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Frasnian vertebrate taphonomy and sedimentology of macrofossil concentrations from the Langsede Cliff, Latvia

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LETHAIA

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The siliciclastic sequence of the Upper Devonian of Kurzeme, Western Latvia, is renowned for abundant vertebrate fossils, including the stem tetrapods Obruchevichthys gracilis and Ventastega curonica. During the first detailed taphonomic study of the vertebrate assemblage from the Ogre Formation cropping out at the Langsede Cliff, Imula River, abundant vertebrate remains have been examined and identified as belonging to one psammosteid, two acanthodian and three sarcopterygian genera; the placoderm Bothriolepis maxima dominates the assemblage. Besides fully disarticulated placoderm and psammosteid plates, separate sarcopterygian scales and teeth, and acanthodian spines, partly articulated specimens including complete distal segments of Bothriolepis pectoral fins, Bothriolepis head shields and sarcopterygian lower jaws have been found. The size distribution of the placoderm bones demonstrates that the individuals within the assemblage are of approximately uniform age. Distinct zones have been traced within the horizontal distribution of the bones. These linear zones are almost perpendicular to the dominant dip azimuth of the cross-beds and ripple-laminae and most probably correspond to the depressions between subaqueous dunes. Concavity ratio varies significantly within the excavation area. The degree of fragmentation of the bones and disarticulation of the skeletons suggest that the carcasses were reworked and slightly transported before burial. Sedimentological data suggest deposition in a shallow marine environment under the influence of rapid currents. The fossiliferous bed consists of a basal bone conglomerate covered by a cross-stratified sandstone with mud drapes, which is in turn overlain by ripple laminated sandstone, indicating the bones were buried by the gradual infilling of a tidal channel. All the Middle-Upper Devonian vertebrate bonebeds from Latvia are associated with sandy to clayey deposits and have been formed in a sea-coastal zone during rapid sedimentation episodes, but differ in fossil abundance and degree of preservation. D Agnathans, Devonian, facies analysis, fish, fossil assemblage, 2 palaeoenvironment.

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The origin and early evolution of tetrapods are among the most significant questions about vertebrate evolution. During the last two decades, new members of the tetrapod stem group including both 'Devonian tetrapods' (i.e. forms with limbs) and 'tetrapodomorph fishes' (i.e. forms with paired fins) have been discovered in Pennsylvania (Daeschler *et al.* 1994), China (Zhu *et al.* 2002), Belgium (Clément *et al.* 2004), Arctic Canada (Daeschler *et al.* 2006; Shubin *et al.* 2006) and Russia (Lebedev 2004), whereas tetrapod tracks have been found in the lower Middle Devonian of Poland (Niedźwiedzki *et al.* 2010). These discoveries have provided a wealth of new data on the sequence of morphological changes during the fish-tetrapod transition, the timing of these evolutionary events, and their possible geographic and environmental settings.

Middle and Upper Devonian deposits of Latvia yield a number of important taxa belonging to the tetrapod stem group, including *Panderichthys* and *Livoniana* from the uppermost Middle Devonian (Vorobyeva 1962; Ahlberg & Clack 1998; Ahlberg *et al.* 2000), *Obruchevichthys* from the Frasnian (Vorobyeva 1977; Ahlberg & Clack 1998) and *Ventastega curonica* from the Upper Famennian (Ahlberg *et al.* 1994, 2008). *Panderichthys* has paired fins (e.g. Vorobyeva 1992; Boisvert *et al.* 2008), whereas *Ventastega* almost certainly had limbs judging by its pectoral and pelvic girdle morphology (Ahlberg et al. 2008). The appendages of Livoniana and Obruchevichthys are unknown, but both are phylogenetically intermediate between Panderichthys and Ventastega. Furthermore, the two lower jaw fragments that constitute the total material of Obruchevichthys gracilis Vorobyeva (Vorobyeva 1977; Ahlberg & Clack 1998) closely resemble the jaws of Elginerpeton pancheni Ahlberg from Scat (or Scaat) Craig in Scotland, which are associated with the oldest known tetrapod limb and girdle elements (Ahlberg 1991, 1995, 1998; Ahlberg & Clack 1998). The Latvian fossil record of the tetrapod stem group in the Middle to Upper Devonian thus straddles the morphological fish-tetrapod transition and has the potential to illuminate this important event in some detail.

The ecological and environmental preferences of the first tetrapods, where they originated and lived, are still debatable issues (for the summary of the discussion, see Lebedev 2004 and Blieck et al. 2007). Taphonomic studies of the vertebrate assemblages may provide valuable information on the formation of the taphocoenoses, with the possibility of using this information to make palaeoecological reconstructions. However, the taphonomy of Palaeozoic vertebrate assemblages has not been well studied. In Latvia, Lyarskaya (1971) initiated taphonomic studies of the fossil vertebrate assemblages of different ages, while later studies of the rich assemblage of fish, agnathan, plant and invertebrate remains from the Lode locality (Lode Formation, upper part of the Middle Devonian; for discussion concerning the age of the Lode Formation, see Mark-Kurik et al. 1999) added significantly to knowledge of the taphonomy of the Devonian vertebrates, including Panderichthys, within this delta front sedimentary environment (Lyarskaya 1981; Kuršs 1992; Kuršs et al. 1998, 1999; Upeniece 1999; Zupinš 2003). Lukševičs & Zupinš (2004) provided a taphonomic analysis of the late Famennian vertebrate assemblage from the Pavāri site, which yields Ventastega, concluding that the taphocoenosis formed in a shallow sea under the influence of tidal processes.

