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Taphonomy of the vertebrate bone beds from the Klūnas fossil site, Upper Devonian Tērvete Formation of Latvia

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Abstract. Combined sedimentological and taphonomical study of the siliciclastic sequence of the Tērvete Formation in the stratotypical area was aimed at revealing the formation of the three oryctocoenoses discovered and related structural and textural features of the deposits, as well as at detailed observation of the taphonomical peculiarities of the obtained palaeontological material. The fossil vertebrate assemblage is represented by 14 taxa comprising placoderms, acanthodians, sarcopterygians and actinopterygians. The three oryctocoenoses, first recognized in 2010, differ in the proportions of repeatedly buried material, in the number and degree of preservation of small and fragile skeletal elements, as well as in the evaluated current velocity and the transportation distance. Sedimentary concentrations of marine vertebrate remains, dominated by the antiarchs *Bothriolepis ornata* and *B. jani*, have been formed under the influence of fluvial and tidal processes in the shallow-water environment, deltaic or estuarine settings. Elongated placoderm and sarcopterygian bones are probably better indicators of the palaeoflow direction than acanthodian spines or sarcopterygian teeth.

Key words: East Baltic, fossil fish assemblage, sedimentary environment, taphonomy.

INTRODUCTION

The Middle and Upper Devonian sequences of Latvia have been well known for vertebrate fossils for about two centuries. Several publications provide information about the stratigraphic distribution of vertebrates and composition of their assemblages (Lyarskaya & Lukševičs 1992; Esin et al. 2000). Palaeoecology and taphonomy of Late Devonian fish and tetrapod assemblages of Latvia have attracted attention relatively recently (Kuršs & Lyarskaya 1973; Lyarskaya 1981; Lukševičs 1992b; Lukševičs & Zupiņš 2004; Lukševičs et al. 2011). The Klūnas fossil fish locality on the right bank of the Skujaine River corresponds to the mainly clastic deposits of the Tērvete Formation (Fm; coincides approximately with the *trachytera* and possibly *postera* conodont zones of the Standard Conodont Zonation, the Famennian Stage of the Upper Devonian), and yields a rich assemblage of fossils represented by fish, charophyte algae and vascular plant remains, as well as rare trace fossils. Devonian fishes from the outcrops along the Skujaine River were first mentioned by Toll (1893). Later Vasiliauskas (1963) provided the description of the placoderm *Phyllolepis tolli* and a list of vertebrate taxa from this locality. Since then several excavations organized by the Natural History Museum of Latvia and the University of Latvia have taken place at the Klūnas site during the time span 1983–1998, as well as in 2009 and 2010. The results of these excavations concerning the palaeoecology of the assemblage (Lukševičs 1992b) and the description of bothriolepid placoderms (Lukševičs 1986, 1992a, 2001) have been partly published. The excavations of 2009 and 2010 were aimed at detailed sedimentological and taphonomical studies and resulted in valuable palaeontological material concerning the variability of taphonomical peculiarities of the site, where three different oryctocoenoses have been discovered; sedimentological data were additionally collected in the autumn of 2011. The main aim of this article is to describe in detail the taphonomical peculiarities of the palaeontological material collected during the 2009 and 2010 excavations and related structural and textural features of the deposits of the Tērvete Fm, as well as to discuss the formation of these three oryctocoenoses.

MATERIAL AND METHODS

The Klūnas site is located in southern Latvia, Zemgale, Tērvete municipality, downstream of Klūnas on the right bank of the Skujaine River (Fig. 1). A detailed geological section of the Tērvete Fm was compiled in

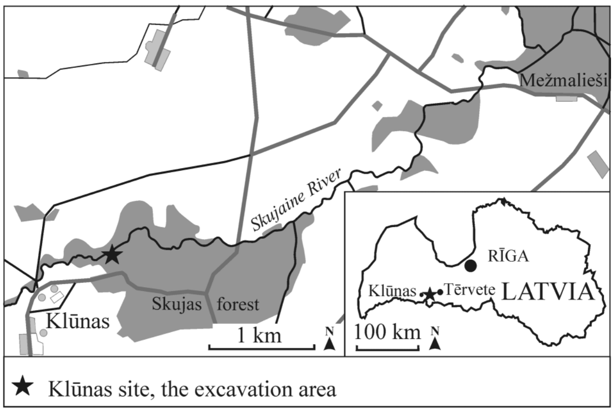

Fig. 1. Map of the vicinity of Tērvete showing the location of the Klūnas fossil site.

the northern and southern parts of the outcrop and the strata containing vertebrate remains were described in 2009 and 2011. Cross-stratification measurements were taken to compile the rose diagram of palaeocurrent directions. Because of the small size of the outcrop and post-depositional deformations only 13 measurements were made. Thirteen samples of deposits were taken. Seven samples, representing almost unconsolidated sandy material, were sieved to determine the grain size. Five samples, representing mixtures of sand, clay and carbonate material, were first dried and weighed, then processed with 5% HCl to remove and calculate carbonates, afterwards washed to remove the <0.05 mm fraction and calculate its content, and finally dried and sieved to determine the distribution of sandy fraction. All analyses were done in the Rock Processing Laboratory of the University of Latvia. The average grain size and sorting of the clastic material were calculated from the data of grain-size analysis according to the measuring method of R. Folk and W. Ward (McManus 1988). An approximate water depth that could have existed during the accumulation of sandy material in subaqueous dunes was calculated from the thickness of trough cross-beds (Leclair & Bridge 2001).

Two layers of sandstone at the Klūnas site yielded abundant vertebrate remains. Within these layers three distinct oryctocoenoses of vertebrate fossils, differing in taphonomical features, were first recognized in 2010. Almost 1500 fish fossils were found in 2009. In 2010 more than 970 vertebrate fossils were detected, whereas 722 specimens were identified to the generic/species level. Horizontal plans of the excavation area, showing the exact location of each bone, have been created during the excavations of 1990 and 2010. Material collected in previous years (1983–1998, 2009) comes mainly from the level of the 1st oryctocoenosis. All the material excavated at the Klūnas fossil site is kept at the Natural History Museum of Latvia (collection No. LDM G 100).

Selected taphonomic attributes such as size, articulation and skeletal preservation, fragmentation, azimuthal orientation and concavity ratio, as well as abrasion (edge rounding) were documented. All measurements of the taphonomic attributes were made directly at the outcrop. The number and relative abundance of taxa as well as bone sizes have been quantified. The number of identified specimens is designated as NISP. The azimuthal orientation of the bones and teeth was compared to the dip direction of the cross strata. The concavity orientation of such strongly convex skeletal elements as the dorsolateral and ventrolateral plates of placoderm fishes was taken into consideration in particular as an indicator of the hydrodynamics of the sedimentary environment. The concavity ratio was calculated as the proportion of vaulted bones lying with the convex side upwards, expressed in per cent. The articulation index Ai was calculated as the ratio between the number of all articulated skeletal element specimens and the minimum number of individuals (MNI). Hence, the disarticulation index is the expression $\mathrm{Di} = 1 - \mathrm{A}$. The representation of various skeletal elements of the placoderms *Bothriolepis ornata* and *B. jani* was calculated and the representation of fossils of different size was counted to characterize the sorting of the remains. Only fossils larger than 0.5 cm were counted; this size limit was selected to identify most of the fossil remains immediately in the field and assign them to a higher taxonomic group (genus, family or order). The specific distribution of the fossils of different size was analysed using the Student's t-test (see for example McDonald 2009, pp. 118–122) for assessing the statistical significance of the difference between two sample means.

