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**A specimen of *Psammolepis* in the Gauja Formation (Estonia)**

**BSc thesis**

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## Introduction

The Devonian Period is sometimes called „The Age of the Fishes“. It is the period when fish and agnathan diversity exploded and many modern fish families developed. Studies on Devonian agnathans and fishes represent an important part of evolutionary research telling us how physiology and morphology of aquatic animals changed in changing environment. The evolution of Devonian fishes and agnathans was related to the evolution of first tetrapods in mid-Devonian when vertebrates moved to the terrestrial environment.

In Estonia, the Devonian System has long time been a subject of studies. One of the first to describe fossil fishes in Estonia was Hermann Martin Asmuss (1812-1859). Thanks to his excavations of fishes in the Aruküla Caves, the Estonian fish fossils became known around the world. Thanks to extensive studies by Elga Mark-Kurik, the collection of Devonian agnathans and fishes in Estonia has grown considerably and is today one of the best in the world.

The Devonian of Estonia is rich in psammosteids. According to E. Mark-Kurik, they were likely the dominant species during the Middle Devonian (Mark-Kurik, 2007). Thanks to this, psammosteids can be used in stratigraphy as they are quite common in the Devonian outcrops of the Baltic area. Fish fossils are one of the few sources of biostratigraphic information that can be used in the Devonian stratigraphy of Estonia. Fish species are also known to have large distribution areas. They can be used for correlation of the Estonian sections to the global stratigraphic standard and support comparisons with other regions, e. g. Scotland. Fish fossils can also be used in palaeoenvironmental and palaeoecological studies. All the same is valid for agnathans.

Material for the present study was collected in the Kalmetumägi locality. The recovered specimen was particularly hard to prepare because of extensive fragmentation. Fragmented material, however, contained pieces of a shield with fragmentarily preserved sensory system, thus making the material potentially very rare and important.

Our sense of hearing is the most familiar example of a sensory system that is sensitive to changes in pressure when sound is transmitted through air. The lateral line system in Devonian agnathans and fishes could provide similar type of information. It was sensitive to changes of pressure transmitted through water. The lateral line system allows the animal to determine direction and rate of water movement. The animal could then gain a sense of its own movement, on the activities of nearby predators or prey and even the displacement of non-living objects in water. More complex canal systems are indicative of more turbulent and dynamic living environment which required better movement control for maintaining a stable position (Elliott & Mark-Kurik, 2005). Furthermore, the electroreceptors of sharks are also derived from the lateral line system. The lateral line system is of vital importance within the sensory system of aquatic vertebrates but is different in different taxa. It may slightly vary also between the individuals of same species, but also due to the age of the animal, but can still be used as a species character in taxonomy.

This study is positioned on the border between geology and biology. It implies basic understanding of fish anatomy, physiology, palaeoecology and sedimentology, in order to describe a vertebrate fossils and differentiate between the anatomical and *post-mortem* features. Uncovering and identifying a new fossil is a challenge and opportunity to acquire various experiences and valuable

information. Various publications in English, Russian and German were used to get more information about the subject. The database of the Estonian geological collections was used to learn about other fossils from the same area. The Latvian Museum of Natural History and the Geological Institute of Tallinn University of Technology were visited to study fossils from the same area. The geological maps of the Land Board of the Republic of Estonia were used to study and discuss stratigraphy of the area.

The primary aim of this thesis was to identify the collected material. This was a stepwise procedure starting with preparation and assembling the fragments, figuring and describing the fossil in order to find characters of identification. The second of this study was to analyse the geological (biostratigraphic, taphonomic, etc.) value of the material. This required access to geological databases and literature on the fossils from the same area.

## Terminology

basal layer – a layer of tissue on visceral surface that interacted with inner body organs.

branchial plates – two triangular plates on the left and right sides of psammosteid body, covered by tubercles on both sides. Pleromin tissue mostly occurs on antero-lateral edges. Proximal sides that were attached to the body are thicker and larger and may bear some tesserae.

dorsal plate – a plate that covers dorsal side of psammosteid body, it is normally of round or oval shape and flat compared to a ventral plate, has neither a posterior notch nor pleromin tissue. It may be partly or entirely covered with tesserae.

pleromin tissue – the term was introduced by Ørvig (1976) to designate a hypermineralized tissue reinforcing important carapace parts.

proximal side – external side of psammosteid body plates.

ridge scales – elongated or rhomb shaped convex scales, covered by tubercles externally and in part also internally. Ventral ridge scales also contain pleromin tissue in posterior part.

scales (body scales) – thin rhomb shaped scales are usually flat and covered with tubercles.

spongy tissue (*spongiosa*) – porous tissue between the superficial and basal layers.

tesserae – small bony plates that cover body between larger plates but sometimes may cover large plates also. They are irregularly shaped and externally covered with tubercles. Normally quite thin.

tubercles/ornamentation – superficial layer of bony tissue, consists of small tooth like structures of different shape and size. Ornamentation is one of the basic characters for identification of psammosteid species.

ventral plate – a plate that covers ventral side of psammosteid body, normally oval or elongated in shape, usually rather convex, having pleromin tissue and a posterior notch. Sometimes partly covered with tesserae.

visceral side – internal side of psammosteid body plates.

## Former studies on *Psammolepis*

The rich Baltic Middle Devonian vertebrate assemblages represent the flourishing period of the Devonian faunas. The Devonian assemblages were represented by agnathans (Heterostraci, Thelodonti, Anaspida and Osteostraci) and by gnathostomes (Acanthodii, Chondrichthyes, Osteichthyes, Placodermi and Tetrapoda). Psammosteids (Heterostraci) were likely a group of dominant species in Middle Devonian (Mark-Kurik, 2007) but research on psammosteids has not been very popular as most of the findings comprise isolated plates or fragments. The material is mainly coming from the Main Devonian Field (Baltic States, Leningrad, Pskov and adjacent regions of Russia) that was the main distribution area of psammosteids in the world (Tarlo, 1964, Obruchev & Mark-Kurik, 1965).

Today, psammosteiformes are represented by families Drepanaspididae, Obrucheviidae, Psammolepididae, Psammosteidae and Pycnosteidae (SARV: Eesti geokogude infosüsteem ja andmerekasutamine, 2015). Obruchev and Mark-Kurik (1965) include most of the Middle and Upper Devonian psammosteid genera into the family Psammosteidae Traquair, 1896. Tarlo (1962, 1964, 1965) establishes a larger number of families. He supposes (Tarlo, 1964, figs 30, 32) that ancestors of psammolepidids were the Emsian/Eifelian guerichosteids: *Guerichosteus* Tarlo, 1965 and advanced genus *Schizosteus* Obruchev, 1940 (today assigned to Pycnosteidae – Sarv, 2015). Pycnosteids formed a parallel development line to psammolepididae in the Middle Devonian (SARV: Eesti geokogude infosüsteem ja andmerekasutamine, 2015).

The family Psammolepididae comprises nine species of the genus *Psammolepis* Agassiz, 1854. The psammolepidids are characterized by narrow, solid ventral median plates that differ from the deeply notched plates of the pycnosteids, and by broad and long branchial plates, different of the short branchial plates of psammosteids.

The genus *Psammolepis* was established by Agassiz in 1844. The type species of this genus is *Psammolepis paradoxa* Agassiz, 1844. The species occurs in the middle and upper Old Red Sandstone (Middle and Upper Devonian) of Baltic Region, Timan, Donbas, Scotland and Ellesmere Island in Arctic Canada (Mark-Kurik, 1968). The genus *Psammolepis* is readily recognized by its ornamentation of superficial scale-like tesserae (Tarlo, 1965).