Of the two known specimens of *Obruchevichthys gracilis*, one (the holotype) comes from Latvia and was found in the Ogre Formation at Velna Ala by the river Abava. The other specimen comes from an unknown locality, probably in western Russia (Vorobyeva 1977; Ahlberg & Clack 1998). The Ogre Formation is thus of considerable interest when investigating the environmental preferences of the earliest tetrapods. The poorly fossiliferous sandstones and siltstones of the Ogre Formation, widely distributed almost over the whole of Latvia and cropping out in Kurzeme and Vidzeme, contain rare fossils of conchostracans and lingulate brachiopods, as well as a rather

diverse vertebrate assemblage (Esin et al. 2000). Gross (1933, 1942) provided the first descriptions of the vertebrate fossils from this stratigraphic level; additional taxa were described by Obruchev (Obruchev & Mark-Kurik 1965), Vorobyeva (1962), and Lyarskaya (1981, 1986). Lyarskaya & Lukševičs (1991) compiled a list of all the vertebrate taxa reported from the Ogre Formation of Latvia including the erroneously determined Obruchevia (syn. Aspidosteus), which has been recorded only from contemporaneous deposits in Russia. The Ogre Formation correlates with the Pamūšis Formation in Lithuania and Prilovat' Formation in northwestern Russia; all these lithostratigraphic units correspond to the Pamūšis Regional Stage of the Main Devonian Field (Rzhonsnitskava & Kulikova 1990) and rhenana conodont Biozone. The complete list of vertebrates from the Pamūšis Regional Stage of the Main Devonian Field (Esin et al. 2000) contains 13 vertebrate taxa.

In the early 1980s, a group of palaeontologists under the guidance of L. Lyarskaya investigated the palaeofauna from the Langsede site (Fig. 1), collecting many well-preserved disarticulated plates of Bothriolepis maxima and a lower jaw of Platycephalichthys bischoffi, as well as some other material, now kept at the Natural History Museum of Latvia. Then, for a period of more than 20 years, the interest of palaeontologists in the Devonian vertebrate remains of Latvia was focused elsewhere and it was not until the summer of 2008 that excavations were organized at the Langsede outcrop. The goal of this article is to discuss the results of the taphonomic analysis of the vertebrate assemblage from the Langsede site, which may cast light on the palaeoecological peculiarities of the agnathan, gnathostome, and basal tetrapod communities of the Late Frasnian.

Regional and geological setting

The Langsēde site is located in western Latvia, in the vicinity of Langsēde hamlet, on the right bank of the river Imula 640 m upstream from its confluence with the river Abava (Fig. 1), just a few kilometres west of the Velna Ala, type locality of *Obruchevichthys* (Vorobyeva 1977). Deposits of the Upper Devonian Ogre, Stipinai and Amula formations crop out in the Langsēde Cliff, which has been designated as a geological and geomorphological nature monument.

The Upper Devonian is the most complete and widely exposed part of the Devonian section in Latvia with both the Frasnian and Famennian stages being present. The lithostratigraphy of this sequence in Latvia is well-established (Sorokin 1981a): the Frasnian section consists of the Plavinas, Salaspils, Dubnik

3



Fig. 1. (A, B) Location maps showing the investigated outcrop relative to A, Europe; B, Latvia; and C, vicinity of Sabile.

(lateral equivalent of the Salaspils Formation), Daugava, Katleši, Ogre, Stipinai, and Amula formations (Fig. 2). However, the definition of the lower boundary of the Frasnian sequence in Latvia, as well as the chronostratigraphy, is still debatable due to the rarity of index conodonts in these mainly shallow-water and mixed-composition carbonate and siliciclastic deposits (e.g. Mark-Kurik *et al.* 1999). Nevertheless, it has been possible to trace most conodont zones by extrapolation (Esin *et al.* 2000).

During the almost 20-Myr-long time span of the Late Devonian carbonate sedimentation dominated, while the territory was covered by a shallow, sometimes restricted basin, with fluctuating salinity (Fig. 3). Although carbonate sedimentation was predominant, there were several comparatively short episodes of clastic sedimentation during the Frasnian and Famennian, and the deposits of the Ogre Formation represent the results of one such event. The Ogre Formation is composed of sandstone, siltstone, dolomitic marl, clay and gypsum, overlying the eroded surface of the Katleši Formation, but in the northwestern and northeastern Latvia it disconformably covers the Daugava Formation.

The Ogre Formation consists of a 15–18 m (western Latvia) up to 50-m-thick (eastern Latvia) mainly siliciclastic sequence, composed of three members: the Lielvārde Member at the base, the Rembate Member in the middle, and the uppermost Suntaži Member. The Lielvārde Member consists of sandstone, clay, dolomitic marl, siltstone, dolomite and gypsum-rich dolomite. Fish remains often form clusters, the socalled 'fish breccia' (Sorokin 1978). The middle part of the Ogre Formation, the Rembate Member, is composed of cross-stratified feldspar-quartz sandstone with high mica content and carbonate cement, rhythmically alternating with argillite (clay), siltstone and dolomitic marl in eastern Latvia. The sandstone is found at the base of the rhythms. In the Abava River basin, this interval is represented mainly by sandstone, but in some places in southern Kurzeme the deposits contain gypsum. The Suntaži Member comprises clay and dolomitic marl with siltstone and sandstone interbeds. The Ogre Formation vertebrate assemblage corresponds to the Psammosteus falcatus and B. maxima biozones, which correlate with the late rhenana Standard Conodont Biozone (Esin et al. 2000); conchostracans and lingulid brachiopods, although not abundant, have also been found in this formation (Sorokin 1981b).

Later, the clastic sedimentation was replaced by carbonate sedimentation: the deposits of the Stipinai Formation consist of dolomite, dolomitic marl with sandstone inclusions, siltstone, clay and gypsum interbeds. These deposits are distributed throughout western Latvia, but occur as separate erosional remnants in eastern Latvia.

