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Environmental differentiation reflected by vertebrate faunal diversity in the Lower Devonian of the Holy Cross Mountains, Poland

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The Lower Devonian of the Holy Cross Mountains is well-known in the field of vertebrate palaeontology but remains unrecognized as regards palaeoenvironmental reconstructions. We therefore analysed the spatial distribution and relative abundance of fossil vertebrates in this area within one time interval. The fauna from an Early Devonian (Emsian) siliciclastic bone-bearing breccia (the "Placoderm Sandstone") exposed in four sections of the Łysogóry region and five sections of the Kielce region was analysed with respect to the frequency of the remains and their taxonomic affinity. The relative abundances of agnathans, acanthodians, placoderms, osteichthyans and chondrichthyans suggest more open marine conditions in the Łysogóry region and more terrestrial-influenced in the Kielce region during the Emsian. The results show that the average agnathan and acanthodian content of the Łysogóry region is significantly larger than that in the Kielce region. On the other hand, there are relatively fewer osteichthyans in the Łysogóry region and a significantly higher proportion of bony fishes was recorded in the fauna of the Kielce region. Placoderms are characterized by their generally similar frequency in both regions and from site to site in each of them, though a greater abundance was noted from the Kielce region. Likewise differences in the proportions of particular groups in the Kielce region suggest a large variety of marginal-marine environments under the influence of factors that might have included marine currents and variable conditions around a river mouth.

Key words: vertebrates, Lower Devonian, Emsian, Holy Cross Mountains, environment.

INTRODUCTION

The Lower Devonian of the Holy Cross Mountains has been debated in many publications (Kontkiewicz, 1882; Gürich, 1896; Czarnocki, 1919, 1936; Tarlo, 1957, 1961a, b, 1964, 1965; Kulczycki, 1960; Szrek et al., 2014; Szrek and Dupret, 2017; Szrek, 2020; Szrek et al., 2021) as regards its stratigraphy, palaeontology and palaeoenvironments. For many years, the only accessible locality with a reasonably informative section containing Polish Lower Devonian fossils was that at Podłazie Hill near Kielce in the western part of the Holy Cross Mountains. There, a bone-bearing breccia known as the Placoderm Sandstone is exposed. The site is now the best studied Lower Devonian locality of the region. The section, belonging to the Emsian Winna Formation, was discovered in an old, completely overgrown and partially buried sandstone quarry which, when it was active, was the only source of Placoderm Sandstone for scientific study (Kulczycki, 1960) and for academic collections (Kozak and Król, 2021). Unfortunately, the section and its sedimentological details are not known to have been documented at that time. During the past two decades one of us (PS) has made excavations at the site, primarily for obtaining new fossils, and several hundred specimens have been collected and are under study (Burrow and Szrek, 2018; Dec, 2019; Wilk et al., 2020; Szrek et al., 2021); it forms the largest collection of Early Devonian vertebrates from the region assembled so far.

The vertebrate fossils in the Placoderm Sandstone, with their ornamentation, are preserved as cavities in a hard sandstone. Such negative forms (natural moulds) used to be studied only after partial destruction of the rock and infilling the moulds with latex rubber or silicone. The casts were then observed and photographed, though much information was lost in this destructive process. Nowadays, the sandstone samples can be analysed by CT-scanner (high resolution computer tomography) and the images of specimens hidden in the rock examined on computer screen, completely non-destructively. The preliminary trials of this technique applied to the Placoderm Sandstone gave remarkable results. Even the tiny tubercles on the bones are visible (Fig. 1).

Since the second half of the 19th century, the Devonian vertebrate fauna of the Holy Cross Mountains, consisting mainly of