As a result of extensive collection work carried out by Elga Mark-Kurik and her colleagues, lots of findings of this genus are known. In one instance, a post-orbital plate was found in natural association with a branchial plate (GIT 116-212, formerly numbered as Pi 239). Based on this material, E. Mark-Kurik was able to give a detailed reconstruction of the dorsal side of *Psammolepis venyukovi*, published by Heintz in 1957 (see also Figure 1).

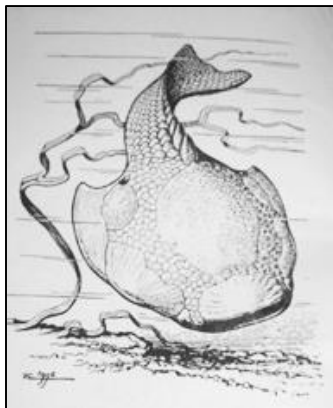


Figure 1.

Reconstruction on *Psammolepis venyukovi* by Mark-Kurik (1965).

## Morphology

Agnathans had well developed exoskeleton already in the Ordovician and Silurian. The question what stimulated the development/growth of agnathans exoskeleton remains unanswered for the time being. A possible explanation is that the appearance of exoskeleton was related to certain environment conditions or chemical properties of water, thus suggesting the environment to be quite different from modern situation (Mark-Kurik, 1992). Yakovlev (1966) suggests that strong exoskeleton further compensated weakness of cartilage inner skeleton.

*Psammolepis* was a typical representative of agnathans. Fossil remains of *Psammolepis* consist of isolated plates and scales. The branchial ('lateral') plates and ridge scales are rather common. Dorsal and ventral plates are twice as rare as the branchial plates. Other plates (rostrals, pineals, orbitals, postorbitals, cornuals and the anterior plates of ventral carapace – see Figure 2) have been discovered only in a few cases (Obruchev & Mark-Kurik, 1965, table I; Mark-Kurik 1968).

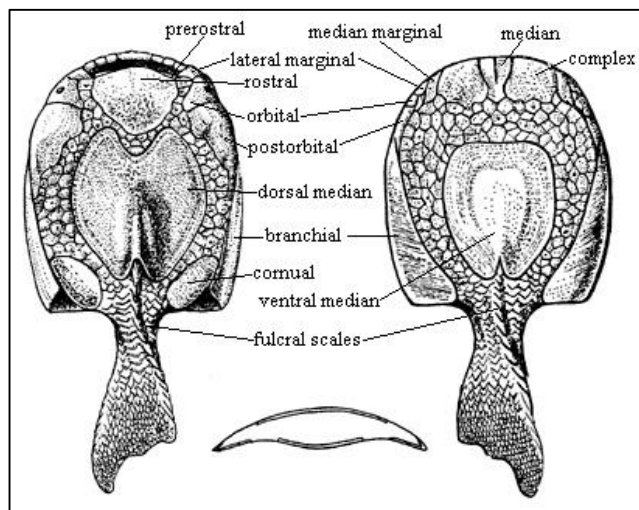


Figure 2.

Reconstruction and morphology of *Drepanaspis* Traquair, 1889 (Tarlo, 1964).

The tail in *Psammolepis* was longer than  $\frac{1}{4}$  of overall length of the body. The tail parts found so far indicate that it was large and strong, serving as strong 'engine' in swimming and/or escaping from predators. A caudal fin was present but is only rarely preserved. The fin has five spreading rows of consolidating bigger scales. *Psammolepis proia* Mark-Kurik, 1965 was one of the largest psammosteids, 70 to 90 cm in length.

Oblong dorsal plates of *Psammolepis* are partly or entirely covered with tesserae and their growth centres are situated anteriorly, with few exception. The pattern of sensory canals on dorsal plates of *Psammolepis* is known: it is very symmetrical and consists of two medial dorsal canals and 1-3 transverse commissures (Elliott & Mark-Kurik, 2005). The ventral plates of psammosteids are oval shaped. Two kinds of branchial plates have been found in *Psammolepis*, long and narrow ones and long and wide ones.

A posterior notch exists in juvenile specimens of *Psammolepis*. In adults, the notch and major part of dorsal plate are covered with tesserae.

*Psammolepis* differs from *Drepanaspis* Traquair, 1889 mainly in the structure of dorsal and ventral plates and the shape of branchial plates. However, in some species like *Psammolepis toriensis* Mark-Kurik, 1965, *P. proia* and *P. paradoxa*, the branchial plates are very similar to those of a young *Drepanaspis*. *Psammolepis undulata* Agassiz, 1845 differs from other species in its

bottle-shaped dorsal plate and well-developed lateral angles of the body. *Psammolepis venyukovi* Obruchev, 1965 had a broad rostral plate and a dorsal plate that is wider anteriorly (Mark-Kurik, 1968).

The squamation of psammosteids consists of different kind of scales. Scales *sensu stricto* (*squama*) cover lateral sides of the body. The ridge scales (*squama fastigiata*) mark longitudinal axis of the animal in ventral and dorsal sides. The dorsal (*squama fastigiata dorsalis*) and ventral (*squama fastigiata ventralis*) ridge scales of the Mid-Devonian psammosteids are different. Ventral ridge scales show mechanical abrasion and presence of pleromin tissue, i.e. dentine filling of spongy tissue (Mark-Kurik, 1984).

The only completely known psammosteid species, with a complete assembly of scales and plates, is *Drepanaspis gemuendenensis* Schlüter, 1887 from the Lower Devon of Germany. This species has been studied and illustrated thoroughly by Gross in 1963 (Figure 3). Also some other important specimens of *Drepanaspis gemuendenensis* have been studied by other authors (Traquair, 1905, Obruchev & Mark-Kurik, 1965). The listed specimens are the only well preserved complete set of scales and plates known up to now.

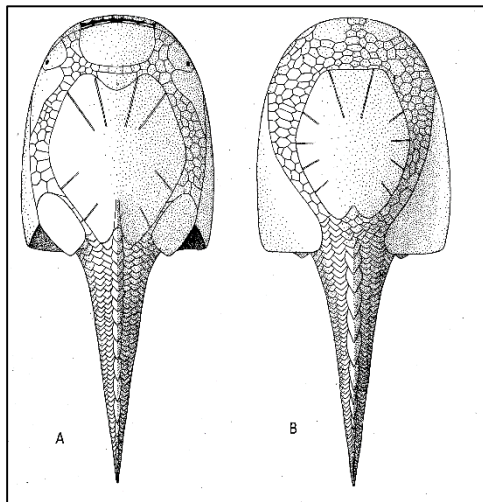


Figure 3.

Reconstruction of dorsal (A) and ventral (B) sides of *Drepanaspis gemuendenensis* Schlüter, 1887 (Gross, 1963).

Reconstructions of isolated plates and scales of *Psammolepis toriensis*, *P. abavica* Mark-Kurik, 1965, *P. paradoxa*, *P. venyukovi* (Figure 2), *P. alata* Mark-Kurik, 1965, *P. undulata* and other psammosteids are also available (Obruchev & Mark-Kurik, 1965; Mark-Kurik, 1968, Lyarskaya, 1971). A rare find of Eifelian age, *Schizosteus striatus* Gross, 1933 shows a large fragment of lower part of the tail squamation (GIT 116-70 in the collections of Tallinn Technical University).

The bony exoskeleton of psammosteids that contained soft tissue was not heavy. The scales and plates did not give the animal a negative buoyancy as they were very thin and relatively light regarding the size of the animal. It is suggested that agnathans were able to compete ray-finned fishes in swimming speed but their manoeuvrability was more limited (Mark-Kurik, 1992).