During the Stipinai time the territory was covered with a shallow sea, which deepened to the southeast. Judging from carbonates with almost no admixture of



Fig. 2. Stratigraphical nomenclature and schematic geological section of the Frasnian deposits in Latvia.



Fig. 3. Palaeogeographical map of the Main and Central Devonian fields during the late Frasnian, with study area indicated (modified after Lebedev *et al.* 2010).

clastic particles and a rather diverse fauna of marine invertebrates, an open shelf sea existed in the central part of this basin (the southern part of Kurzeme). The thickness of the Stipinai Formation in the southern part of Kurzeme reaches 18 m thick and the prevailing deposits are dolomites with rather abundant invertebrate fossils including articulate brachiopods, gastropods, bryozoans, etc. In the near-shore areas, in the northern part of Kurzeme and eastern Zemgale, there is a clastic material admixture in the carbonate deposit. Fossils consist of ostracods, lingulid brachiopods and fish (Sorokin 1981c).

At the end of Amula time, the sea retreated from the major part of the territory. For this reason, the Amula Formation, deposited in shallow sea and lagoonal environments, occurs only in southwestern Latvia (Sorokin 1978). The thickness of the Amula Formation varies between 17 and 28 m and environments varied in different parts of the basin. In the northern and northwestern part of the distribution area, besides the dominating dolomites and dolomitic marls, sand and clay deposits accumulated. There are gypsum inclusions, especially in the southern part of the territory. Fossils are represented by fish and lingulid brachiopod remains, the green algae *Chaetocladus* and, notably, a rich miospore assemblage (Sorokin 1978; Lyarskaya & Lukševičs 1991).

Materials and methods

A detailed geological section of the Ogre and Stipinai formations cropping out at Langsēde was compiled and strata containing vertebrates were described. There are four layers of sandstone that yield vertebrate remains at the Langsēde site, all of them belonging to the Ogre Formation. The analysed specimens were collected from the most fossiliferous of these sandstones. A horizontal area of 8.1 m² was excavated during the expedition of 2008. Material collected in 1981 likely came from the same level; this material is kept at the Natural History Museum of Latvia (collection No. LDM G 99).

A horizontal plan of the excavation area shows the exact location of each bone (Fig. 8). As the bones are fragile, the specimens were put in plaster jackets for transportation to Riga. Because the bones were abundant and closely spaced it was often not possible to extract a plaster jackets without destroying underlying fossils. The greater part of the material is still being processed, and is housed in the Natural History Museum of Latvia.

Selected taphonomic attributes such as size sorting, articulation, fragmentation, left/right skeletal element proportion, azimuthal orientation and concavity ratio, skeletal preservation, and abrasion (edge rounding) were documented. All measurements of the taphonomic attributes except the edge rounding were made directly at the outcrop. The number of taxa and their relative abundance has been quantified, as have bone sizes. The azimuthal orientation of the bones and teeth was compared to the dip direction of the ripple marks. The concavity orientation of such strongly convex skeletal elements as the dorsolateral and ventrolateral plates of placoderms has been taken into consideration in particular as an indicator of the water energy of the sedimentary environment. The representation of different skeletal elements of the placoderm B. maxima was counted to characterize the sorting of the remains. Only fossils larger than 1 cm were counted. This size limit was selected to directly identify in the field most of the fossil remains and assign them to a higher taxonomic group (genus, family, order). More than 650 vertebrate fossils were found and 550 specimens were identified to the generic/species level.

Results

Sedimentology

Sandstone, siltstone and clayey deposits of the Ogre Formation (Rembate Member), dolostone, clayey dolostone and dolomitic marl of the Stipinai Formation (Imula and Bauska members), as well as clayey deposits of the lower part of the Amula Formation are exposed at the Langsēde outcrop (Fig. 4). The lower part of the Ogre Formation was covered by a several metres thick talus and thus not available for study. The lithological section starts at 1.26 m above the Imula level. The lower part of the section, at the 0–2.73 m interval (layers 1 through 7) is represented by very fine-grained sandstone with current ripple lamination and fine-grained sandstone, as well as clayey siltstone with sub-vertical burrows. Fine and medium-grained sandstone (layer 8, interval 2.73–3.16 m) yields abundant vertebrate remains and clay rolls. These remains are present mostly in a 20–40 cm thick conglomerate bed, which is rich in pebble-sized clay rolls and clay inclusions of irregular shape. Conglomerate is covered by cross-stratified fine-grained sandstone.

The fossil-bearing bed is covered by fine-grained cross-stratified sandstone and very fine-grained sandstone with current ripple lamination (layers 9-10, interval 3.16-4.74 m). These deposits are rich in clay and mica, forming drapes on the cross-laminae. Thickness of the cross-stratified beds decreases upwards, while the abundance of mud drapes on the cross-strata increases. Clay and mica content on the cross-strata varies cyclically, which possibly indicates spring and neap tide influence. The structures become indistinct upwards, and the upper part of layer 10 is almost homogenous, which, most probably, is due to the bioturbation. The dominant dip azimuth of the cross-stratification for this interval is 200-240°, while ripples on the surface of the cross-laminae have a dip azimuth of 9°, which is almost the opposite direction.

The upper part of the Ogre Formation at the interval of 4.74–8.27 m (layers 11 through 21) is composed of alternating clastic deposits, clayey siltstone, with problematic burrows, cross-stratified fine-grained and medium-grained sandstone, sometimes with clay rolls and vertebrate remains, and fine-grained sandstone with current ripple lamination.