RESULTS

Lithology

Four beds have been recognized within the section of the Tērvete Fm in the Klūnas outcrop (Fig. 2). The lower part of the section comprises at least 0.5–1.4 m thick fine-grained weakly cemented sandstone (bed 1). The lower contact of this sandstone bed was not uncovered. Sandy material is well sorted. Cross-stratification dominates, and quite often mud and mica drapes occur on the surface of the cross-strata indicating tide-influenced sedimentation. The thickness of the cross-beds is relatively small and changes from 10 to 20 cm. A layer of conglomerate composed of clay clasts and vertebrate remains is present in bed 1 in the southern

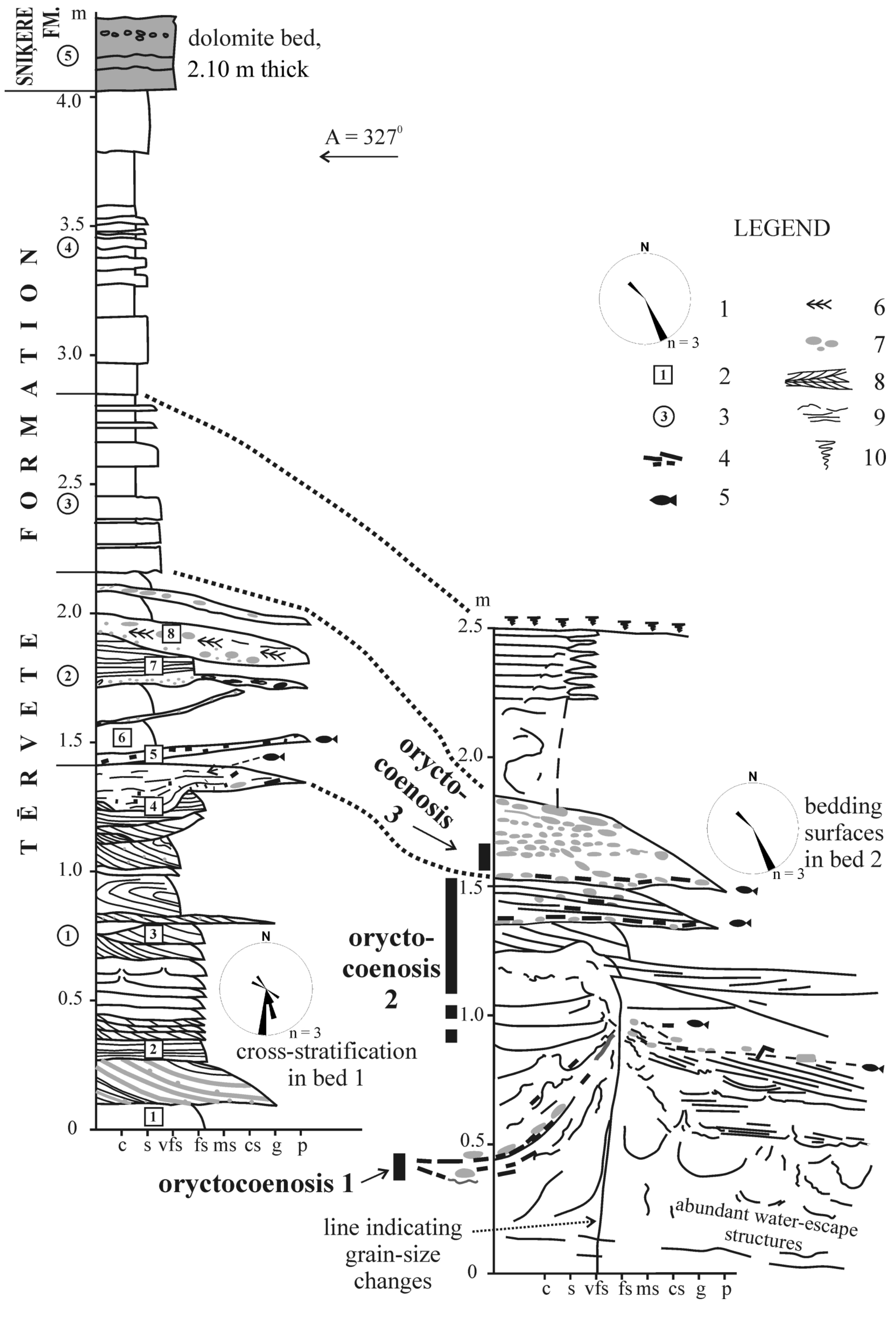

Fig. 2. Geological section of the Klūnas outcrop, Tērvete Formation. Grain size of siliciclastics: c, clay; s, silt; vfs, very fine-grained sand; fs, fine-grained sand; ms, medium-grained sand; cs, coarse-grained sand; g, gravel; p, pebbles. 1, rose diagrams, showing the cross-stratification dip azimuth for bed 1 (*n* = 10) and bedding surface dip azimuth for bed 2 (*n* = 3); 2, sampling site; 3, bed number; 4, vertebrate remains and their position; 5, intervals of the geological section where vertebrate remains have been found; 6, plant remains; 7, clay clasts; 8, cross-stratification; 9, various sedimentary structures, and post-depositional deformations; 10, talus.

part of the outcrop. According to data of previous studies, it continues in the northern direction, but likely downwards from the part of the section exposed in 2009–2011. This conglomerate layer corresponds to the 1st oryctocoenosis represented mainly by separate compactly lying bones including large and very large plates, sometimes partly articulated skeletons and aggregates of sarcopterygian scales, as well as many fragments of bones. The 1st oryctocoenosis is represented by a large lens with a maximum thickness of about 15 cm in the northern part of the outcrop (judging from previous excavations) and diminishing to some centimetres in the southern part of the outcrop. The conglomerate layer has been partially deformed in post-depositional processes. In the southern part of the outcrop the fossils are also situated parallel to the deformations, sometimes lying even vertically.

Vertebrate remains are found also above this conglomerate layer almost through the entire upper part of bed 1, but their content increases towards its top, in a cross-bed rich in clay clasts. The 2nd oryctocoenosis is associated with that part of bed 1. It contains mainly small plates, scales and their fragments, which do not form compact accumulations. Bed 1 is rich in flame and ball-and-pillow structures, however, they are most possibly related to the water-escape processes and other post-depositional deformations associated with the Pleistocene glaciations. These features hinder studies of primary sedimentary structures. The fish remains representing the 2nd oryctocoenosis lie mostly parallel to the surface of the cross-strata and thus the bones have been involved in the process of the formation of subaqueous dunes. The dip azimuth measurements of cross-stratification in bed 1 indicate that the dominant direction of the palaeocurrent was SSE (see Fig. 2).

The overlying bed 2, 0.35–0.70 m thick, is rather complicated in its structure. In the northern part of the outcrop this bed is formed by alternating conglomerate and siltstone layers. The conglomerate layers are 0.01–0.12 m thick and comprise clay and siltstone clasts included in the silty to very fine-grained sandy matrix containing plant macrofossils. Plant macrofossils are rather poorly preserved impressions of possible trimerophytes, represented by up to 50–60 mm long and 3.5 mm wide fragments of axes and lateral branches, as well as probable sporangial clusters. The siltstone layers are rather homogeneous, with mica and dolomite admixture. In the lower portion of this bed in the northern part of the outcrop even silty to sandy dolomite is found. Conglomerate beds cross-cut each other and mark the base of several erosional channels. In the southern part of the outcrop bed 2 comprises almost pure fine-grained sandstone rich in clay clasts. Here, at the bottom of bed 2 the fossils of the 3rd oryctocoenosis are found within an intraformational conglomerate. The 3rd oryctocoenosis consists of medium large bones and contains a rather large proportion of fragmented skeletal elements. Clastic material of bed 2 is moderately well sorted. Bed 2 is disturbed by Pleistocene glacial processes and possibly also recent slump processes obscuring primary structures of deposits. The dolomitic to silty parts of this bed may have been incorporated there from the overlying beds by glaciotectonic processes, but this has not been documented in detail. The bases of the erosional channels dip to the SSE and NNW, therefore the channels were probably oriented in the SWW–NEE direction; however, it is possible that the measurements do not show the precise directions due to post-depositional deformations.