Wearing of margins of branchial plates and the central part of ventral plate in particular is a characteristic feature of psammosteid exoskeleton. Heintz (1957) suggested that the wear of psammosteid shields was caused by rubbing or friction against a more or less firm and even surface. It is likely that the animal rubbed its shields against rocks and stones, attempting to keep steady in the current. It is also possible that the clumsy animal occasionally turned upside down.



## Data on the lateral line systems

The lateral line system allows the animal to sense movement of water. It responds to water flow on the skin and is sensitive to different flow patterns over the body, responding to changes in hydrodynamics of nearby environment.

The former data on sensory line canals is based mainly on the dorsal plates of Middle and Devonian species of the genera *Psammolepis*, *Psammosteus* Agassiz, 1844, *Tartuosteus* Obruchev, 1961 and *Drepanaspis*. In general, there are two medial canals and 1-3 transverse commissures (Elliott & Mark-Kurik, 2005; Figure 4). Sensory canals are generally situated just under the external tuberculate layer (Figure 5) and become visible only in rare cases when the tubercles are worn off (Elliott & Mark-Kurik 2005) (Figure 4).

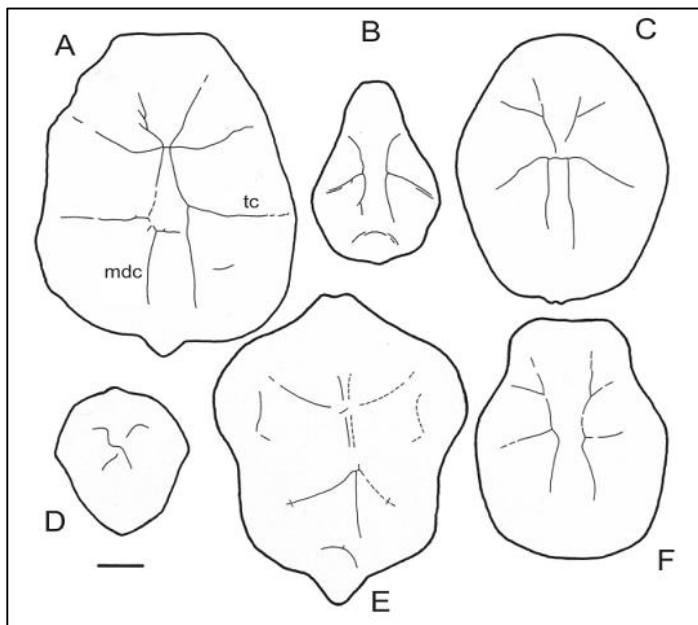


Figure 4.

Lateral line patterns in the dorsal plates of psammosteids. A – *Psammolepis proia*, adult plate, Pi 123; B – *P. undulata*, juvenile plate, Pi 247; C – *Psammosteus praecursor* Obruchev, 1947, adult, Pi 164; D, E – *P. bergi* (Obruchev, 1943); D – juvenile, Pi 912; E – adult, Pi 739; F – *P. livonicus* Obruchev, 1965, adult, Pi 722. Abbreviations: mdc – median dorsal canal; tc – transverse commissure. Scale bar = 50 mm (Elliott & Mark-Kurik, 2005).

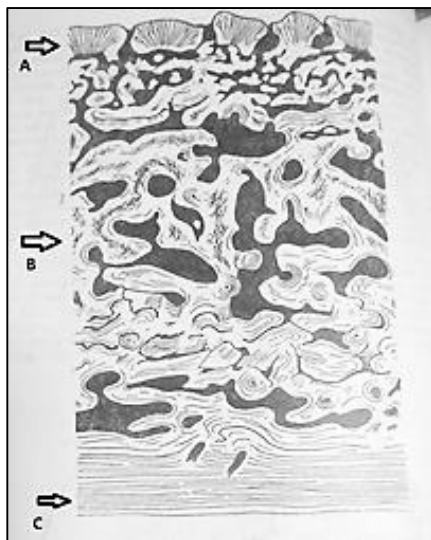


Figure 5.

Cross-section of a *Psammolepis paradoxa* plate. A – tuberculate layer; B – spongy layer; C – basal layer (Obruchev & Mark-Kurik, 1965)

Canals can be recognized as 0.5-1 mm wide grooves or tubes. Sometimes a series of small pores in scales may indicate the position of a sensor canal beneath. In some cases, elongated tesserae mark the position of sensory canals in a plate.

Radial ridges in dorsal and ventral plates of *Drepanaspis gemuendenensis* were identified as sensory line canals by Gross (1963). The ventral and dorsal plates in this species have canal systems of similar configuration (Figure 3).

In different specimens of *Psammolepis undulata* the sensory lines look very similar, with only small differences. The lateral line system in *P. undulata* was earlier known from juveniles only. It is also known that a parallel canal system may occur in *P. undulata* (Elliot & Mark-Kurik, 2005) but there is no information about the visceral side system of *P. undulata*.

The lateral line system in *Drepanaspis* from the Early Devonian was rather simple, compared to more complicated sensory systems of *Psammolepis* and *Psammosteus* from the Late Devonian.

## Materials and methods

### Locality/ Environment

Estonia is located in the north-western part of the Devonian Main Field of the East European Platform. The Devonian Baltic Basin was situated in equatorial latitudes on the margin of the Laurussia Supercontinent. The basin was characterized by siliciclastic deposition, with input of clastic material from the Scandinavian Caledonides (Kleesment & Mark-Kurik, 1997). Its development was influenced by both tectonic movements and eustatic sea-level oscillations (Ziegler, 1988). In the area under consideration, the tide-dominated river delta plain sediments accumulated (Tänavsuu-Milkevičiene, 2009). The basin was situated in the western part of the Baltic Shield and surrounded by deserted land mass. The psammosteids and other Devonian vertebrates lived in the near-coastal brackish sea areas.

### Stratigraphy

The Gauja Stage (Middle Devonian, Figure 6) is distributed in a restricted area in south-eastern Estonia but extends further to the south and east. The total thickness of the stage in Estonia varies from 78 to 79.8 m. The lower and upper parts of the Gauja Formation contain different in fossil

AGE Ma	GLOBAL STANDARD			REGIONAL STANDARD		MAIN LITHOSTRATIGRAPHICAL UNITS (FORMATIONS)			NOTATION		
	SYSTEM	SERIES	STAGE	STAGE	SUBSTAGE	SE ESTONIA	SW ESTONIA	NE ESTONIA	STAGE	FORMATION	MEMBER
358.9	DEVONIAN	UPPER DEVONIAN	FRASNIAN								
372.2				DAUGAVA		DAUGAVA			D <sub>3</sub> dg	D <sub>3</sub> dg	
				DUBNIK		DUBNIK			D <sub>3</sub> db	D <sub>3</sub> db	
						CHUDOVO				D <sub>3</sub> ch	
				PLAVIŅAS		PSKOV			D <sub>3</sub> pl	D <sub>3</sub> ps	
						SNETNAYA GORA				D <sub>3</sub> sn	
382.7		MIDDLE DEVONIAN	GIVETIAN	AMATA		AMATA			D <sub>2</sub> am	D <sub>2</sub> am	
				GAUJA		Lode Mb GAUJA Sietini Mb			D <sub>2</sub> gj	D <sub>2</sub> gj	D <sub>2</sub> gj <sup>L</sup> D <sub>2</sub> gj <sup>S</sup>
				BURTNIĒKI		Abava Mb BURTNIEKI Kooriküla Mb Härma Mb			D <sub>2</sub> br	D <sub>2</sub> br	D <sub>2</sub> br <sup>A</sup> D <sub>2</sub> br <sup>K</sup> D <sub>2</sub> br <sup>H</sup>
				ARUKÜLA		Tarvatu Mb ARUKÜLA Kureküla Mb Viljandi Mb			D <sub>2</sub> ar	D <sub>2</sub> ar	D <sub>2</sub> ar <sup>T</sup> D <sub>2</sub> ar <sup>K</sup> D <sub>2</sub> ar <sup>V</sup>
387.7			EIFELIAN		KERNAVE		KERNAVE			D <sub>2</sub> kr	
				NARVA	LEIVU		LEIVU		D <sub>2</sub> nr	D <sub>2</sub> lv	
					VADJA		VADJA			D <sub>2</sub> vd	
				PÄRNU		PÄRNU Tamme Mb Tori Mb			D <sub>2</sub> pr	D <sub>2</sub> pr	D <sub>2</sub> pr <sup>Tm</sup> D <sub>2</sub> pr <sup>T</sup>
393.3		LOWER DEVONIAN	EMSIAN	RĚZEKNE		RĚZEKNE	LEMSI		D <sub>1</sub> rz	D <sub>1</sub> rz / D <sub>1</sub> lm	
407.6				ĶEMERI		ĶEMERI			D <sub>1</sub> km	D <sub>1</sub> km	
410.8			LOCHKOVIAN	TILŽĒ		TILŽĒ			D <sub>1</sub> tl	D <sub>1</sub> tl	
419.2				OHESAARE		OHESAARE					