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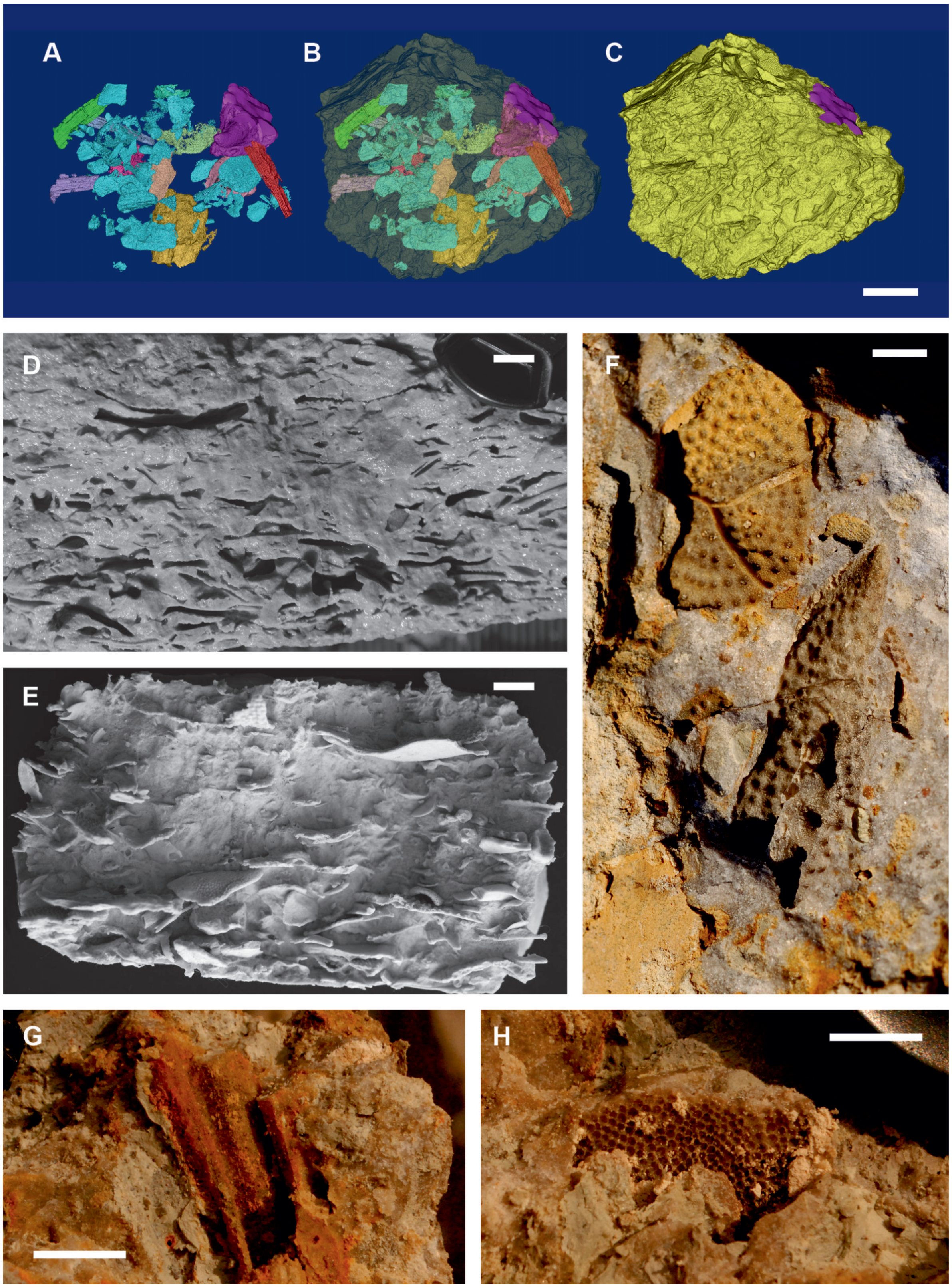

Fig. 1A–C – CT scan of a Placoderm Sandstone block modelled with Mimics 19.0; A – 3D extracted bones (some modelled individually, others as a single set (in pale blue), B – block shown semi-transparent, C – outer surface of the block; scale bar: 5 cm, D – cross-section of the Placoderm Sandstone bed with empty spaces representing bone; E – silicone cast of the surface of the specimen illustrated in D; F–H – surface of the Placoderm Sandstone block with vertebrate remains of placoderm (F), acanthodian (G) and psammosteid (H) elements representing empty spaces after skeletal tissues, scale bars: 1 cm

placoderms, has been used as a stratigraphic tool (Kontkiewicz, 1882) until the times of Czarnocki (1919 and later – see Szrek, 2020). By analysis of "placoderm fossils" in various Paleozoic clastic formations of the Holy Cross Mountains, Czarnocki (1919) was able to resolve an important question regarding the age of the sandstones that build the Łysogóry Range in the Holy Cross Mountains, previously considered as Cambrian and finally dated to the Early Devonian. The so-called placoderm remains were also the basis for naming the the sandstones containing such fossils (Gürich, 1896) as the Placoderm Sandstones. However, not until the last decade (Szrek et al., 2014, 2015; Szrek and Dupret, 2017), were placoderms from the Lower Devonian of the Holy Cross Mountains and (paradoxically) from the Placoderm Sandstone described. The armoured vertebrates described and illustrated were in most cases the more abundant agnathans, such as heterostracans (e.g., Tarlo, 1964, 1965). Probable reasons for this nomenclature (discussed by Szrek, 2020) include the generalizing approach of earlier researchers (Georg Gürich, Jan Czarnocki) to bone remains in Lower Devonian sandstones, lumping all armour-bearing fishes under the name of placoderms. The first certain (illustrated and verified) remains of placoderms from the Placoderm Sandstone were described by Szrek et al. (2014: fig. 5A), based on silicone casts (see also Szrek and Dupret, 2017).