Bed 3 in the northern part of the outcrop is 0.60–0.70 m thick and comprises silty clay intercalated with very fine sand and silt. To the south it contains more clay, especially in the lower part. This bed is largely disturbed as a result of the Pleistocene glacial processes and recent slumps, so it is hard to estimate its thickness and to describe the depositional structures. The clastic material of bed 3 is poorly sorted. In the northern part of the outcrop loose sandy material contains rich accumulations of charophyte gyrogonites, previously tentatively identified as belonging to the genus *Trochiliscus* (Savvaitova 1977).

Bed 4 is represented by alternation of yellow siltstone with dolomite cement and very fine-grained light-yellow loose sandstone. Vertebrate macrofossils were not found here during this study. The trace fossil *Rhizocorallium devonicum* Hecker, identified by N. Delle in 1937, and vertical and horizontal burrows within the clayey carbonate deposits most probably have been reported from bed 4 (Savvaitova 1977).

The Tērvete Fm in the Klūnas outcrop is covered by the Sniķere Fm, well exposed due to the landslide in 2010–2011. It is represented by yellowish-grey, grey and violet dolomite, at least 2.1 m thick, which is glacially dislocated in the upper part.

The uppermost part of the section is composed of Pleistocene till deposits rich in boulders, and the soil cover. The contact between Pleistocene and Devonian deposits is irregular.

Taphonomy

Taxonomic representation

The vertebrate assemblage of the Klūnas site represents all known taxa of the Spārnene Regional Stage of the Baltic Devonian (Mūri Regional Stage in Esin et al. 2000). Also, all the three oryctocoenoses under discussion have similar taxonomic composition which includes placoderms *Bothriolepis ornata* Eichwald, *B. jani* Lukševičs, *Phyllolepis tolli* Vasiliauskas, *Dunkleosteus* sp. and *Chelyophorus* sp., acanthodians *Devononchus tenuispinus* Gross and *Homacanthus sveteensis* Gross (were not found in 2009 and 2010), sarcopterygians *Holoptychius* cf. *nobilissimus* Agassiz, *Platycephalichthys skuenicus* Vorobyeva, *Cryptolepis* sp., *Glyptopomus*? sp., *Glyptolepis*? *dellei* (Gross), *Conchodus* sp. and Dipnoi gen. et sp. indet., as well as an actinopterygian Cheirolepididae gen. indet. The tooth plates of *Conchodus* sp. are known only from the 1st and the 3rd oryctocoenosis, while the remains of Dipnoi gen. et sp. indet. come from the 2nd and the 3rd oryctocoenosis.

The minimum number of individuals (MNI) for the three oryctocoenoses counted from the material of 2009 and 2010 totals 126, despite the great number of identified specimens (Table 1). This may be due to the dominance of sarcopterygian scales and teeth or fragmentary remains. Summarizing all data of 2009 and 2010, the skeletal elements of *Holoptychius* cf. *nobilissimus* dominate the assemblage, forming about one third of all identified remains (Tables 2, 3), while placoderms *Bothriolepis jani*, *B. ornata* and acanthodian *Devononchus tenuispinus* dominate by the MNI, which was estimated by count of the maximum number of identical skeletal elements among all macroscopic fossils, including acanthodian spines.

Bothriolepis ornata dominates the 1st and the 3rd oryctocoenosis (35.3% and 31.3% of all individuals), while the 2nd one is dominated by *B. jani* (21.1%). The MNI of *Phyllolepis tolli* and *Devononchus tenuispinus* (see Tables 2, 3) is only slightly smaller than that of the antiarch placoderms (*Bothriolepis*), whereas other taxa, constituted by *Dunkleosteus*, *Chelyophorus* and sarcopterygians, are represented by minor MNI, but the actual number of remains varies greatly from only one specimen of *Dunkleosteus* sp. to 745 for *Holoptychius* cf. *nobilissimus*. The comparison of all three studied oryctocoenoses by the number of identified specimens (NISP) shows absolute dominance of *H.* cf. *nobilissimus* remains, mainly constituted by scales and teeth, in the 1st and the 2nd oryctocoenosis, as well as the Klūnas site on the whole. The 1st oryctocoenosis is characterized by the dominance of the remains of *H.* cf. *nobilissimus*, *B. ornata* and *Ph. tolli* with the sum of the respective NISPs equal to 86.8%; the 2nd oryctocoenosis is dominated by *H.* cf. *nobilissimus*, *B. ornata* and *D. tenuispinus* forming 74% of all the NISPs; similarly to the 1st oryctocoenosis, the 3rd oryctocoenosis shows dominance of the remains of *B. ornata*, *H.* cf. *nobilissimus* and *Ph. tolli*, but with a smaller sum of the respective NISPs reaching only 66%. *Chelyophorus* has been found only in the 2nd oryctocoenosis; the 2nd oryctocoenosis also differs from both the 1st and the 3rd oryctocoenosis in the smaller proportion of the remains of *Platycephalichthys skuenicus* (see Tables 2, 3) and the larger proportion of spines of *D. tenuispinus* and scales and bones of *Cryptolepis* sp. The 1st and the 3rd oryctocoenosis demonstrate resemblance in the large proportion of the remains of *B. ornata* and *P. skuenicus*, and the smaller proportion of *Cryptolepis* sp. and *Glyptopomus*? sp., but differs in the smaller proportions of plates of *B. jani* in the 1st oryctocoenosis and smaller proportions of *Ph. tolli* in the 3rd oryctocoenosis. The most significant feature which reflects the differences between the three oryctocoenoses is the ratio of NISP *B. ornata*/NISP *B. jani*, which varies between 17.1 in the 1st, 8.2 in the 3rd and 4.9 in the 2nd oryctocoenosis, whereas the same ratio counted for the MNI (MNI *B. ornata*/MNI *B. jani*), changes from 0.74 for the 2nd to 2.5 for the 3rd and 6.0 for the 1st oryctocoenosis. These differences are clearly related to the size of skeletal remains of these two species: *B. ornata* is a rather large fish, while *B. jani* is one of the smallest representatives of this genus.

Table 1. Basic taphonomical data gained in 2009 and 2010 at the Klūnas site. NISP, number of identified specimens; MNI, minimum number of individuals

	2009	2010		
	The Klūnas oryctocoenosis*	1st oryctocoenosis	2nd oryctocoenosis	3rd oryctocoenosis
Number of taxa	12	10	12	10
NISP	1416	337	327	168
MNI	89	18	19	16
Convex-up, %	72	54.7	71.3	83.7
Abrasion, %	–	32.1	29.4	29.8
Disarticulation, %	91	56	100	94

* Not subdivided.