Figure 6.

Stratigraphy of the Devonian System in Estonia (Põldvere, 2014).

content. The lower, Sietiņi Member has yielded fossil agnathans: *Psammolepis venyukovi*, *P. paradoxa*, *P. heteraster* Gross, 1930, *P. alata* (Mark-Kurik 2000). In the Lode Member, only plant macroremains and miospores are known (Kleesment & Mark-Kurik, 1997).

Material of this study, an almost complete psammosteid shield, was collected by Elga Mark-Kurik and Ivars Zupinš in 2010 from the Kalmetumägi locality (Figure 7). The section is located in the Võru Region, Meremäe County, within the Piusa National Park. The height of Kalmetumägi (also called Jõksi) outcrop on the right bank of the Piusa River reaches about 9 m and its length about 25 m. The section is subdivided into two parts by a steep V-shaped valley. The downstream part of the section with two large caves is the best known fossil site of the Gauja Formation in Estonia. The richest collection of vertebrate fossils with bite marks is also coming from the Kalmetumägi locality (Lebedev et al. 2009).



Figure 7. Ivars Zupinš and the Kalmetumägi locality dig site (Photo by E. Mark-Kurik). The red line in the left picture indicates the level where the fossil was found.

The investigated psammosteid shield was uncovered from the coastal outcrop slightly above the water level (Figure 7). The yellowish-brown sandstone was partly very strongly cemented but mostly quite loose and the fossil was collected as fragments of different size. The sediment matrix comprises almost pure very hard cemented sandstone that was difficult to remove. Identification of the species was not possible in its fragmentary state.

The specimen is stored in the Institute of Geology at Tallinn University of Technology (collection number GIT 683-1). For the present study the specimen was wrapped into double layer of bubble wrap, covered with soft paper and transported to Tartu.

### Description of principles and practice of assembly of fragmented vertebrate specimens

Fragments were sorted into groups according to size before cleaning. Softer sediment was cleaned away with a tooth brush or toothpick, harder sediment was removed with a steel needle. Needles were sharpened regularly in circular motion for precise work, and bilaterally (to get a pad like point) for cleaning a bigger area at once. It should be noted that stronger sediment requires harder steel and sharper instrument. Very strongly cemented grains were locally removed by means of a

small drill. Heads of dentist drills are of different size and shape. The drilling instrument lost its sharpness quite fast, so using stronger steel is highly preferable. The needles and drill were used the same way, pulling the sediment particles towards the preparator. Each quartz grain was removed separately, with great care, under the binocular microscope.

The glue was made of polyvinyl buteral dissolved in ethanol. Alcohol was mixed with glue powder until no visible particles were left in the glue. The glue was delivered to the fossil fragments by means of small wooden sticks (for avoiding damage of the fossil with steel needles). The contact surfaces were impregnated twice, as most of the first glue layer was absorbed by the spongy tissue. Only the second glue layer fixed fossil fragments strongly enough to each other.

A preliminary montage of the dorsal shield was performed without gluing the pieces together. The margins of the fossil that matched 100% were put together around the largest fragment. Other (succeeding) pieces were glued to this 'nucleus'. The anterior and posterior parts of the shield were mounted separately as their contact line was a 100% match and no small pieces were absent. No pieces were glued together which did not match exactly. The positions of pieces were guessed according to their thickness, colour, properties of cement, morphology, etc. (Figures 8-11).



Figure 8.  
Matching the fragments.

Photos were taken in the dark cellar laboratory. The fossil was laid down on the paper-covered floor. Photos were taken by Canon Eos 40D camera using both the universal and microphotography lenses. Microscope photos were taken by Leica DFC495 stereozoom 3D microscopy system, using 3 light sources for creating the best illumination of the lateral line canals.





Figure 9.

All the fragments that matched were glued together.



Figure 10.

Fragments that did not match clearly were put into positions they seem to fit the best (compare to the Figure 9).

### Description of the mounted shield

The shield (Figure 9) is at least 285 mm long and 195 mm broad. The shield is moderately convex - the greatest height being approximately 35 mm slightly closer to the front edge of the shield (Figure 11). The posterior part of the shield is flatter than the anterior – the greatest height being 8-10 mm (Figure 11). The anterior-median point of the shield is located somewhat higher (ca 5 mm) than the lateral sides, thus the convexity across the body is stronger than the longitudinal convexity. The length of the median longitudinal thickening and related elevation is about 102 mm and width 17-30 mm.

The shape of the shield is more or less oval. The shield is the broadest between the lateral corners and the line connecting them almost crosses midpoint of the shield. The surface of the shield is without tubercles and only faint marking of tesserae is visible on the proximal surface of the plate (Figure 12). The plate consists only of the basal and median layer, the superficial layers are lacking. According to Heintz (1957), the plate was situated under the skin in a living animal and was therefore invisible.

The shield is comparatively thin (3-4 mm) in frontal and antero-lateral parts, reaching about 5-6 mm thickness in the medial part. Growth centre is located in anterior part of the shield. It is surrounded with small rhomb-shaped scale-like tesserae of about 3 mm size, gradually increasing up to 10mm towards the margins of the plate (Figure 12). No growth lines can be recognized in the specimen. Only the visceral surface bears a faint mark of growth line. It is approximately 160 mm

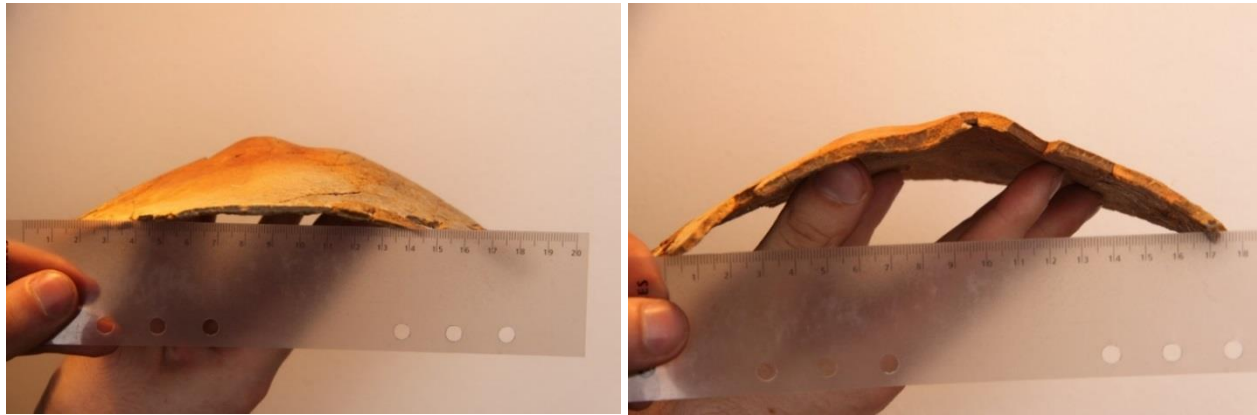


Figure 11. Posterior part of the shield is quite flat (left), but the anterior one rather convex (right).