The lower part of the Stipinai Formation begins with carbonate clayey siltstone at the interval of 8.27–8.33 m (layer 22), with rare sandstone intercalations. The deposits also contain desiccation cracks, while such features have not been found in the sedimentary rocks of the Ogre Formation. The following interval of the section (layers 23–30) comprises thin alternating beds of varying composition: clayey dolomite, carbonate siltstone and conglomerate beds with graded bedding which may represent tempestites (storm deposits), carbonate clay and dolomitic marl. This interval is rich in desiccation cracks and halite pseudomorphs.

The first dolomite layer occurs at the interval of 9.11–9.39 m (layer 31). Brachiopods and small vertical cavities, probably burrows, are present here, as well as halite pseudomorphs. Layer 32 (interval 9.39–9.57 m) is composed of clayey dolomitic rocks with clayey dolomite and dolomitic marl inclusions; it is followed



Fig. 4. Lithological section of the Ogre, Stipinai and Amula formations at the Langsēde Cliff, Latvia. Grain-size of siliciclastics: c, clay; s, silt; vfs, very fine sand; fs, fine sand; ms, medium-grained sand; cs, coarse sand; g, gravel; p, pebbles. Types of clayey-carbonate deposits: dm, dolomitic marl; cd, clayey dolomite; d, dolomite. Numbers: 1, vertebrate fossils and their location; 2, intervals of geological sequence where vertebrates are present; 3, burrows and their orientation; 4, cross-stratification; 5, various structures; 6, clay and mica drapes on cross-laminae; 7, clay interlayers; 8, current ripples; 9, ripples on cross-laminae; 10, desiccation cracks; 11, halite pseudomorphs and glyptomorphs; 12, empty vugs; 13, vugs filled with secondary calcite; 14, carbonate cement in sandstones; 15, soil; 16, till deposits; 17, scree.

by clayey silt and coarse-grained siltstone (layer 33, interval 9.57–9.67). This is the last interval of the Stipinai Formation that has comparatively coarse-grained material inclusions. The upper part of the geological section (9.67–12.47 m) is represented by clayey dolomitic rocks, with the content of dolomite increasing upwards (layers 34 through 36). The uppermost layer 36 (11.09–12.47 m) comprises hard platy dolomite having no pores or vugs. The change from clayey dolomitic deposits with desiccation cracks and halite pseudomorphs to dolomites with brachiopods indicates that during the Stipinai time the water depth gradually increased and the clastic supply decreased.

The dolomites of the Stipinai Formation are covered by a clay stratum, at least 50 cm thick (layer 37), that most probably belongs to the Amula Formation. A Pleistocene till more than 2 m thick covers the Palaeozoic rocks.

Taphonomy

Taxonomic representation

Although there are four levels of fish-yielding sandstone in the Ogre Formation at the Langsēde outcrop, only one was examined in detail, and all the excavations took place at the level of the eighth layer (Fig. 4). In the field, seven genera were identified, belonging to four groups: heterostracans, placoderms, acanthodians and sarcopterygians (Table 1).

No remains of *Obruchevichthys* or any other tetrapods have been found at the Langsede site. Macroscopic remains of acanthodians and psammosteids are rare, but there is a large amount of microscopic material, such as acanthodian scales and psammosteid tubercles. These microscopic remains are not further discussed here.

In comparison with the vertebrate assemblage characteristic for the Pamūšis Regional Stage of the Main Devonian Field, the faunal diversity of the Langsede site is slightly lower (see Table 1). The placoderms, Bothriolepis maxima, Bothriolepis evaldi, and Asterolepis? amulensis, occur at the Langsede site, but only B. maxima was excavated during the expedition of 2008; while from the territory of the Main Devonian Field five species, including B. maxima, B. evaldi, Asterolepis? amulensis, Grossilepis spinosa, and Walterilepis speciosa have been reported (Esin et al. 2000). Outside the studied area, B. maxima is widely distributed in various formations of Latvia, Lithuania and northwestern Russia (Lukševičs 2001a); B. evaldi is known from two localities in Kurzeme and one in Vidzeme; Asterolepis? amulensis and G. spinosa are known only from the Ogre Formation outcropping in a very small area in Kurzeme around the Langsede site (Lyarskaya & Lukševičs 1991), and W. speciosa has been described from the Ogre Formation cropping out along Daugava River in Vidzeme (Gross 1933). Four sarcopterygian fish genera have been mentioned from the territory of the Main Devonian Field (Esin et al. 2000): Holoptychius, Platycephalichthys, Eusthenodon and 'Dipterus', but Eusthenodon was included in the list erroneously. Two genera, Holoptychius and Platycephalichthys (Table 1), as well as an unidentified dipnoan, represent sarcopterygians at the Langsede site. One of the earliest tetrapods known from body fossils, Obruchevichthys (Ahlberg et al. 1994), was originally described from the Frasnian of western Russia and from the Ogre Formation of Latvia at the

Table 1. List of identified taxa from the Langsede site and vertebrates from the Pamūšis Regional Stage of the Main Devonian Field (MDF; after Esin et al. 2000).

		Langsede site		
Group	Genus/species	Coll. LDM G 99	Material of 2008	MDF
Heterostracomorpha	Psammosteus falcatus Gross	+	+	+
11000100011001pina	Psammosteus tenuis Obruchev	_	_	+
	Psammosteus sp.	+	+	_
	Obruchevia heckeri (Obruchev)	_	_	+
Placodermi	Bothriolepis maxima Gross	+	+	+
	Bothriolepis evaldi Lyarskaja	+	_	+
	Asterolepis? amulensis Lyarskaja	+	_	+
	Grossilepis spinosa (Gross)	_	_	+
	Walterilepis speciosa (Gross)	?	_	+
Acanthodii	Devononchus laevis Gross	+	+	+
	Acanthodii gen. et sp. indet.	+	+	_
Sarcopterygii	Holoptychius cf. nobilissimus Ag.	+	+	+
	Platycephalichthys bischoffi Vorobyeva	+	+	+
	'Dipterus' cf. marginalis Agassiz	_	_	+
	Dipteriformes gen. et sp. indet.	_	+	_
	Obruchevichthys gracilis Vorobyeva	-	-	+

Table 2. Number of skeletal elements, percentage (%) and minimum number of individuals (MNI) from the Langsēde site.