Table 2. Comparison of the oryctocoenoses by the number of identified specimens (NISP) and the minimum number of individuals (MNI)

Taxon	2009		2010						2009 and 2010 in total	
			1st oryctocoenosis		2nd oryctocoenosis		3rd oryctocoenosis			
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Bothriolepis ornata	288	21	103	6	93	3	75	5	559	28
Bothriolepis jani	216	35	6	1	19	4	9	2	250	41
Phyllolepis tolli	51	2	46	2	22	1	12	2	131	3
Dunkleosteus sp.	1	1	0	0	0	0	0	0	1	1
Chelyophorus sp.	3	1	0	0	1	1	0	0	4	2
Devononchus tenuispinus (spines)	176	18	11	2	27	3	4	1	218	24
Holoptychius cf. *nobilissimus*	458	2	141	1	122	1	24	1	745	5
Platycephalichthys skuenicus	11	1	7	1	3	1	7	1	28	3
Cryptolepis sp.	131	1	13	1	26	1	33	1	203	4
Glyptopomus? sp.	18	1	4	1	9	1	2	1	33	3
Glyptolepis? *dellei*	14	1	2	1	1	1	0	0	17	3
‘*Conchodus*’ sp.	0	0	1	1	1	1	1	1	3	3
Dipnoi indet.	45	3	0	0	3	1	1	1	49	5
Cheirolepididae indet.	4	1	0	0	0	0	0	0	4	1
Total	1416	88	334	17	327	19	168	16	2245	126

Table 3. Comparison of the oryctocoenoses by the number of identified specimens, NISP (%) and the minimum number of individuals, MNI (%)

Taxon	2009		2010						2009 and 2010 in total	
			1st oryctocoenosis		2nd oryctocoenosis		3rd oryctocoenosis			
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Bothriolepis ornata	20.3	23.9	30.8	35.3	28.4	15.8	44.6	31.3	24.9	22.2
Bothriolepis jani	15.3	39.8	1.8	5.9	5.8	21.1	5.4	12.5	11.1	32.5
Phyllolepis tolli	3.6	2.3	13.8	11.8	6.7	5.3	7.1	12.5	5.8	2.4
Dunkleosteus sp.	0.1	1.1	0	0	0	0	0	0	0.04	0.8
Chelyophorus sp.	0.2	1.1	0	0	0.3	5.3	0	0	0.2	1.6
Devononchus tenuispinus (spines)	12.4	20.5	3.3	11.8	8.3	15.8	2.4	6.3	9.7	19.0
Holoptychius cf. *nobilissimus*	32.3	2.3	42.2	5.9	37.3	5.3	14.3	6.3	33.2	4.0
Platycephalichthys skuenicus	0.8	1.1	2.1	5.9	0.9	5.3	4.2	6.3	1.2	2.4
Cryptolepis sp.	9.3	1.1	3.9	5.9	8.0	5.3	2.0	6.3	9.0	3.2
Glyptopomus? sp.	1.3	1.1	1.2	5.9	2.8	5.3	1.2	6.3	1.5	2.4
Glyptolepis? *dellei*	1.0	1.1	0.6	5.9	0.3	5.3	0	0	0.8	2.4
‘*Conchodus*’ sp.	0	0	0.3	5.9	0.3	5.3	0.6	6.3	0.1	2.4
Dipnoi indet.	3.2	3.4	0	0	0.9	5.3	0.6	6.3	2.2	4.0
Cheirolepididae indet.	0.3	1.1	0	0	0	0	0	0	0.2	0.8

Size-specific distribution

Size-specific distribution has been evaluated only for the material of 2010 (Fig. 3). The longest bone from the Klūnas site collected in 2010 is the posterior ventrolateral (PVL) plate of *B. ornata* reaching 154 mm in length. The best sorting by size is demonstrated by the fossils of the 2nd oryctocoenosis, where the maximum length of bones reaches 56 mm, but 75% of all bones fit within the 1–24 mm range. The 1st oryctocoenosis shows a slightly poorer sorting, 75% of all bones are 1–36 mm long, and reach the maximum length of 138 mm.

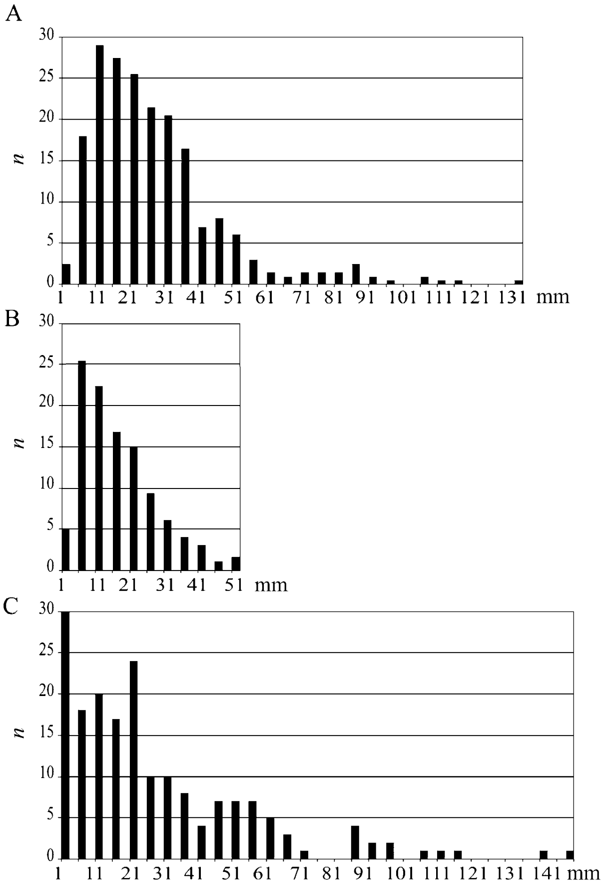

Fig. 3. Size-specific distribution of the fish fossils from the Klūnas site, according to data of excavations of 2010. **A**, the 1st oryctocoenosis; **B**, the 2nd oryctocoenosis; **C**, the 3rd oryctocoenosis; *n*, the number of specimens.

Within the 3rd oryctocoenosis 75% of all bones are 1–39 mm long, the maximum length being 154 mm. The specific distribution of the fossils of different size has been analysed using the Student's t-test. The analysis shows that the 1st and the 2nd, and the 2nd and the 3rd oryctocoenosis significantly differ in size distribution, while the difference between the 1st and the 3rd oryctocoenosis is statistically insignificant.

Disarticulation of skeletons

Vertebrate remains at the Klūnas site are represented in general by completely disarticulated placoderm plates and plate fragments, sarcopterygian scales and teeth, rarely bones of the head and shoulder girdle, and acanthodian spines and scales. Some articulated placoderm skeletal elements are known from the 1st and the 3rd oryctocoenosis, two specimens consisting of several scales of *Holoptychius* in partial articulation, as well as articulated lower jaws of *Holoptychius* and *Platycephalichthys*, while only separate bones are present in the 2nd oryctocoenosis. Among placoderm remains there are some distal segments of the pectoral fin and incomplete head shields of *B. ornata*, as well as a part of the trunk armour of *B. ornata* including anterior median dorsal (AMD), posterior median dorsal (PMD) and both mixilateral (MxL) plates. The disarticulation index for the whole Klūnas site is very high, exceeding 90%.