Figure 12. Figure of canals and faint marking of tesserae. Canals are marked in red, tesserae are in black, bite mark in yellow and growth centre with a black circle.

long and located on the left side of the plate. This line was used to reconstruct the shape of the shield (Figure 13). Various radial canal openings and a line of small pores are seen on the right side of visceral surface of the plate. A series of small holes and tubes can be found also on the visceral side, being oriented towards the growth centre (Figure 14).

A small thin piece with ornamentation was also found in the same assemblage of plate fragments and first thought to belong to the same specimen although the margins of the piece did not fit the larger plate. It bears large pyramidal tubercles, with smaller tubercles between them. (Figure 15).

After assembling the fossil, an extensive system of canals was revealed on the external surface of the shield. Two median canals (mdc) run longitudinally approximately in the middle of the shield. Left median canal is about 220 mm in long and 1 mm wide. Right median canal is about 150 mm long and 1 mm wide. Both canals are discontinuous. Distance between the median canals is 270-420 mm. Canals ran underneath the tesserae (Figure 12)

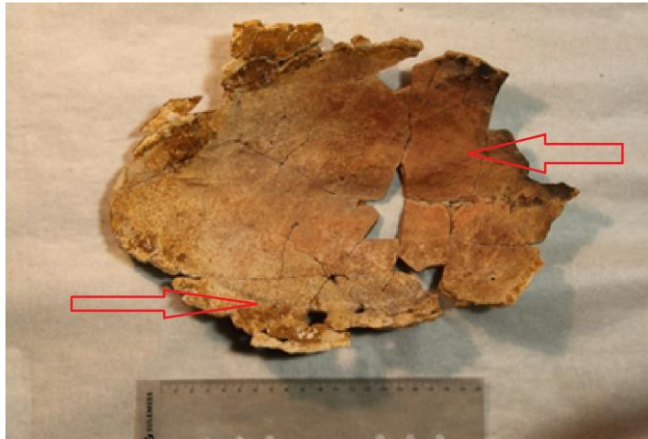


Figure 13.

Visceral side of the plate showing a faint outline of a former edge of the plate in bottom mid area (left arrow). The right arrow points at thickening of the shield mid-anteriorly.



Figure 14.

Radial canals on the visceral side of the plate.

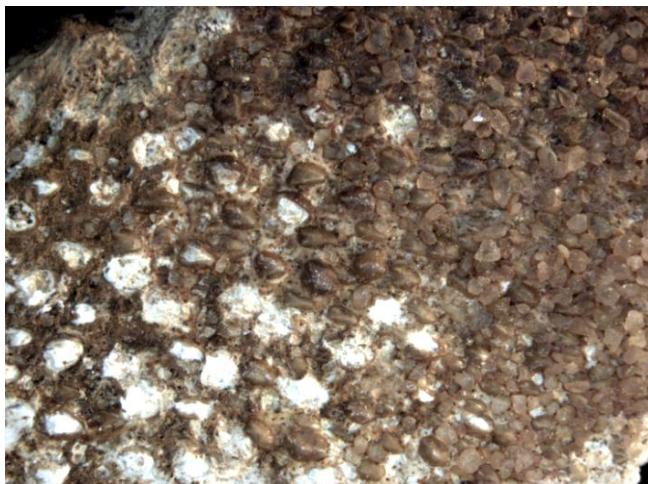


Figure 15.

The isolated fragment with tuberculate ornamentation.



At least 3 transverse commissures (tc) are visible on the proximal surface. These canals reach almost the lateral margin of the preserved part of plate, suggesting that they continued underneath tesserae towards the branchial plates. The length of the left posterior tc is approximately 30 mm and width about 1 mm. The left median tc is about 60 mm long and 1 mm wide. The left anterior tc is very difficult to detect as only faint openings can be seen. Right posterior side tc is not visible. Right median side tc is approximately 60 mm long and 1 mm wide, right anterior side tc 30 mm long and 1mm wide. Both anterior tc's consist of series of small openings that follow a canal seemingly connecting two median canals. Both median canals and transverse commissures have short branches. They are oriented in various directions.

The lateral dorsal canals (ldc) are very rare in psammosteids and they are absent also in the present specimen. The lateral canals are known in several species of the genus *Psammosteus*.

The bite mark in the left anterior part of the shield is small, about 2.2 mm long (parallel to the longitudinal axis) and 1.5 mm across. The dimensions of the corresponding opening on the visceral surface are about 1.5x1.0 mm. There are three cracks originating from the corners of the triangular bite mark and originally reached about 1.5 mm length. The cracks are partly regenerated, this is evident from ridges on the surface that follow the primary crack (Figures 16-19).

A possible scratch mark is located in anterior part of the shield, being of about 10 mm in length (Figure 20).



Figure 16.

The bite mark in the left anterior part of the plate (visceral side).

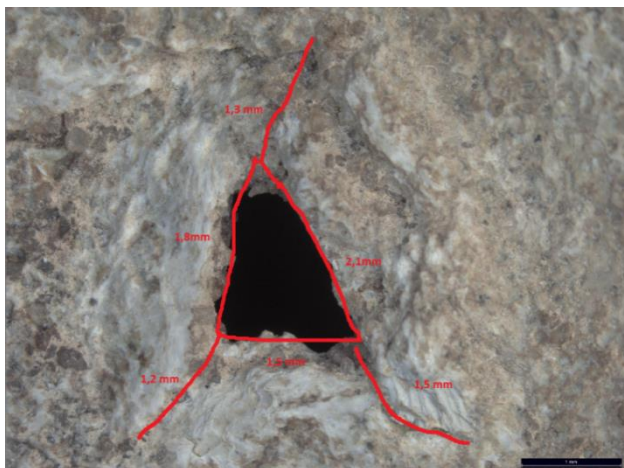


Figure 17.

The bite mark with annotated, partly regenerated cracks (visceral side).



Figure 18.

The bite mark in the left anterior part of the plate (proximal side).



Figure 19.

The bite mark with annotated, regenerated crack (proximal side).



Figure 20.

A possible scratch in the anterior part of the plate.

## Discussion

### Identification and comparison

Already during the excavation it was suggested that the shield belonged to a psammosteid. A number of species of the genus *Psammolepis* is known in the Gauja Formation whilst the other psammosteids disappeared earlier. Unfortunately, the fossil had no ornamentation left. As it probably was primarily covered with tesserae, it could be either dorsal or ventral plate. After preparation and gluing it was clear that the shield belonged to a large specimen of a species of *Psammolepis* but the primary position of the shield (ventral or dorsal), its orientation (anterior-posterior) and species affinity were still unclear.