Taxon	No. elements	%	MNI	MNI, %
Bothriolepis maxima	339	67.1	74	89.2
Holoptychius sp.	136	26.9	3	3.6
Platycephalichthys bischoffi	19	3.8	1	1.2
Psammosteus sp., Ps. falcatus	8	1.6	4	4.8
Devononchus laevis	3	0.6	1	1.2

Velna ala site. No specimens of this taxon were recovered during the present excavation.

The minimum number of individuals (MNI) was estimated using the maximum number of identical skeletal elements among macroscopic fossils, including acanthodian spines (Table 2). Placoderms represented by only one species, *B. maxima*, are markedly dominant in the vertebrate assemblage, with 89% of the total MNI, followed by psammosteids (5%) and sarcopterygians (5%). Acanthodians are less abundant, comprising 1% of the total MNI.

Size- and age-specific distribution

The specific distribution of the fossils of different size from the Langsede site has three obvious maxima (Fig. 5). The first one is associated with the elements having a length or diameter of 4–5 cm and is mostly represented by sarcopterygian scales; the second is formed of bones 11–14 cm in length; and the third one of bones 17–18 cm long. Placoderm remains are predominant among the fossils of the second and the third groups.

The anterior median dorsal (AMD) bones of *B. maxima* reach a maximum length of 26 cm, and 72% of these skeletal elements belong to the interval of 17–26 cm (number of measured bones, n = 39; Fig. 6A). The largest specimens from the Langsēde site are also the largest known AMD of *B. maxima*. These



Fig. 5. Size-specific distribution of the vertebrate fossils from the Langsēde site.



Fig. 6. Length distribution of the placoderm bones from the Langsēde site. A, *Bothriolepis maxima*, anterior median dorsal plate. B, *Bothriolepis maxima*, posterior median dorsal plate.

plates, having a length of 22–26 cm exceed the largest complete 21.6-cm-long AMD previously described by Lukševičs (2001a). The length of the posterior median dorsal (PMD) bones (n = 26) varies between 8 and 19 cm, and 81% lie within the interval of 13–19 cm (Fig. 6B). Most probably this size distribution shows that *Bothriolepis* is represented mainly by adults. Large bones may indicate the presence of older individuals, but no remains of juveniles have been found at the Langsēde site so far.

Disarticulation of skeletons

Vertebrate remains at the Langsede site are represented in the main by fully disarticulated placoderm and psammosteid plates and plate fragments, sarcopterygian scales, and teeth. The remains are well-preserved and complete bones are more abundant than fragments. Articulated elements are very rare and are limited to distal segments of the pectoral fin (n = 7) and a head shield of *B. maxima* (almost complete (Fig. 7A), lacking only the premedian, postmarginal and right lateral bones), and a large lower jaw of a sarcopterygian.

Articulated remains of psammosteids are generally very rare. At Langsede, only disarticulated plates representing this group have been found, including



Fig. 7. Bothriolepis maxima Gross. A, head shield LDM G 99/68 in dorsal view, with abraded and rounded margins. B, premedian plate LDM G 99/2, with abraded and rounded margins. C, premedian plate LDM G 99/72, with abraded and rounded margins. D, articulated nuchal and postpineal plates LDM G 99/73, with abraded and rounded margins. E, nuchal plate LDM G 99/5. Langsēde site, right bank of Imula River, Latvia. Upper Devonian, Frasnian, Ogre Formation.

several branchial and one ventral plate. No ornamentation is left on most of the branchial plates, but on the surface of the ventral plate there are well-preserved, separate tubercles and tesserae. Acanthodians are represented only by spines and isolated scales.

The disarticulation index was calculated as the ratio between the number of all articulated skeletal element specimens and MNI. Counted for all macroscopic remains excluding acanthodian spines, the disarticulation index is rather low reaching only 1.2%, and the same index measured for the head shields of *B. maxima* only slightly exceeds the latter, reaching 1.4%. The disarticulation index for the distal segments of pectoral fin is about four times higher reaching 5.4%, suggesting this skeletal element was the most resistant against disarticulation, similarly as in another placoderm *Asterolepis ornata* demonstrated pectoral fins with plates tightly connected by serratiform sutures long after disintegration of the trunk shield (Upeniece 2005).

Representation of skeletal elements

Among the skeletal elements of *B. maxima* the best represented are AMD plates, which are used for estimating MNI (Table 3, see also Table 2). PMD plates are also represented well (62% of the expected number). There is a distinct gap between the percentage of PMD and the next skeletal element in the range, posterior ventral lateral plates (PVL, 24% of the expected number). Other skeletal elements are poorly represented; none of them exceeds 20% of the expected number. Some isolated bones of the head shield are found, such as the lateral plate, which is a paired bone

Table 3. The representation of some skeletal elements belonging to *Bothriolepis maxima*.

	Number o	f specimens			
Plate	Total	Expected number	Representation of plates (%)		
AMD	74	74	100		
PMD	46	74	62.1		
PVL	36	148	24.3		
AVL	28	148	18.9		
MV	12	74	16.2		
MxL	18	148	12.1		
Cv_1	18	148	12.1		
ADL	16	148	10.8		

(La; n = 9), and the unpaired premedian (Prm; n = 5), postpineal (Pp, n = 2), nuchal (Nu; n = 2), and pineal (Pi, n = 1) plates.