Taking all macroscopic remains into account, the articulation index in the 1st oryctocoenosis is the highest, reaching 44%, and the same index counted for the head shields of *B. ornata* reaches 50%. The articulation index for the distal segments of the pectoral fin of *B. ornata* in this oryctocoenosis is 17%. In the 3rd oryctocoenosis the articulation index for the head shields of *B. ornata* is 20%, while for all macroscopic remains this index is only 6%. Thus, *B. ornata* head shields at the Klūnas site are the most resistant against disarticulation, similarly to what has been shown for *B. maxima* from the Langsēde site (Lukševičs et al. 2011) and the antiarch placoderm *Asterolepis ornata*, demonstrating head shields with plates tightly connected long after disintegration of the trunk shield (Upeniece 1999).

Representation of skeletal elements

Analysis of the representation of skeletal elements is possible only for two species of placoderm fishes found in the material from the excavations of 2009 and 2010 by numerous individuals, namely *B. ornata* and *B. jani*, with the MNI 28 and 41, respectively (Table 4). The comparison of representation of various skeletal elements of these two species shows that the remains of the smaller fish, *B. jani*, are much better sorted than those of the larger species, *B. ornata*. Almost all plates of the trunk shield of *B. ornata* are well represented, except the median ventral (MV) plate, almost flat and relatively thin bone. Surprisingly well are represented also such bones of the head shield as nuchal (Nu), lateral (La) and premedian (Prm) plates, and even complete head shields form 21.4% of the expected number of the heads (which should be 28 according to the MNI). Only slightly vaulted AMD and PMD plates of *B. jani* are well represented among the trunk shield plates, similarly to *B. ornata*, whereas strongly vaulted plates with lateral walls, anterior dorsolateral (ADL), anterior ventro-lateral (AVL), MxL and PVL are underrepresented. Only one complete head shield has been found; MV, paranuchal (Pn), postpineal (Pp), pineal (Pi) and postmarginal (Pmg) plates of *B. jani* have not been found in the material collected in 2009 and 2010, thus the plates of the head shield are strongly underrepresented.

Table 4. The representation of some skeletal elements belonging to *Bothriolepis ornata* and *B. jani*, based on material of 2009 and 2010

Plate	*Bothriolepis ornata*			*Bothriolepis jani*		
	Number of specimens		Representation of bones, %	Number of specimens		Representation of bones, %
	Total	Expected number		Total	Expected number	
AMD	23	28	82.1	41	41	100.0
PMD	28	28	100.0	24	41	58.5
AVL	31	56	55.4	20	82	24.4
PVL	27	56	48.2	24	82	29.3
Nu	16	28	57.1	8	41	19.5
MxL	23	56	41.1	18	82	22.0
ADL	22	56	39.3	13	82	15.9
La	26	28	46.4	5	41	12.2
Prm	12	28	42.9	2	41	4.9
Head shield	6	28	21.4	1	41	2.4
MV	2	28	7.1	0	41	0

Detailed analysis of the representation of skeletal elements of *B. ornata* and *B. jani* from the three compared oryctocoenoses is impossible due to the small MNIs of the respective species. Nevertheless, some trends could be traced. For instance, *B. ornata* is better represented in the 1st and the 3rd oryctocoenosis than *B. jani*. Although the MNI of *B. jani* is the same as the MNI of *B. ornata* in the 2nd oryctocoenosis, the remains of *B. jani* are rather well sorted and many plates are absent from here.

Phyllolepis tolli in comparison with bothriolepid placoderms is represented rather poorly by six spinal plates, two ADL plates, a single AVL, PVL and Pn plate, as well as abundant indeterminable fragments. The MNI in the species is only 3, which is rather low taking into account more than 120 fragments identified as belonging to this species. Other placoderms are known from minor fragmentary findings, but acanthodian macroremains are represented by spines alone.

No sharp differences were observed between the three oryctocoenoses in the representation of sarcopterygian skeletal elements. Sarcopterygian remains mainly comprise scales, teeth or tooth plates, rarely separate skull bones or bones of the shoulder girdle, as well as two partial lower jaws belonging to *Holoptychius* cf. *nobilissimus*.

Breakage and abrasion of bones

One of the main characteristics of the Klūnas fossil site is the great amount of fragmentary remains several times exceeding the number of intact bones, which in the material of 2010 reaches only 132 bones out of 733 analysed specimens. The proportion of complete, intact bones varies from 10.1% in the 1st oryctocoenosis to 21.7% in the 2nd and 29.5% in the 3rd oryctocoenosis. The 1st oryctocoenosis is characterized by a relatively low number of intact or almost complete bones which lost less than 10% of their full size (about 24% of all analysed specimens), a relatively high proportion of bones that preserved about one half of their full size (8.9%), and many small fragments (18.1%) forming less than 10% of the intact bone each (35.9% belong to the fragments forming less than 25% of the skeletal element, Fig. 4). The 2nd oryctocoenosis differs from the 1st oryctocoenosis in a higher proportion of intact bones, reaching 21.7% and even 27.4% if including almost complete bones which lost less than 10% of their volume. On the other hand, contrary to the 1st oryctocoenosis, the proportion of bones broken into

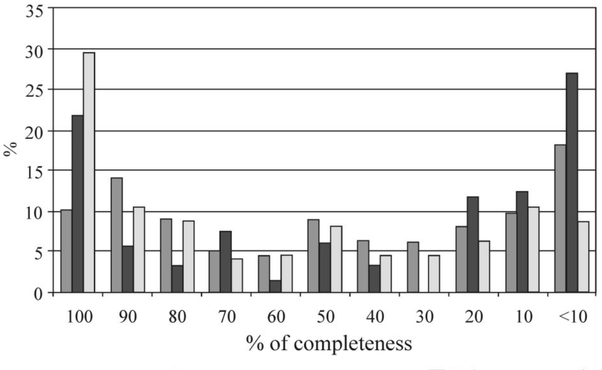

Fig. 4. Proportions of intact and broken skeletal elements from the three oryctocoenoses, Klūnas site, according to data of excavations of 2010.

large parts is much smaller, while the number of small fragments is the highest among all compared oryctocoenoses, reaching 26.9% for fragments forming less than 10% of the intact bone and 50.9% for the fragments forming less than 25% of the respective skeletal element. The 3rd oryctocoenosis differs from the other two in the higher proportion of intact bones (29.5%) and almost complete bones that lost less than 10% of their full size (10.4%), and the smallest number of very small fragments (only 8.7% are fragments forming less than 10% of the intact bone).

In the material collected in 2009 none of the plates of the articulated specimen of the dorsal armour of *B. ornata* (AMD, PMD and both MxL, collection number LDM G 100/542) is complete. Within the range of variously preserved bones of the head shield (collection number LDM G 100/543) only Pmg and Pn are intact, while Nu is preserved only by 60% and La by 40%.

Behrensmeyer (1990) reported that weathered bones are more vulnerable to abrasion and breakage during the fluvial transportation than fresh bones, and roundness of edges of the bones is an important indicator of re-deposition of fossils. The Klūnas site on the whole contains 71% of bones with almost intact, well-preserved margins; in 21% the edges are slightly rounded and 8% of those are heavily rounded. Fossils with rounded edges might have been abraded and re-deposited, while the elements with intact, well-preserved edges have never been reworked.