The shield was convex, oval in shape and relatively thick, the latter fact suggesting first a ventral shield. Glinskiy (2014) described a ventral plate of *Psammolepis proia* from the Aruküla Stage and its main characteristics are largely similar to the new material. The present plate also has a pattern of well-preserved sensory system. Having a sensory system on ventral side could be helpful for a bottom dwelling animal to sense the bottom. It is known that *Drepanaspis* had sensory lines on the ventral shield (Gross, 1963). This means that the presence of a sensory system is not contradictory to the suggestion that the material represents a ventral plate. Among the species of *Psammolepis*, the sensory system is previously known only in a dorsal plate of *P. undulata*. A similarity between the dorsal and ventral sensory systems could be expected, based on example of *Drepanaspis* (Figure 3).

A closer examination in low light conditions revealed a faint pattern of tesserae. This pattern enabled to locate the growth centre and revealed the orientation of the plate. The growth centre in a ventral plate of *Psammolepis* is located in the anterior part (Obruchev & Mark-Kurik, 1965). In the new specimen the growth centre was located in the anterior part as well.

A similar plate of *Psammolepis venyukovi* (GIT 166-216, figure 21) has different shape of the growth centre. This suggests that shape of the plate changed during ontogeny. Another specimen (GIT 116-230, *Psammolepis undulata*) shows that the adult dorsal plate was covered with tesserae (Figure 22). The specimen (GIT 116-231, *Psammolepis undulata*) shows a lateral line system that is almost identical to that in new specimen (Mark-Kurik, 1965), a similar plate thickness and similar faint outline of tesserae (compare to Figure 23). The similarity increases due to the fact that the particular specimen seems to lack upper layer of tubercles as well. There are several examples that tubercles in *P. undulata* can easily be removed in course of transportation and burial.



Figure 21.

A ventral plate of *Psammolepis venyukovi* (GIT 116-216), with well-expressed growth centre.





Figure 22.

An adult dorsal plate of *Psammolepis undulata* (GIT 116-230) with a distinct pattern of tesserae.



Figure 23.

A juvenile dorsal plate of *Psammolepis undulata* (GIT 116-231) lacking visible pattern of tesserae. The sensory system is well observable.

Heintz (1957, p.158) mentions that the dorsal and ventral shields do not come into direct contact with other body plates, such as branchial plates. They are separated by zones of minute tesserae that surrounded the larger plates and became gradually merged into the shield while new plates probably grew in the zone between the larger body plates.

The new specimen shows that the whole upper layer of tubercles is absent, apparently due to heavy wear. In a living specimen, this would result in development of secondary dentine – pleromin – filling in cavities in the spongy tissue (spongiosa; Mark Kurik, 1984). However, the specimen reveals no indication of pleromin tissue and this suggests that abrasion took part after death of the animal. Based on this evidence, the new specimen most likely represents a dorsal shield.

Various species of the genus *Psammolepis* are known in the Gauja Formation. *P. paradoxa*, *P. alata*, *P. venyukovi* and *P. undulata* have been recorded but the latter is reported only from Latvia (Mark-Kurik, 2000). Identification of the new specimen is based on the comparison of shape of the plate, tesserae and lateral lines with those in the species previously known in the Gauja

Formation (Table 1). The Table 1 does not contain *P. toriensis* Mark-Kurik, 1965 that is much older and *P. abavica* Mark-Kurik, 1965 that always bears a strong ornamentation.

Table 1. Comparison of species of *Psammolepis* known in the Gauja Formation. The best fit with the new specimen is indicated in bold.

Species	<i>Psammolepis undulata</i>	<i>Psammolepis venyukovi</i>	<i>Psammolepis alata</i>	<i>Psammolepis paradoxa</i>
Formation	Gauja, Amata	Gauja	Gauja	Gauja
Tesserae	<b>dorsal plate covered with tesserae, peripheral zone without tesserae</b>	covers entire plate, except growth centre	posterior half has a faint outline of tesserae	covers entire dorsal plate, except growth centre
Sensory system	<b>two median dorsal canals and three transverse commissures</b>	unknown	unknown	unknown
Dorsal plate	flat, bottle-shaped, sometimes <b>no ornamentation left</b>	flat, round in outline.	unknown	fairly round in outline, flat
ventral plate	unknown	unknown	long and narrow, convex bend anteriorly, flattens out posteriorly.	<b>oval, convex bend anteriorly, flattens out posteriorly</b>
growth centre	<b>anterior half of the plate</b>	anterior third of the plate	Anterior, mid-part	<b>anterior half of the plate</b>

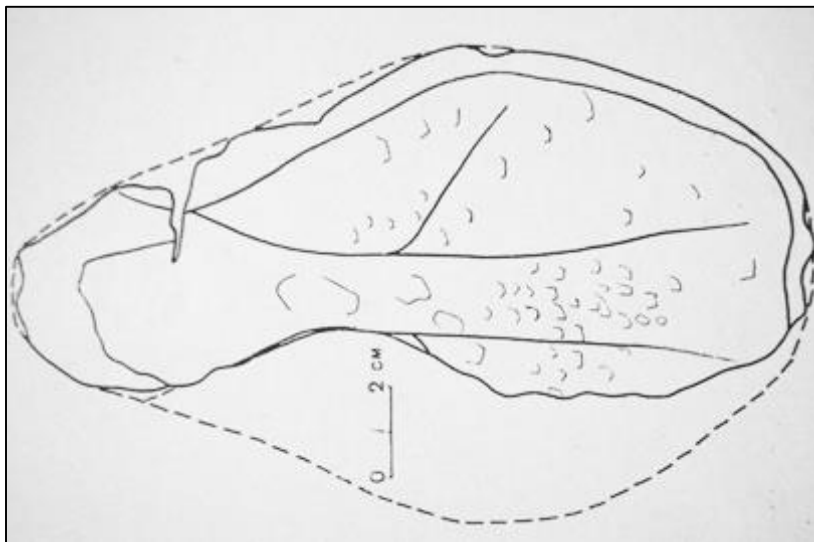


Figure 24.

A juvenile dorsal plate of *Psammolepis undulata* (from Lyarskaya 1971).

Lateral line system of the specimen described in this study closely resembles that in *Psammolepis undulata* (Figures 4B and 24). In another specimen of *P. undulata* (GIT 116-231=*Pi* 247), the commissures almost reach the lateral margins of the plate, leaving no space for lateral canals. The median canals are situated in the middle of the plate. It looks likely that the lateral canals existed in the band of tesserae between the plates.

There are also minor differences. The short parallel sections of sensory lines can be seen at the distal ends of commissures in a specimen GIT 116-231 of *P. undulata* (Elliott & Mark-Kurik, 2005; see Figures 4 and 23) but this feature could not be observed in the present specimen. However, this may also be due to the fact that the marginal parts of the plate where the parallel sensory lines may have occurred could not be assembled from the available pieces.

Visceral side of the plate is relatively smooth but bears some thickenings (Figure 25). Large area of a thickening is also observed in a dorsal plate of *P. undulata* (GIT 116-231, Figure 23, see above). This feature is likely somehow related to anatomy of *Psammolepis*. A row of small thickenings in the peripheral area of the visceral surface likely marks the previous margin of the plate and can be used for reconstructing tentatively its proportions (Figure 25)

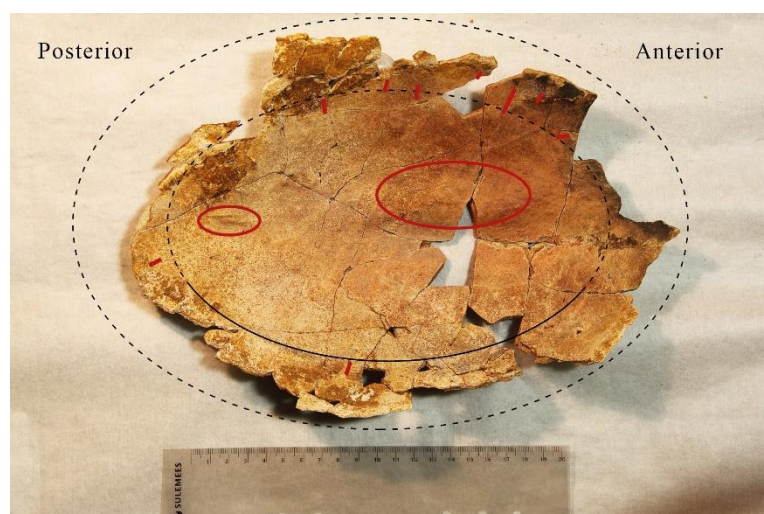


Figure 25.