The sarcopterygian remains mainly comprise scales and teeth, which have been identified as belonging to *Holoptychius* sp. and *Platycephalichthys* sp. Also a preopercular bone and cleithrum probably belonging to *Holoptychius* sp., have been identified. Among the collected specimens is some lower jaw material as well: a nearly complete lower jaw and a detached prearticular of *Platycephalichthys*, and a fragmentary lower jaw which presumably belongs to *Holoptychius*.

Psammosteid macroscopic remains are represented mainly by branchial plates (n = 7), and a single complete and well-preserved ventral plate. The branchial plates were used for estimating the MNI (n = 4) and identified as belonging to *Psammosteus* sp. and *Psammosteus* cf. *falcatus*. No ventral plates belonging to *Ps. falcatus* have been described so far.

Breakage, wearing and abrasion of bones

Although the bones in general are well preserved and many are almost perfectly complete, there are also hardly determinable fragments. Among the *B. maxima* bones about 20% are fragmented. Sarcopterygian scales and teeth are represented with both complete and fragmented specimens. Other sarcopterygian remains available for study are generally relatively well preserved. Bone surface on the edges of the lower jaw of *Platycephalichthys* is just slightly abraded. The prearticular is not complete as a part of its posterior (proximal) end is missing. Otherwise the bone shows just minor evidence of abrasion on the thin edges along the dorsal and ventral margins of its front end. Psammosteid branchial plates lack proximal and distal parts.

Wear of the bones is seen along the lateral margins of the bothriolepid fins. Other bothriolepid bones have no evidence for unambiguous wear. The middle part of the psammosteid ventral plate is significantly worn, as is characteristic for this group (Obruchev & Mark-Kurik 1965). Many branchial plates of the psammosteids lack ornamentation, most probably due to abrasion, and not wear; no tubercles at all are preserved on the surface of several plates.

The overlapping areas of such bones of the bothriolepid head shield as Nu and Prm are abraded and have rounded margins (Fig. 7B–E). Also the posterior part of many PMDs is abraded in the area of the dorsal median ridge. This feature apparently should be explained by the fact that the centre of gravity of the PMD is located in this area. Among the fragmented bones of the bothriolepids many have rounded edges. Although this is compatible with longdistance transportation, it is, in the context of other sedimentological and taphonomic data from Langsēde like occurrence of bones together with clay rolls on the bottom of channel, most probably evidence for having been reworked.

Orientation of skeletal elements

The horizontal distribution of the bones over the studied area is not homogenous, distinct linear zones of increased density of fossils can be traced. These zones are oriented almost perpendicular to the dip azimuth of the ripple marks. Concavity ratio varies in different areas of the studied area: in the northern part of the excavation area convex bones mainly lie with their convex surface upwards, but in the southern part of the area the number of bones lying with their concave surface upwards increases up to 50% of all the bones. Prevailed azimuthal orientation of the fossils is SWW–NEE, while the most common azimuth of the ripple-mark dip in the bone-bed is SSW (Fig. 8).

Discussion

Lithofacies analysis

A detailed sedimentological interpretation of the deposits of the Ogre Formation has never been performed. In the most exhaustive description of the formation provided by Sorokin (1978) and Sorokins (1997), deposits of the Ogre Formation, cropping out **4** along the northern border of their distribution area in Kurzeme, have been broadly interpreted as having been deposited 'within the shallow-water zone of subaqeous deltas and lagoons', characterized by reduced salinity.

Sedimentological analysis of the geological section at the Langsede site shows that during the Ogre time sand was deposited by flowing water, but the clayey and silty particles settled in slack water episodes. The dip azimuth measurements of the cross-stratification of the siliciclastic sequence (n = 24) show that the dominant direction of the palaeo-stream flows was SSW. More exact evidence of the sedimentary environment is found in the middle Ogre sequence (layers 8 through 10), which is here interpreted as a tidally influenced channel. The bone-bed (layer 8) lies at the bottom of an erosion channel, and the overlying sequence of the cross-stratified sandstone is the result of the gradual infilling. The thickness of the cross-laminae series decreases upwards, indicating gradual shallowing. The climbing ripples on the cross-laminae have a northerly dip azimuth, opposite to that of the cross-stratification. This feature, as well as the mud drapes on the cross-strata, is indicative of tide-influenced sedimentation. The evidence of tidal signatures supplements data of previous studies, which proved tidal influence on sedimentation in the Baltic palaeobasin during the Middle Devonian and Middle/Upper Devonian transition (Tovmasyan 2004; Pontén & Plink-Björklund 2007; Tänavsuu-Milkeviciene & Plink-Björklund 2009).

The transition between the land and the sea in tidedominated coastal environments is very complex because of the interaction of numerous physical, chemical and biological processes (e.g. Dalrymple & Choi 2007). A more exact sedimentological interpretation of the succession of the Ogre formation requires further facies study and sequence-stratigraphical analysis including data from other localities.

The composition and structure of the Stipinai Formation indicate gradually deepening water with a simultaneously decreasing clastic supply. The Imula



Fig. 8. Horizontal plan and rose diagrams illustrating orientation of fossils from the Langsēde site and dip azimuth of the cross-stratification of the Ogre Formation. A, azimuthal orientation of all the bones measured (n = 198). B, azimuthal orientation of sarcopterygian teeth and acanthodian spines (n = 113). C, azimuthal orientation of bones, teeth and spines altogether (n = 311). D, dip azimuth of the cross-stratification of the Ogre Formation (n = 24).