Orientation of skeletal elements

The horizontal distribution of bones over the studied area is not homogeneous. Distinct zones of increased or decreased density of fossils can be traced (Fig. 5). Zones of increased density usually contain many elements of various sizes, whereas zones of decreased density might be subdivided into two types: (1) containing a limited number of large bones and (2) containing scattered relatively small scales or fragments. The shape and size of zones of increased density of fossils slightly resemble those of subaqueous dunes, but this observation needs to be proved on a larger exposed area. The highest concavity ratio is characteristic of the 3rd oryctocoenosis where 83.7% of all bones are found in the convex-up position. The concavity ratio is 71.3% for the 2nd oryctocoenosis and the smallest for the 1st oryctocoenosis, reaching only 54.7%. The measurements of azimuthal orientation made in 2009 and 2010 demonstrate two prevailing directions for the acanthodian spines ($n = 115$): NNW–SSE and NE–SW, with the mean maximum almost coinciding with the N–S direction (Fig. 5D; note that the diagram shows bidirectional distribution). Sarcopterygian teeth ($n = 38$) are oriented by their tips mostly from north to south or in the opposite direction, and to the WSW; however, the mean vector is directed to the NW (Fig. 5E). This could be explained by orientation of the teeth mainly by their tips against the dominant flow direction. Elongated bones of placoderms and sarcopterygians with the length/width ratio larger than 3 (e.g., plates of the pectoral fin of *Bothriolepis*, complete distal segment of the pectoral fin, fragments of cleithra of *Holoptychius*, etc.; $n = 33$) also show two dominant directions: almost directly to the south and perpendicular to that, almost exactly to the east, with the mean maximum only slightly deviating to the west from the south direction (Fig. 5F). Sum of all measurements ($n = 186$) clearly demonstrates the dominant orientation exactly to the south (Fig. 5G). Measurements of the dip azimuth of the cross-stratification indicate that the palaeostream has flown to the SSE.

DISCUSSION

The stratigraphical position, distribution, correlation and age of the Tērvete Fm in the Baltic are debatable. The Tērvete Fm was established by L. Savvaitova in 1967 (Savvaitova 1977) by separation of sandy deposits of the lower part of the Svēte Fm. The Svēte Fm has been described by Liepiņš (1959) as being located between sandstones of the Mūri Fm below and dolostones of the Žagare Fm above. Later the new name of the Sniķere Fm was given for the remaining, upper part of the Svēte Fm, since the name Svēte appeared to be used for the other unit (Savvaitova 1981). The specific structure and composition of the middle Famennian mainly clastic deposits have been used as a base for treating the Mūri Fm as the Mūri Regional Stage (RS; Savvaitova 1977, 1981); the Tērvete Fm has been separated either as corresponding to the specific age of the Tērvete RS (Savvaitova 1977), or united together with the Sniķere Fm into the Švėtė RS (Savvaitova 1981), or united together with the Mūri Fm into the expanded Mūri RS (Gailīte et al. 2000). The Tērvete and the Sniķere Fms of Latvia correspond to the Švėtė Fm in Lithuania (Žeiba 1981). A similar composition of vertebrate assemblages, restricted distribution of typical deposits of the Tērvete Fm, rather similar composition of sandy deposits of the Mūri and Tērvete Fms and the cyclic structure of the section lead to the conclusion that L. Savvaitova was correct in merging these two lithostratigraphical units into one regional stage. Since the name Mūri RS is used for the regional stage corresponding to the Mūri Fm alone, the name Spārnene RS was proposed by L. Savvaitova (Lukševičs et al. 1999) for this regional stage corresponding to the Mūri and Tērvete Fms, as well as the

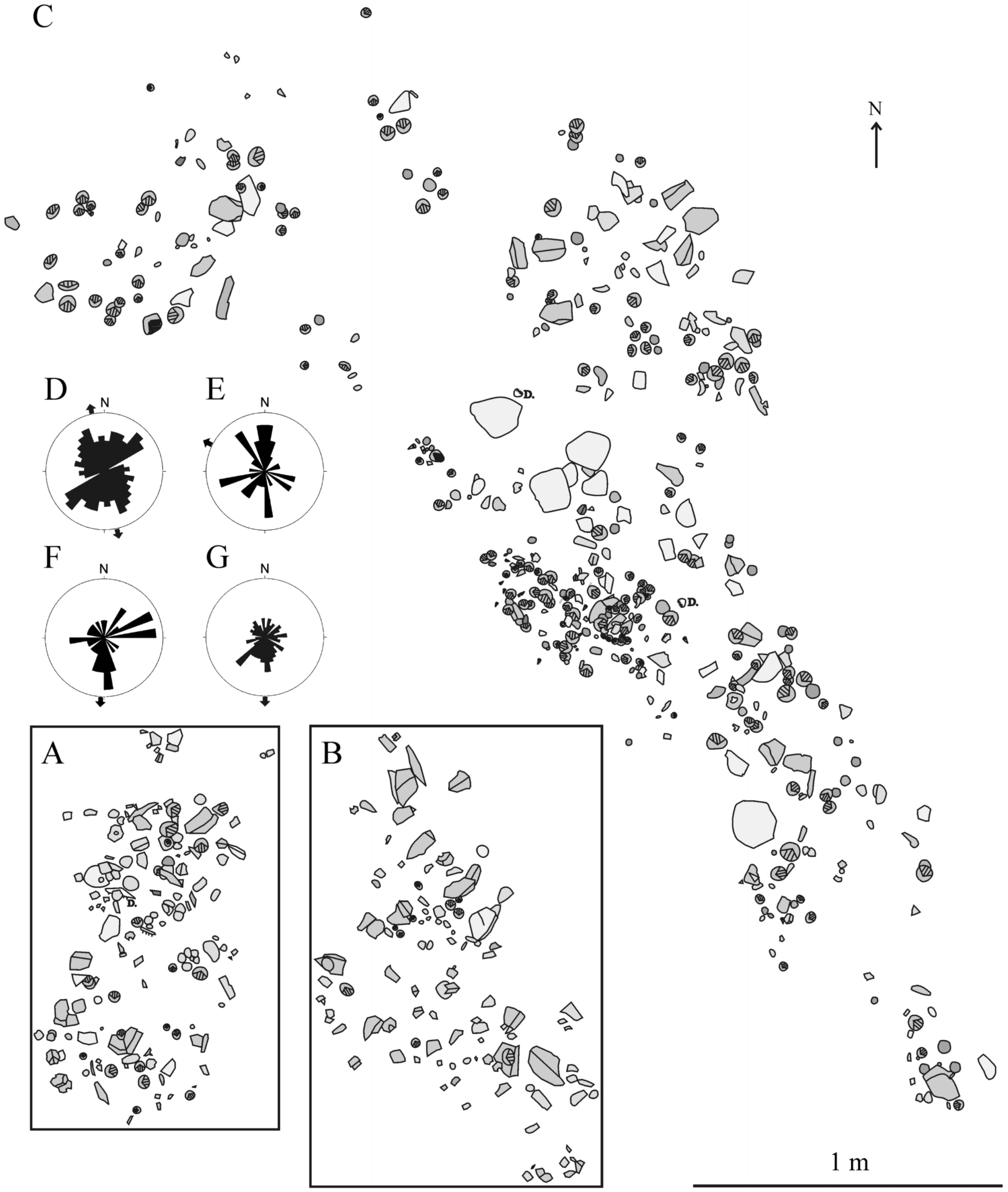

Fig. 5. Horizontal plan and rose diagrams, illustrating orientation of fossils at the Klūnas site (measurements of azimuthal orientation made in 2009 and 2010). **A**, the 1st oryctocoenosis; **B**, the 3rd oryctocoenosis; **C**, bone bed corresponding to the 1st oryctocoenosis, according to the data of excavations of 1990. Rose diagrams show the orientation of: **D**, acanthodian spines (*n* = 115); **E**, sarcopterygian teeth (*n* = 38); **F**, elongated bones of placoderms and sarcopterygians with the length/width ratio larger than 3 (*n* = 33); **G**, sum of all measurements (*n* = 186).

lower part of the Šventė Fm. Unfortunately, conodonts are still poorly known from the interval under discussion and correlation with the Standard Conodont Zonation still remains unclear. Only the restricted assemblage from the Šventė Fm in Lithuania allows correlation of the Sniķere Fm with the *postera* Zone (Middle–Lower *styriacus* Zones of the previous conodont zonation; Žeiba & Valiukevičius 1972).