As well as the Podłazie Hill locality, the Placoderm Sandstone *sensu* Szrek (2020) with its typical fauna can be found also at the following localities in the Kielce Region (southern Holy Cross Mountains, Fig. 2): Dębska Wola, Bieliny, Masłowiec and Kopiec, as well as from the Barcza Mountain, Bukowa Góra, Grzegorzowice-Skały Quarry, and Podole representing the northern, Łysogóry region. The vertebrate remains belonging to placoderms, chondrichthyans, acanthodians, osteichthyans and agnathans from these sections have been identified and counted in this study, and statistical data on the relative abundances of various groups of vertebrates obtained. The results provide insights into the geographic differentiation of the vertebrate fauna, particularly between the northern and southern regions.

MATERIAL AND METHODS

Fossils of the Placoderm Sandstone from the nine localities listed above and four museum collections (Geological Museum of the Polish Geological Institute – National Research Institute: Muz PGI-NRI 1733.II; Holy Cross Mountains Branch of the PGI-NRI: OS-223; Polish Academy of Sciences, Museum of the Earth: MZ-VIII/Vp and the University of Warsaw, Faculty of Geology: MWG UW ZI/43) have been studied. Our research develops the methodology of Szrek et al. (2014), extending it to eight more localities after field collecting made possible by heavy excavators (Podole, Podłazie, Kopiec) and manual excavation (the rest of the localities). Large pieces of Placoderm Sandstone (~1 m^2 in size) found in the exposures were broken up and subjected to surface analysis, counting all visible specimens (Table 1 and 2). The number of specimens studied depended on the richness of the sandstone in vertebrates, the thickness of the unit and overall access to the rock. Each vertebrate fragment, intraclast and quartzite pebble was treated as a separate object. Non-vertebrate remains were treated separately where clearly outlined and not in contact with any other object. Due to the very high degree of fragmentation of almost all vertebrate elements (dermal plates, scales, teeth, fin spines, etc.), each object was counted as one regardless of its state of preservation. For example, a small fragment of a dermal plate had the same value as a complete scale during counting. The identification of vertebrate elements as belonging to a particular group (agnathans, placoderms, chondrichthyans, acanthodians, and osteichthyans) was made based on general, but clearly distinctive morphological features, while specimens of unclear taxonomic affinity were classified as "unidentified". In total 2115 vertebrate remains and other elements were analysed and evaluated. Details on their systematic affiliation are shown in Table 1. Additionally, taking into consideration differences between the numbers of specimens of different groups at the localities, especially among the Łysogóry and Kielce regions, the Pearson correlation coefficient was calculated for those areas. Two variables (Kielce and Łysogóry regions) were measured at the interval level (vertebrate groups) thus each observation in the dataset has a pair of values (e.g., values of placoderms in both regions). Data were calculated using the Pearson formula in the *Microsoft Excel* programme (Table 3) which evaluates the effect of change in one variable on the other.

GEOLOGY AND AGE OF THE SECTIONS STUDIED

Differences in facies development of the Holy Cross Mountains during the Devonian include predominantly marine conditions in the Łysogóry region and more continental conditions in the Kielce region (Szulczewski, 1995). Moreover, the Lower Devonian succession in the Łysogóry region is almost complete, whereas in the Kielce region it is characterized by several unconformities and gaps (see Szulczewski, 1995: fig. 1). The differences in the palaeontological record of the Lower Devonian deposits are also significant. The Łysogóry region has yielded a rich assemblage of invertebrate fossils and ichnofossils (Szulczewski, 1995; Szulczewski and Porębski, 2008), as well as vertebrate remains (Szrek et al., 2015). In the Kielce region, there are no discernible invertebrate fossils (Szrek et al., 2014, 2016), while the vertebrate remains are numerous and diversified (Tarlo, 1957, 1961a, b, 1962, 1964, 1965; Kulczycki, 1960; Blieck, 1980; Szrek et al., 2014, 2015; Szrek and Dupret, 2017).