Member is divided into two parts. The basal unit, beds 22 through 32, represents an intertidal flat. This interval of alternating beds of varying composition (clayey dolomite, carbonate siltstone, conglomerate beds, carbonate clay and dolomitic marl) is rich in desiccation cracks and halite pseudomorphs, indicating periodic sub-aerial conditions in a shallow-water basin. The upper part of the Imula Member and the lower part of the Bauska Member (layers 33 through 35) are interpreted as a subtidal flat, whereas the deposits of the uppermost part of the Stipinai Formation correspond to the deeper part of the sea (layer 36). This interpretation corresponds well to the conclusions that the sea basin developed transgressively during the Stipinai time interval (Sorokin 1981c).

Taphonomic analysis

The Langsēde vertebrate bone-bed was examined for taphonomic factors that could be relevant to the taxonomic composition of the assemblage and disintegration of carcasses. Five species of placoderms (*B. maxima, B. evaldi, Asterolepis? amulensis, G. spin*osa and *W. speciosa*) are known from the Pamūšis Regional Stage of the Main Devonian Field (Esin *et al.* 2000), but only one species of placoderm, namely B. maxima has been found at the Langsede site during the excavations of 2008; two taxa, B. evaldi and Asterolepis? amulensis, are represented by a few specimens in the material collected in 1981. There could be several possible explanations for this difference, the most obvious being sorting of the vertebrate bones during deposition. At the Langsede site the greater part of the bones exceed 10 cm in length, and small, fragile remains are underrepresented. The remains of relatively small placoderm fishes such as Asterolepis? amulensis, G. spinosa, W. speciosa and B. evaldi belong to another size group and, most probably, would be associated with a different sedimentary environment characterized by lower hydrodynamic activity, where smaller remains settled together with fine-grained sandy and silty material in slow currents. Grossilepis spinosa has been reported from another level of sandstone at Velna Ala (Gross 1942), while B. evaldi and Asterolepis? amulensis originally come from the siltstone at the Kalnamuiža site (Lyarskaya 1986). Bothriolepis evaldi is also known from the fine-grained sandstone at the Kaibala site close to the Daugava River in Vidzeme (Lukševičs 2001a), close to the type area of W. speciosa (Gross 1933). The same reason, that is lower hydrodynamic activity and deposition in slow currents, may explain why there are no juveniles among the remains of *B. maxima* at Langsede.

Although placoderm bones dominate the assemblage, among more than 650 specimens representing at least 74 individuals only one articulated head shield of B. maxima has been found. This demonstrates the existence of a time interval between death and final burial, significant enough for disintegration of the bodies, including rather solid parts of the armour. The degree of fragmentation and disarticulation of the bones most probably shows that carcasses have been reworked: possibly carcasses were deposited on a muddy bottom of the basin and the soft tissues at least partially decomposed; later the sediments were eroded and partially articulated or separate plates were transported to a short distance before final burial. At the same time, some isolated bones of the head shield, such as La, Prm and Pi plates, are present at the Langsede site, although not abundant. The presence of these large, but easily breakable skeletal elements with varying thickness suggests that the bones cannot have been transported very far.

The concavity ratio may serve as an indicator for the energy of the water currents and specific depositional mechanisms or conditions. As has been shown for mollusc shells (Clifton 1971; Seilacher 1973), concave-up is a stable position for shells in still water. However, as vertebrate remains differ significantly from bivalve shells in density, shape and dimensions, hypotheses about hydrodynamically stable positions of plates need to be tested experimentally. In the northern part of the excavation area vaulted bones mainly lie with the convex side upwards, possibly in a hydrodynamically stable position, whereas in the southern part of the area the number of concavedown bones increases thus indicating variable speed of current and increasing turbulence in the southern part of the area.

The horizontal distribution of the bones is not homogeneous; there are distinct linear zones oriented almost perpendicular to the dominant dip azimuth of cross-strata and ripple-laminae in the Ogre sandstone. This distribution suggests that the bones may have become concentrated in the depressions between subaqueous dunes. The vertebrate remains at the Langsēde site most probably were deposited in a shallow marine environment on the bottom of a tidal channel under the influence of rapid water currents.

Comparison of taphonomic and sedimentological data from the Langsede site with similar data obtained in the other well-studied localities of Devonian vertebrates from Latvia, such as Pavāri, Skujaine, kūki and Lode, shows some resemblances between these oryctocoenoses despite the great differences in age and taxonomic composition of assemblages. The Pavāri site in western Latvia, where the upper Famennian Ketleri Formation crops out, demonstrates the same taxonomical diversity (eight species of fishes and tetrapod), but better preservation of the remains including articulated head shields and pectoral fins, as well as several partially articulated trunk armour of the placoderm Bothriolepis ciecere, skull roof and associated cheek of the tetrapod Ventastega curonica, and several lower jaws of the tetrapod and sarcopterygian fishes Holoptychius, Cryptolepis, and Glyptopomus. The placoderm B. ciecere dominates the assemblage. The specific distribution of the fossils of different size showing only two maxima, dominance of the small bones, partial articulation of skeletons, more uniform representation of skeletal elements of placoderm armour in comparison with that from the Langsede site, good preservation, no traces of wearing and abrasion of fossils, and rather strong azimuthal orientation are characteristic for the Pavāri site. The sedimentary environment has been interpreted as a shallow sea, where the vertebrate remains have been deposited in the fine-grained sand infilling an erosional channel (Lukševičs & Zupinš 2004).