The deposits of the Tērvete Fm, comprising weakly cemented sandstone and sand intercalated with dolomitic marls, siltstone and clay, containing a relatively low-diversity assemblage of fish, charophytes and rare trace fossils determined by Delle (1937) as *Rhizocorallium devonicum*, have been traditionally interpreted as having formed in a shallow, rather restricted sea of lowered salinity (Savvaitova 1998). However, no direct indications of lowered salinity have ever been reported. Accumulations of charophyte calcified oospheres, the gyrogonites, were previously usually interpreted as indicators of lowered salinity, however, many charophyte species from the Devonian sections have been found to be associated with typical marine assemblages, showing that the first representatives of the Charophyta were adapted to a wider variety of sedimentary environments than their modern relatives (Georgescu & Braun 2006). *Rhizocorallium*, a horizontally or obliquely oriented, U-shaped burrow with spreite between the limbs of the U, is usually interpreted as fodinichnia, a feeding burrow where the animal moved horizontally through the sediment in a systematic feeding pattern, and corresponds to the *Glossifungites* ichnofacies related to the erosion surfaces on semi-consolidated mud, which suspension feeders dug shelters into (Seilacher 1967). The study of the environmental significance of the trace fossil *Rhizocorallium* from the Lower Triassic of Spitsbergen demonstrated that these burrows are generally found associated with storm-generated siltstone and sandstone beds of the shoreface zone (Worsley & Mørk 2001). Sedimentological analysis of the geological section at the Klūnas site shows that the deposits have formed under the influence of fluvial and tidal processes. During the formation of bed 1 the sand was accumulated in subaqueous dunes, which migrated downstream in a southerly direction. Erosional channels marked by conglomerate containing clay clasts and vertebrate remains developed in at least two episodes. The conglomerate of bed 2, also composed of clay clasts and fish bones, marks the base of a larger erosional channel, which seems to have been filled with clayey material of bed 3. The water depth during the formation of bed 1 was approximately 2.5–4 m as calculated from the thickness of the sandstone cross-beds. The influence of tidal processes on sedimentation is identified by mud and mica drapes on the cross-strata of the sandstone of bed 1 and obviously also by sandy and silty intercalations in clayey deposits of bed 3. The remains of the land plants (possibly trimerophytes), being of low density and high buoyancy, were most probably floated into the basin by the river and hence transported over a longer distance than fish bones. Plant tissue of all types sinks only after it becomes waterlogged; agitation of the water, e.g. by storm, may increase the rate of waterlogging (Nichols 1999). The occurrence of plant macrofossils in the same bed with trace fossils suggests the role of storms in the accumulation of plant remains in a shallow-water environment, but detailed studies are needed to understand the hydrodynamic behaviour of plant debris. The indications of tidal processes suggest that these deposits are not alluvial and have formed in deltaic or estuarine settings. The occurrence of plant macrofossils, charophyte gyrogonites and trace fossils in these deposits does not contradict this suggestion. More detailed sedimentological interpretation of the Tērvete Fm in the Klūnas outcrop is problematic due to considerable post-depositional deformations. The features like water-escape structures, disrupted bedding and sharp changes in layer surface orientation in bed 1, irregular layering in bed 2 and considerable folding in bed 3 are most probably related to Pleistocene glacial processes. These processes have influenced also the overlying dolomites of the Sniķere Fm. Even the thickness and inclination of individual beds as well as the character of their contacts have obviously been changed by these processes. The influence of recent slump processes is not excluded as well.

Analysis of similarities and differences between the three studied oryctocoenoses demonstrates that these are all sedimentological concentrations and have to be assessed as allochthonous assemblages differing in various taphonomical attributes starting from the geometry of a fossil deposit. Still, judging from the short distance of transportation and good preservation of vertebrate fossils, most probably all fishes represented in the studied oryctocoenoses lived in the same environment where their remains have been buried. Thus the deltaic and/or estuarine environment was favourable for burial, but also appropriate for the existence of Devonian vertebrates. The 1st and the 2nd oryctocoenosis are three-dimensional deposits differing in a much greater thickness of the fossil-bearing lens in the case of the 2nd oryctocoenosis, while the 3rd oryctocoenosis looks like a typical two-dimensional deposit of pavement type (Martin 1999), which usually forms in the channels. However, the similarity of the taxonomic composition and NISP, as well as many other taphonomical features including size-specific distribution, representation of various skeletal elements, orientation and sorting, make the 1st and the 3rd oryctocoenosis more similar to each other than to the 2nd oryctocoenosis. Differences in taxonomic representation such as the ratio NISP *B. ornata*/NISP *B. jani*, ratio MNI *B. ornata*/MNI *B. jani* and the presence of the placoderm *Chelyophorus* only in the 2nd oryctocoenosis could have the same reason, namely the small size of *B. jani* and *Chelyophorus*, as well as overall rarity of *Chelyophorus*.

Size-specific distribution of fossil bones shows the best sorting by size of various skeletal elements within the 2nd oryctocoenosis, which coincides with the highest proportion of taxa characterized by tiny bones (*B. jani*, *Cryptolepis* sp., *Devononchus tenuispinus*) or relatively small skeletal elements (scales of *Holoptychius*) on the one hand, and total disarticulation of skeletons on the other hand. Comparison of representation of the skeletal elements of the two antiarch placoderm fishes shows that the same number of individuals of *B. ornata* and *B. jani* buried within the 2nd oryctocoenosis is represented by almost all skeletal elements of a larger fish *B. ornata* and only few, presumably most easily transportable elements of *B. jani*. These differences in representation of various skeletal elements of *B. ornata* and *B. jani* clearly demonstrate the significance of size and shape of the analysed bones in the sorting of the remains. A rather large fish with the dorsal length of the trunk armour reaching 230–240 mm and the length of the head shield of at least 100 mm (Lukševičs 2001), *B. ornata*, is well represented by various skeletal elements except MV and some small bones of the head armour. The other species of the same genus, *B. jani*, is a small fish with an estimated median dorsal armour length reaching only about 65 mm (Lukševičs 2001). This demonstrates rather good sorting depending on the shape of the plates: slightly vaulted AMD and PMD plates are represented in much larger quantities than the strongly vaulted trunk shield plates with two laminae. Most probably the underrepresentation of such strongly vaulted bones could be explained by the equilibrium between the velocity of the current needed to lift and transport these bones, higher velocity which may cause damage to particular elements, content of clastic particles in the flow and transportation distance. Mixture of large and small skeletal elements characteristic of the 1st and the 3rd oryctocoenosis, better representation of skeletal elements of various shapes and proportions, lower disarticulation index in comparison with the 2nd oryctocoenosis – all these features suggest weak sorting, most probably due to a shorter distance of transportation within the sediment load. Significant difference between the 1st and the 3rd oryctocoenosis in the proportion of the intact bones (10.1% and 29.5%, respectively) and different content of small fragments (many in the 1st oryctocoenosis and few in the 3rd oryctocoenosis) might suggest that skeletal elements within the 3rd oryctocoenosis have been buried in the calmest sedimentary environment or that the remains have been transported over the shortest distance. This is evidenced also by sedimentological data suggesting that the fish remains of both the 1st and 3rd oryctocoenoses accumulated on the bottom of erosional channels, but the presence of clayey material (probable channel infilling) forming bed 3 may suggest a slightly deeper sedimentary environment. The highest concavity ratio and hence the strongest convex-up orientation characteristic of the 3rd oryctocoenosis suggest a rather great influence of the water current. Therefore the most reliable explanation for the differences between the 1st and the 3rd oryctocoenosis could be a stronger current, but a much shorter distance of transportation of remains before the final burial. The concavity ratio may serve as an indicator for the energy of the water currents and for some specific depositional mechanisms or conditions: as has been shown for the mollusc shells (Clifton 1971; Seilacher 1973), concave-up is a stable position for the shells in still water, whereas the convex-up position is stable in flowing water.

