125.

Lebedev, O. and Lukševičs, E. 2017. *Glyptopomus bystrowi* (Gross, 1941), an "osteolepidid" tetrapodomorph from the Upper Famennian (Upper Devonian) of Latvia and Central Russia. *Palaeodiversity and Palaeoenvironment*, **97**(3), 615–632. https://doi.org/10.1007/s12549-016-0249-9

Lebedev, O. and Lukševičs, E. 2018. New material on *Ventalepis ketleriensis* Schultze, 1980 extend the zoogeographic area of a Late Devonian vertebrate assemblage. *Acta Geologica Polonica*, **68**(3), 437–454. https://doi.org/10.1515/agp-2018-0023

Liepiņš, P. 1951. Daži devona stratigrāfijas jautājumi galvenā devona lauka rietumu daļā (Some questions on stratigraphy of the western part of the Main Devonian field). *Latvijas PSR ZA vēstis*, **6**, 983–988.

Liepiņš, P. 1964. Об унифицированной субрегиональной схеме стратиграфии девонских отложений (On the unified subregional stratigraphic chart of the Devonian deposits). *Izvestija Akademii nauk Latvijskoj SSR*, **1**, 21–26.

Lukševičs, E. 2001. Bothriolepid antiarchs (Vertebrata, Placodermi) from the Devonian of the north-western part of the East European Platform. *Geodiversitas*, **23**(4), 489–609. https://sciencepress.mnhn.fr/en/periodiques/geodiversitas/23/4/bothriolepides-antiarches-vertebrata-placodermi-du-devonien-du-nord-ouest-de-la-plateforme-est-europeenne

Lukševičs, E. 2017. Kāds klimats valdīja Baltijā vēlajā devonā? (What climate dominated in Baltics during Late Devonian?). In *75th Scientific Conference of the University of Latvia. Geography. Geology. Environmental Science. Abstracts*. University of Latvia, Riga, 152–155.

Lukševičs, E. 2023. Augu atliekas un eksistences liecības no devona nogulumiem Latvijas teritorijā (Plant remains and evidences of the existence from the Devonian deposits of Latvia). In *Koks un cilvēks Ziemeļeiropā no senvēstures līdz mūsdienām* (Kalna, S. and Šabanovs, J., eds). *Latvijas Nacionālā vēstures muzeja raksti*, **31**, 7–15.

Lukševičs, E. and Stinkulis, Ģ. 2018. Nogulumiežu segas stratigrāfiskais iedalījums, uzbūve, sastāvs un reģionālās atšķirības (Stratigraphic subdivision, structure, composition and regional differences of sedimentary cover). In *Latvija: zeme, daba, tauta, valsts* (Nikodemus, O., Kļaviņš, M., Krišjāne, Z. and Zelčs, V., eds). Academic Publisher of University of Latvia, Riga, 38–58.

Lukševičs, E. and Stinkulis, Ģ. 2024. The Upper Famennian Ketleri Formation of Latvia: data on the fauna and flora from tide-dominated delta deposits in a seasonal climate. In *XI Baltic Stratigraphical Conference, Abstracts and Field Guide* (Hints, O., Männik, P. and Toom, U., eds). Geological Society of Estonia, Tallinn, 23.

Lukševičs, E. and Zupiņš, I. 2004. Sedimentology, fauna, and taphonomy of the Pavāri site, Late Devonian of Latvia. *Acta Universitatis Latviensis, Earth and Environment Sciences*, **679**, 99–119.

Lukševičs, E., Mešķis, S. and Linde, K. 2015. Vertebrate remains and trace fossils from the Ketleri outcrop. In *73rd Scientific Conference of the University of Latvia. Geography. Geology. Environmental Science. Abstracts.* University of Latvia, Riga, 206–210.

Lukševičs, E., Stinkulis, Ģ. and Lebedev, O. 2017. Late Devonian vertebrate, plant and trace fossils from the Ketleri Formation, south-western Latvia: biostratigraphic and palaeobiogeographic significance. In *10th Baltic Stratigraphic Conference, 12–14 September 2017, Chęciny, Poland. Abstracts and Field Guide* (Żilińska, A., ed.). Faculty of Geology, University of Warsaw, 50–51.

Lukševičs, E., Ješkins, J., Bērtiņa, L., Matisone, L., Visotina, T. and Alksnītis, V. 2022. Jauna vēlā devona mugurkaulnieku oriktocenoze "Pavāri-2". In *80th Scientific Conference of the University of Latvia. Section "Pre-Quaternary deposits, processes, organisms and climate"*, book of abstracts, 1–2.