The vertebrate fauna is represented in the middle Famennian Tervete Formation, cropping out at the Skujaine site in southern Latvia, by 14 species of placoderms, acanthodians, sarcopterygians and actinopterygians. In comparison with the Langsede locality, smaller bones dominate the vertebrate remains

from the Skujaine site in total, with few larger than 10 cm. Fossils from the Skujaine locality are overall better preserved in comparison with those from the Langsede site, e.g., several partially articulated head shields of the placoderms Bothriolepis ornata and Bothriolepis jani (Lukševičs 2001a), as well as articulated lower jaws of Holoptychius and Platycephalichthys have been collected there. The placoderms B. ornata and B. jani compose more that 60% of all vertebrate individuals. In many cases broken plates, sometimes with strongly marked traces of wearing and abrasion, represent the remains. The Tervete Formation comprising weakly cemented sandstone and sand intercalated with dolomitic marls, siltstone and clay, has been traditionally interpreted as a deposit of a shallow sea (Savvaitova 1998). Detailed sedimentological analysis indicates variable hydrodynamic conditions, rapid sedimentation and slump processes, which, probably, not only caused the sudden fish burial in the fine-grained sandstone and sand, but also distorted the underlying beds. Most probably the deposits of the Tervete Formation were formed in estuarine settings.

The vertebrate remains from the upper Givetian k ūki fossil site corresponding to the Gauja Formation (northeastern Latvia) are represented mainly by large psammosteid and placoderm plates, which have been reported from clayey lenses inside the cross-stratified sandstone (Lyarskaya 1981). Among the seven species recognized in Kūki, three are represented by only one specimen; thus the structure of the fossil assemblage (taxonomic representation) rather closely resembles that at the Langsēde site. The preservation of the fossils is much poorer, no articulated portions of the armour having been found. The sedimentary environment of this part of the Gauja Formation has been interpreted by Pontén & Plink-Björklund (2007) as an extensive tide-influenced delta-plain.

The Lode clay pit lies within the upper Givetian Lode Formation, it is located about 20 km to the northeast from the kūki site. Lode site shows the bestpreserved fish remains ever found in Latvia, including complete skeletons of the placoderm A. ornata with articulated scaly tails (Kuršs & Lyarskaya 1973; Lyarskaya 1981; Ivanov et al. 1996) and very fine orbital ossifications (Lukševičs 2001b), several complete carcasses of the sarcopterygians Panderichthys rhombolepis, Laccognathus panderi (Lyarskaya 1981) and Eusthenopteron kurshi (Zupinš 2008), as well as usually complete juvenile skeletons of the placoderm A. ornata and the acanthodian Lodeacanthus gaujicus (Upeniece & Upenieks 1992). Fossil fishes constitute several fossil assemblages/taphocenoses slightly differing in taxonomic composition and varying greatly in preservation (Kuršs et al. 1999). All taphocenoses from the Lode site are believed to have been formed when vertebrates were rapidly buried on a deltaic slope due to slumping processes, thus ensuring fast burial and fossilization in anoxic conditions (Kuršs *et al.* 1999; Upeniece 1999; Zupiņš, 2003).

Summary

Siliciclastic deposits of the Frasnian Ogre Formation cropping out at the Langsede Cliff along Imula River vield a rich vertebrate accumulation. This fish bonebed is a typical example of the Devonian vertebrate assemblages from Latvia, characterized by relatively low diversity, almost uniform age of individuals, low rate of fragmentation, but high degree of bone disarticulation and sorting, which indicate reworking and short transportation prior to the final burial. Sedimentological data suggest deposition in a tidal channel under the influence of rapid water currents. Vertebrate bones were buried after short transportation mostly at the bottom of a channel. All the Middle-Upper Devonian vertebrate assemblages from Latvia compared here have been formed in the shallow water of a sea-coastal zone and all are associated with sandy to clayey deposits. Vertebrate remains have also been reported from carbonate sections (Lvarskava & Lukševičs 1991), but usually these are distributed 5 sporadically and do not form accumulations, contrary to the Silurian of Estonia (Märss et al. 2003) and some Devonian vertebrate localities around the Old Red Sandstone continent, e.g. the Andreyevka-2 site in Central Russia (Alekseev et al. 1994) or the Sosnogorsk site at Izhma River in South Timan (Beznosov 2009). Vertebrate burial patterns are rather similar when comparing Frasnian and Famennian assemblages, demonstrating the significance of the sedimentation rate, hydrodynamic regime and oxygen content within the sediments.

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Many thanks for your assistance.

Query reference	Query	Remarks
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Q2	AUTHOR: Please check authors' affiliations.	
Q3	AUTHOR: Niedźwedski <i>et al.</i> 2010 has been changed to Nied- zwiedzki <i>et al.</i> 2010 so that this citation matches the Reference List. Please confirm that this is correct.	
Q4	AUTHOR: Sorokin (1997) has been changed to Sorokins (1997) so that this citation matches the Reference List. Please confirm that this is correct.	
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Q6	AUTHOR: Please check the author name "Sorokins".	

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USING e-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

Required software to e-Annotate PDFs: <u>Adobe Acrobat Professional</u> or <u>Adobe Reader</u> (version 8.0 or above). (Note that this document uses screenshots from <u>Adobe Reader X</u>) The latest version of Acrobat Reader can be downloaded for free at: <u>http://get.adobe.com/reader/</u>

Once you have Acrobat Reader open on your computer, click on the Comment tab at the right of the toolbar:



3. Add note to text Tool – for highlighting a section to be changed to bold or italic.



Highlights text in yellow and opens up a text box where comments can be entered.

How to use it

- Highlight the relevant section of text.
- Click on the Add note to text icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

4. Add sticky note Tool – for making notes at specific points in the text.



Marks a point in the proof where a comment needs to be highlighted.

How to use it

- Click on the Add sticky note icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted



- Type the comment into the yellow box that appears.

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annotations on proofs and commenting on these marks. Allows shapes, lines and freeform annotations to be drawn on proofs and for

7. Drawing Markups Tools – for drawing shapes, lines and freeform

Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks..

How to use it

- Click on one of the shapes in the Drawing Markups section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.



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