Data on the fragmentation of partially articulated specimens, including the dorsal armour of *B. ornata* LDM G 100/542 and the head shield LDM G 100/543, are not easy to interpret. Most probably all mentioned skeletal elements or partial carcasses have been broken due to some predator or scavenger activity just before the final burial. The most probable large predator of that times capable of making such damage to the armour of the antiarch placoderms could be the giant euarthrodire placoderm *Dunkleosteus* or large sarcopterygian *Holoptychius*. The partly articulated squamation of *Holoptychius* could demonstrate a very fast burial of large segments of skin with attached scales without having been reworked. Contrary to these cases of fast burial, the presence of fossils with rounded margins, especially characterizing the 1st oryctocoenosis, indicates repeated burying. Summing up all taphonomical peculiarities, the degree of fragmentation, as well as the number of abraded fossils, decreases, while the number of convex-up plates and sorting degree increase upwards. Differences between the three studied oryctocoenoses are seen in (1) the admixture of repeatedly buried elements to the very fresh material, which was buried fast after relatively short transportation in a moderate-speed current, characteristic of the 1st oryctocoenosis; (2) very good sorting of completely disarticulated small and fragile, but most easily transportable skeletal elements of various fishes, suggesting lower velocity of the current, which characterizes the 2nd oryctocoenosis, and (3) transportation of the weakly sorted and better articulated skeletal elements by a strong current to a very short distance, except the rewashed elements, characteristic of the 3rd oryctocoenosis.

The azimuthal orientation of fossils is close to the dominant flow direction to the SSE, approximated by measurements of the dip of the cross beds. Elongated skeletal elements, such as acanthodian spines with the length/width ratio varying from about 10 to 17 (depending on the completeness of the spine), sarcopterygian teeth with their characteristic shape of an elongated and sometimes slightly curved cone and with the length/width ratio changing approximately from 2.1 to 5.3, and elongated bones of placoderm and sarcopterygian armour, all show about the same orientation. The main portion of bones has been oriented parallel to the main direction of flow, to the south or opposite to this direction, as demonstrated by the sarcopterygian teeth. Still, a large portion of bones has been oriented perpendicular to the main flow direction. Elongated placoderm and sarcopterygian bones show bidirectional orientation particularly well; acanthodian spines unexpectedly show much more widely dispersed directions of orientation. Differences in the degree of orientation could be most possibly explained by a particular 'behaviour' of various skeletal elements in the current. Due to a relatively higher density, acanthodian spines and sarcopterygian teeth most probably have been able to resist the current flow. It is likely that these elements have not been lifted by the current and have mostly been oriented by the current force while resting on substrate. In contrast to spines and teeth, elongated skeletal elements of placoderms and sarcopterygians most possibly have been transported by the current more easily and deposited in an oriented position, some parallel to the current, some perpendicular to it. Therefore the elongated placoderm and sarcopterygian bones might be used as better indicators of the flow direction than very elongated, but dense and thus relatively heavy acanthodian spines or sarcopterygian teeth.

Among other Upper Devonian oryctocoenoses, predominance of small (<10 cm) bones is also characteristic of the Pavāri site in western Latvia, where the upper Famennian Ketleri Fm crops out (Lukševičs & Zupiņš 2004). In comparison with the Pavāri oryctocoenosis, all three oryctocoenoses from the Klūnas site show much higher fragmentation of skeletal elements and a lower articulation index. The fish fossil bone-bed from the Langsēde site (Lukševičs et al. 2011) differs from the Klūnas oryctocoenoses in the bone size distribution, but resembles them in the degree of disarticulation. By the degree of preservation and the bone size Upper Givetian and Lower Frasnian vertebrate localities, such as the Launagiezis (Ērmaņi in Lyarskaya 1981; Gauja Formation), Ķūķi and Pastamuiža sites (Amata Formation), are much more similar to the Langsēde site than to the Klūnas or Pavāri sites.

CONCLUSIONS

Differences and similarities between the three vertebrate bone-bearing beds in the deposits of the Tērvete Fm cropping out on the right bank of the Skujaine River at the Klūnas site in south Latvia as well as extensive palaeontological material collected there are taphonomically and sedimentologically analysed. Sedimentological analysis shows that the deposits have been formed under the influence of fluvial and tidal processes in the shallow-water environment, at least partly as infilling of erosional channels, thus evidencing deltaic or estuarine settings. All three oryctocoenoses from the Klūnas fossil fish site are sedimentary concentrations and allochthonous assemblages showing various degree of mixing of repeatedly buried and very fresh, partially articulated material. Vertebrates represented in the studied oryctocoenoses most probably lived in the same deltaic or estuarine environment together with the trace makers of *Rizocorallium* and charophyte algae, whereas the remains of the land plants were floated into the basin by the river. Still, post-mortem transportation of fish carcasses from the open sea by storm or tidal currents is not excluded either. All three oryctocoenoses differ from each other. However, the 1st and the 3rd oryctocoenosis, which have been formed as vertebrate bone accumulations on the bottom of an erosional channel, have much in common contrary to the 2nd oryctocoenosis, which exemplifies the lens of fossil-bearing cross-stratified sandstone formed in subaqueous dunes. Vertebrate remains of the 3rd oryctocoenosis were transported before the final burial over the shortest distance. Elongated placoderm and sarcopterygian bones might be better indicators of the palaeoflow direction than very elongated, but dense acanthodian spines or sarcopterygian teeth.

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Ülem-Devoni Tērvete kihistu vertebraatide tafonoomia Klūnase leiukohas Lätis

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On käsitletud Ülem-Devoni Tērvete kihistu sedimentoloogiat ja vertebraadifossiilide tafonoomiat Klūnase leiukohas Lätis. On kirjeldatud kolme 2010. aastal avastatud vertebraadifossiilide kogumit (orüktotsönoosi), mis erinevad üksteisest korduvalt mattunud fossiilide osakaalu ja skeletifragmentide säilivusastme poolest, peegeldades erinevusi vee liikumiskiiruses ning materjali edasikandumise kauguses. Uuritud kooslused on esindatud 14 taksoniga, mille hulka kuulub rüükalasid, akantoode, sagaruimseid ja kiiruimseid. Vertebraadifossiilide kogumid, kus domineerivad antiarhid *Bothriolepis ornata* ja *B. jani*, on moodustunud madalaveelises estuaari- või deltakeskkonnas fluviaalsete või loode-protsesside tagajärjel. On selgitatud, et rüükalade ja sagaruimsete piklikud skeletiosised on tõenäoliselt paremad paleohoovuste suuna indikaatorid kui akantoodide ogad või kiiruimsete hambad.