From a formal lithostratigraphic view, the sandstones exposed in the Kielce region belong to the Winna Formation and those in the Łysogóry region to its equivalent, the uppermost Barcza and Zagórze formations. They represent the middle to upper Emsian (see Fijałkowska-Mader and Malec, 2011, 2018). The analysis of vertebrate content in different sites containing the Placoderm Sandstone is based on the contemporaneous deposition of the bone-bearing horizons analysed. Such dating was available to us thanks to the regional analyses of Tarnowska (1971, 1976, 1981) and Fijałkowska-Mader and Malec (2011).

The localities studied, four in the Łysogóry region and five in Kielce region, represent the western, central and eastern parts of both regions and most of them gave at least hundred counts of vertebrate remains, intraclasts and quartzite pebbles.

KIELCE REGION

The Dębska Wola site is the westernmost locality, ~4 km southwest of Morawica town and 20 km south of Kielce. At Dębska Wola, Czarnocki (1919, 1936) described the Placoderm Sandstone breccia as characterized by an exceptional richness of vertebrate remains such as scales, fin spines, armour fragments, teeth, etc. Later, the examination of the sec-

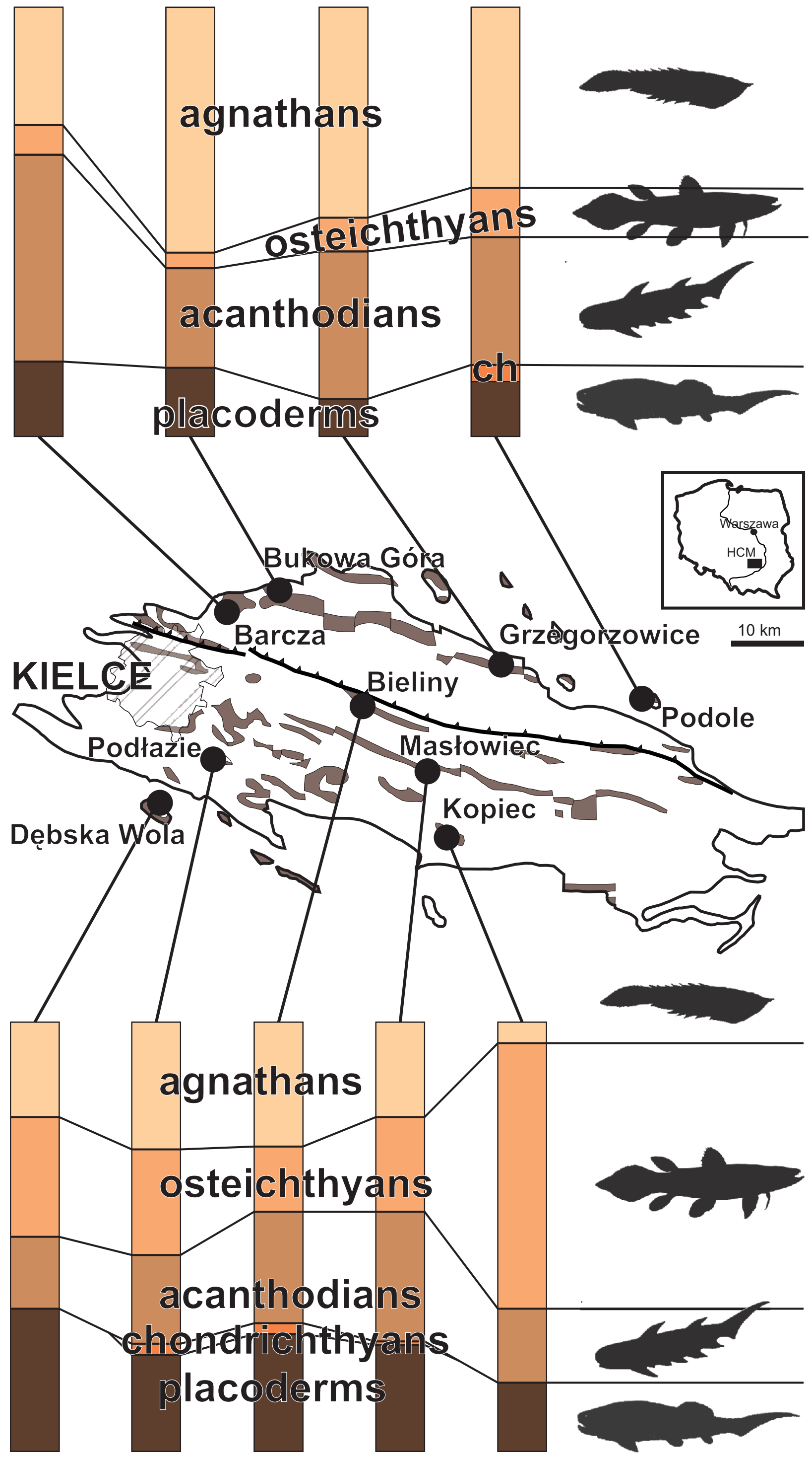

Fig. 2. Locality map of the Placoderm Sandstone outcrops in the Holy Cross Mountains with diagrams showing relative abundances of each vertebrate group

ch – chondrichthyans

tions was difficult as they became increasingly vegetation-covered, and required large-scale excavation (Szrek and Dupret, 2017). According to Czarnocki (1919), the Placoderm Sandstone at Dębska Wola corresponds to the lower Emsian in the terrigenous "Barcza Series" of the Łysogóry region. The Placoderm Sandstone from this locality is <0.5 m thick, but contains abundant remains. It occurs in the same context as the section at Podłazie noted below.

The Podłazie locality was described in detail by Szrek et al. (2014). The light greyish-beige bone-bearing breccia is made of empty spaces after the broken remains of a rich, diverse vertebrate assemblage. It was deposited during high-energy events in shallow water conditions (Johnson and Baldwin, 2012; Szrek et al., 2014). Based on miospores and tephrocorrelation the Placoderm Sandstone in Podłazie Hill is dated as Emsian (407.6 ±2.6–393.3 ±1.2 Ma; Tarnowska, 1976, 1981; Szulcze-