Large thickened part of the shield anteriorly, another smaller one posteriorly (red ellipses). Former edge of the shield (with black line) was used to reconstruct the shape and size of the shield. Radial openings are marked with red lines.

The visceral surface of the plate displays various radial canal openings (Figure 25) and small pores that could be interpreted differently. They seem to be organized in rows pointing towards the growth centre. They could belong to the blood vessel system within the spongy layer or to the secondary sensory canal system. If the second interpretation were correct, it might mean that psammosteids had a double sensory canal system like amphiaspids (Elliott & Mark-Kurik, 2005). The amphiaspid *Siberiaspis plana* Obruchev, 1964 had a proximal sensory system developed as open grooves on the surface and the visceral system as canals within the carapace (Novitskaya, 1983). The new observations may indicate that the double sensory system could be more common than previously expected and be characteristic of at least some psammosteiformes as well.

The assembled plate may still represents a dorsal one, in spite of its remarkable convexity. A dorsal plate can also be convex like a ventral one but it does not have a posterior notch in adult specimens. The notch is lacking in the particular specimen also but this is the strong convexity of the plate that is slightly contradictory to the previous data on *P. undulata*. The remarkable convexity may be due to the specific properties of the Kalmetumägi locality. All vertebrate fossils in this locality seem to be characterized by minute deformation only. It is exemplified by the

specimen (GIT 116-212, *Psammolepis venyukovi*), which does not show deformation at all. Based on this fact, we may suggest that other findings of *P. undulata* may have been deformed (flattened) much more than the present specimen. The possible reasons of unique preservation of vertebrate fossils from the Kalmetumägi locality are unclear at the moment.

A closer examination of the small fragment with ornamentation suggests that this piece was not a part of the studied shield of *Psammolepis*. The piece displays a typical squamation pattern of the sarcopterygian *Laccognathus* Gross, 1941 (Figure 26).

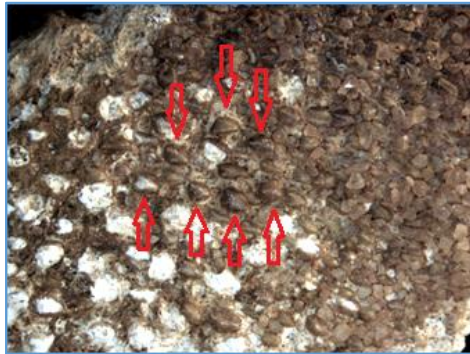


Figure 26.

Piece with *Laccognathus* ornamentation. Red arrows show tubercles.

As a summary, it is very likely that the studied material represents a dorsal plate and belongs to *P. undulata*. This decision is based on close match of the sensory systems, on the data on stratigraphic distribution of the species of *Psammolepis* in the Gauja Formation, on the lack of ornamentation and the pleromin tissue. The identification is based on a process of elimination.

#### Possible origin of bite marks and description of regeneration features

Bite marks found in the fossil were probably produced by a sarcopterygian of the genus *Laccognathus* that has the teeth of similar shape and size (Lebedev et. al, 2009; GIT 365-229). Interesting is the fact that a piece with *Laccognathus*-type of ornamentation was collected together with the fragments of the studied plate. Sarcopterygians were a widely common group of large Middle/Late Devonian predators. As the bite mark and cracks are situated in anterior part of the shield, it suggests a frontal attack. An attack from behind would be a typical hunting strategy for predators (Pihu, 2006) but other directions can be observed also.

#### Stratigraphy

The Kalmetumägi locality is one of the best known Devonian vertebrate fossil sites in Estonia. Various of species of the genus *Psammolepis* have been found there.

The Kalmetumägi locality has been referred to as an outcrop of the Gauja Formation. This looks intriguing as *P. undulata* has not been recorded before in the Gauja Stage in Estonia (Mark-Kurik, 2000). The previous records are known in the Amata Stage (one specimen, TUG 1343-6) but eleven specimens (GIT 116-225 to GIT 116-236) are known in the Gauja Stage in Latvia.

It is unclear if the Kalmetumägi section exposes the Sietiņi or the Lode Member. The fossil dealt with in the present paper was uncovered near the water level. The outcrop belt of the Amata Formation is at about 1 km distance from the current locality in the geological map (1:50 000 – Maa-amet, 2015). The altitude difference between the outcrop belt of the Amata Formation in this

location and the water level of the river is close to thickness of the Lode Member (about 20 m). This means that the border between the two members might be located close to the water level. The lower part of the upper Lode Member is described as white or light yellowish fine-grained cross-bedded sandstone with some clay and silt (Kleesment, 1995). The lower Sietņi Member has been described as yellowish-brown cross-bedded sandstones (Mark-Kurik & Põldvere, 2012). These descriptions are similar but relatively vague, differing only in the dominant colour. The Kalmetumägi outcrop has been previously described by Mark-Kurik as exposing the Sietņi Member (Mark-Kurik, 2000) but by Kleesment as a section of the Lode Member (Kleesment, 2015). The nearby Jõksi locality (GIT 108487, 71-38c) has been described by H. Viiding in his field notes from 1957 (SARV: Eesti geokogude infosüsteem ja andmerekasutamine, 2015) as exposing the Lode Member. No visible boundary can be observed in the succession but the sampling level is rather low in the section.

Another discrepancy is related to the known distribution pattern of the fish remains. In Latvia, both the Sietņi and Lode members contain vertebrate fossils, but in Estonia no vertebrate fossils are found in Lode Member (Table 2).

Table 2. Vertebrate distribution in the Gauja and Amata formations in Estonia and Latvia (based on Mark-Kurik, 2000)

Taxa	Gauja Formation				Amata Form.	
	Sietņi Member		Lode Member			
	Estonia	Latvia	Estonia	Latvia	Estonia	Latvia
<i>Psammolepis venyukovi</i>	x	x				
<i>Psammolepis heteraster</i>	x	x				
<i>Psammolepis paradoxa</i>	x	x				
<i>Psammolepis alata</i>	x	x		x		
<i>Psammolepis undulata</i>		x			x	x
<i>Laccognathus panderi</i>	x	x		x		x
<i>Psammolepis paradoxa</i>				x		

Some decline of fish diversity at the generic level can be observed in the Gauja Formation in Latvia. The Amata Formation reveals the same tendency. The species of *Psammosteus* become dominant, replacing the species of *Psammolepis*. Only *P. undulata* is still rather common in the Amata Formation, other species being relatively rare. The Amata vertebrate assemblage contains several representatives of crossopterygians (*Laccognathus*, *Panderichthys*, *Eusthenopteron*, etc.) (Mark-Kurik, 2000). *Laccognathus* has been documented also in the Kalmetumägi outcrop. A small piece of *Laccognathus* has been observed among the fossil remains also by the author (see page 24).

As the new specimen of *P. undulata* is definitely coming from the Gauja Formation, it represents the first record of this species in the Gauja Stage in Estonia. This new record makes the distribution interval of *P. undulata* more similar to that in the Devonian of Scotland and makes the Gauja Formation faunistically similar to the Nairn Sandstone in Scotland, supporting the biostratigraphic correlation of these two units (see Figure 27).