Lukševičs, E., Ahlberg, P. E., Niedźwiedzki, G., Alksnītis, V., Gess, R. W. and Stinkulis, Ģ. 2024. *Ventastega* and a new tetrapod from the Upper Famennian of Latvia. In *17th International Symposium on Early and Lower Vertebrates* (Mondéjar Fernández, J., Baños-Rodríguez, R., Cloutier, R. and Miyashita, T., eds). *Ichthyolith Issues Special Publication*, **16**, 61.

Lyarskaya, L. and Savvaitova, L. 1974. Строение и ихтиофауна кетлерской свиты Латвии (Structure and fish fauna of Ketleri Formation of Latvia). In *Региональная геология Прибалтики* (*Regional Geology of the Baltic*) (Sorokin V., ed.). Zinatne, Riga, 90–106.

Melezhik, V. A., Fallick, A. E. and Grillo, S. M. 2004. Subaerial exposure surfaces in a Palaeoproterozoic ^{13}C-rich dolostone sequence from the Pechenga Greenstone Belt: palaeoenvironmental and isotopic implications for the 2330–2060 Ma global isotope excursion of $^{13}C/^{12}C$. *Precambrian Research*, **133**(1–2), 75–103. https://doi.org/10.1016/j.precamres.2004.03.011

Mešķis, S. and Lukševičs, E. 2018. Pēdu fosīliju trīsdimensionāls tīkls Ketleru svītā Pavāru atsegumā (Three-dimensional network of trace fossils in the Ketleri Formation from the Pavāri locality). In *76th Scientific Conference of the University of Latvia. Geography. Geology. Environmental Science. Abstracts*. University of Latvia, Riga, 271–274.

Mokany, K., Raison, R. J. and Prokushkin, A. 2006. Critical analysis of root : shoot ratios in terrestrial biomes. *Global Change Biology*, **12**(1), 84–96. https://doi.org/10.1111/j.1365-2486.2005.001043.x

Nichols, G. 2009. *Sedimentology and stratigraphy*. Wiley-Blackwell.

Pipira, D., Ķeipāne, L., Stinkulis, Ģ., Vircava, I. and Martma, T. 2023. Dolocretes in the uppermost Famennian to Mississippian siliciclastic deposits (Šķervelis Formation, Latvia). *Estonian Journal of Earth Sciences*, **72**(2), 211–225. https://doi.org/10.3176/earth.2023.86

Pontén, A. and Plink-Björklund, P. 2007. Depositional environments in an extensive tide-influenced delta plain, Middle Devonian Gauja Formation, Devonian Baltic Basin. *Sedimentology*, **54**(5), 969–1006. https://doi.org/10.1111/j.1365-3091.2007.00869.x

Reineck, H.-E. and Singh, I. B. 1980. *Depositional Sedimentary Environments*. Springer-Verlag, New York.

Savvaitova, L. S. 1977. *Фамен Прибалтики* (*Famennian in the Baltics*). Zinatne, Riga.

Savvaitova, L. 1995. Ketleru svīta (Ketleri Formation). In *Latvijas daba, enciklopēdija* (Kavacs, G., ed.). Latvijas Enciklopēdija, Riga, 240.

Seilacher, A. 1967. Fossil behaviour. *Scientific American*, **217**(2), 72–83. https://www.jstor.org/stable/24926087

Sharp, Z. 2017. *Principles of Stable Isotope Geochemistry*. 2nd ed. University of New Mexico, Albuquerque. https://doi.org/10.25844/h9q1-0p82

Sidaravičienė, N., Valiukevičius, J., Paškevičius, J., Kondratienė, O., Baltrūnas, V., Gaigalas, A. et al. 1999. *Lithuanian Stratigraphic Units*. Lietuvos geologijos tarnyba, Vilnius.

Stinkulis, Ģ. 2003. Latvijas nogulumiežu segas stratigrāfiskā shēma (Stratigraphic chart of the sedimentary cover of Latvia). *Latvijas ģeoloģijas vēstis*, **11**, 14–17.

Szrek, P., Salwa, S. and Niedźwiedzki, G. 2015. A plant-root system in the Lower Devonian of the Holy Cross Mountains, Poland. *Estonian Journal of Earth Sciences*, **64**(1), 95–98. https://doi.org/10.3176/earth.2015.17

Tovmasjana, K. 2013. *Depositional environment of the tidally-dominated transgressive succession: Rēzekne and Pärnu regional stages, Baltic Devonian basin*. Summary of doctoral thesis. University of Latvia, Riga, 43–88.