SCOTLAND			ESTONIA			
Regional stratigraphy		fishes	Formation	Member	Fishes	Stage
<b>Whitemire Beds</b>		<i>Pl.mironovi?</i>	<b>Plavinas</b>		<i>Pl.mironovi</i>	Frasnian
<b>Nairn Sandstones</b>		<i>P.undulata</i>	<b>Amata</b>		<i>P.undulata</i>	?
		<i>Laccognathus</i>	<b>Gauja</b>	Lode, Sietiņi	<i>Laccognathus</i> <i>P.undulata</i>	
<b>John o'Groats Sandstones, Eday Flagstone Formation</b>		<i>Tristichopterus</i> <i>Watsonosteus</i> <i>Microbrachius</i>	<b>Burtnieki</b>	Abava	<i>tristichopterid</i> <i>Watsonosteus</i> <i>Microbrachius</i>	
<b>Upper Caithness</b> Flagstone Group	<b>Mey Subgroup</b> <b>Rousay</b> Flagstone Formation	<i>Millerosteus</i>		Koorküla Härma		Givetian
	<b>Latheron subgroup</b> <b>Ham-Scarfskerry</b> Subgroup <b>Upper Stromness</b> Flagstones		<b>Aruküla</b>	Tarvastu Kureküla Viljandi	<i>Millerosteus</i>	
<b>Lower Caithness</b> Flagstone Group	<b>Achanarras</b> Limestone Member, <b>Sandwick</b> Fish bed	<i>Coccosteus</i> <i>Rhamphodopsis</i>	<b>Kernave</b> <b>Narva</b>		<i>Coccosteus</i> <i>Rhamphodopsis</i>	Eifelian
	<b>Robbery Head</b> Subgroup, <b>Lower Stromness</b> Flagstones	Coccosteus	<b>Leivu</b>			
			<b>Vadja</b>			
	<b>Lybster</b> Subgroup		<b>Pärnu</b>	Tori Tamme		

Figure 27. Devonian correlation between Estonia and Scotland. Two light grey zones represent mark the interval of great similarity, the darker grey zone the distribution interval of *P. undulata*. Modified from Mark-Kurik, 2012 and Mark-Kurik, 2000.

## Conclusion

This contribution summarizes various aspects related to the discovery of a *Psammolepis* in the Gauja Formation in Estonia.

The fragmentary material was identified after assembly as *Psammolepis undulata*. This identification is based on the observations and the process of elimination, as follows:

- the size and shape of the shield suggested that it is a psammosteid;
- the plate lacks pleromin and this suggests it to be a dorsal shield;
- the sensory system closely matches that of a previously known dorsal shield of *P. undulata*, with only minimal differences;
- considering the species previously known in the Gauja Formation, the other characters fit the best *P. undulata*.

A psammosteid shield with well-preserved lateral line system is very rare and fact that the current specimen has preserved an extensive system of canals makes it exceptional. This specimen also shows that the sensory system of *Psammolepis* was larger than previously thought. Features of the visceral surface suggest that *P. undulata* could have a double sensory system like amphiaspids, but these preliminary observations need further approval.

Current specimen bears a partly regenerated bite mark, likely created in course of an attack by a sarcopterygian of the genus *Laccognathus*. As the bite mark and related cracks are situated in anterior part of the plate, it suggests a frontal attack.

Vertebrate fossils in the Kalmetumägi locality are of unique preservation being only weakly deformed.

The new plate represents the first and only specimen of *P. undulata* found in the Gauja Formation in Estonia. The new record makes the distribution interval of *P. undulata* similar to that in Latvia and in the Devonian of Scotland. This supports the suggested correlation of the Gauja Formation to the Nairn Sandstone in Scotland.

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## ***Psammolepis*'e leid Gauja lademest (Eesti)**

### **Kokkuvõte**

Devoni ajastut on nimetatud kalade ajastuks. Sellel ajastul ilmus ning suri välja palju lõuatute ja kalade liike. Eestis on Devoni ladestu ning neist kihtidest pärinevad vertebraadid olnud traditsiooniliseks uurimisobjektiks. Esimeste seas kogus ja kirjeldas Eesti Devoni fossiile Hermann Martin Asmuss (1812-1859). Tänu temale ja Elga Mark-Kurikule on Eesti lõuatute ja kalade fossiilide kollektsioon üks parimaid maailmas.

Käesoleva töö materjal on kogutud 2010. aastal Kalmetumäe paljandist, mis asub Võru Maakonnas, Meremäe vallas, Piusa rahvuspargis. See on Gauja kihistu paljand, kust on leitud palju lõuatute fossiile. Käesolevas töös käsitletav psammosteidi kilp kaevati välja paljandi allosast, veepiiri lähedalt. Eksemplar oli fragmenteeritud, mis tõttu liiki esialgu määrata ei saanud. Töö eesmärgiks oli kogutud materjali identifitseerimine ning leiu geoloogilise väärtuse hindamine.

Leitud tükid jaotati gruppidesse vastavalt suurusele. Pudedam sete eemaldati tükkidelt hambaharja või hambaorgiga, tugevamalt tsementeerunud materjal rauast prepareerimisnõelaga, mida teritati regulaarselt, või siis väikese puuri abi, kasutades hambapuuri otsikuid. Tööd teostati binokulaari all. Fragmentide kokkuliimimiseks kasutati polüviinbuteraali, mis lahustati alkoholis. Liimimist alustati suurematest murdepindadest, mis sobitusid 100%, see järel liimiti tekkinud „tuuma“ külge teised tükid vastavalt sobivusele. Fotod tehti pimedas laboris Canon Eos 40D kaameraga, mikrofotod Leica DFC495 stereozoom 3D süsteemiga.

Kokkumonteeritud kilp on ovaalse kujuga. Kilbi pind on kaetud osaliselt säilinud tesseeride mustriga, kuid ornament ei ole säilinud. Kasvukese asub kilbi eesmises otsas ja on ümbritsetud tesseeridega, mis on väiksemad kui tesseerid kilbi serva-alal. Kasvujooni otseselt näha ei ole, kuid kilbi siseküljel markeerib paksendite rida kohati kilbi varasemat serva. Siseküljel on märgata radiaalselt kilbi keskosa poole suunatud kanaleid. Kilbi välisküljel oli nähtav osaliselt säilinud küljejoonekanalite süsteem: kaks pikka keskkanalit ja vähemalt kolm nendest väljuvat lühemat kanalit, mis ulatuvad plaadi säilinud osa servani. Kilbi eesosas on näha ka hammustusjälge ning sisepinnal selle regenereerumise jälgi.

Koos muu materjaliga leiti ka väike ornamenteeritud tükk, mis arvati alguses kuuluvat antud eksemplari juurde, kuid täpsemal uurimisel selgus, et see kuulub teisele isendile perekonnast *Laccognathus*, mille esindajad olid Gauja eal levinud kiskjad.

Kilbi kuju ja suurus viitavad psammosteiidile. Pleromiini pole näha, mis tähendab, et tegu on dorsaal kilbiga. Küljejoonekanalite süsteemi sarnasuse ning muude tunnuste sobivuse alusel on leid identifitseeritud kui *Psammolepis undulata* dorsaalkilp. See on liik, mida Eestis ei olnud varem Gauja lademest teada.

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### **A specimen of *Psammolepis* in the Gauja Formation (Estonia),**

supervised by Prof. Tõnu Meidla (University of Tartu) and Elga Mark-Kurik (Tallinn University of Technology)

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