Table 1

Number of vertebrate remains and clasts observed on the surfaces of samples of Placoderm Sandstone from the Holy Cross Mountains

	Łysogóry region				
	Barcza	Bukowa Góra	Grzegorzowice	Podole	TOTAL
Placoderms	13	13	8	17	51
Chondrichthyans	0	0	0	5	5
Acanthodians	35	18	30	38	121
Osteichthyans	5	3	7	15	30
Agnathans	20	45	43	54	162
Unidentified	2	5	15	21	43
Clasts	9	23	9	45	86
Total number of vertebrate fragments	73	79	88	129	369
TOTAL	84	107	112	195	498

	Kielce region					
	Dębska Wola	Podłazie	Bieliny	Masłowiec	Kopiec	TOTAL
Placoderms	71	152	33	28	13	297
Chondrichthyans	0	19	3	1	0	23
Acanthodians	35	141	31	34	14	255
Osteichthyans	60	166	18	25	51	320
Agnathans	47	201	35	25	4	312
Unidentified	24	93	21	20	15	173
Clasts	16	148	23	16	34	237
Total number of vertebrate fragments	213	679	120	113	82	1207
TOTAL	253	920	164	149	131	1617

wski and Porębski, 2008; Fijałkowska-Mader and Malec, 2011). Lithostratigraphic considerations suggest that the sandstones exposed at Podłazie Hill belong to the lower part of the Winna Formation (see Fijałkowska-Mader and Malec, 2011). The bone-bearing breccia is at least 40 cm thick.

At the next locality, Bieliny, Czarnocki (1919) distinguished the following sequence: (1) grey and olive clayey and marly shales belonging to the Silurian on which lie (2) the Placoderm Sandstone – compact sandstones, yellowish with lens-shaped inclusions of green clay and placoderm moulds, forming the main part of the section; above them lie (3) pale green clay shales 0.5 m thick, as thin interbeds between sandstone layers. Then (4) conglomerates of the Upper Emsian, up to 5 m thick. The top of the sequence comprises (5) fragile rust-coloured sandstones with an invertebrate fauna. Intercalations of conglomerate in the upper part of the sandstone and shale succession indicate marine transgression. In the uppermost sandstones a marine fauna with *Spirifer* reflects displacement of the shoreline (Pajchlowa, 1957). The bone-bearing unit at this locality is also exposed in the section by the river Belnianka at the foot of Chełm mountain. It is up to 0.5 m thick with an abundance of vertebrate remains similar to those from Dębska Wola and Podłazie.

At Masłowiec near Łagów upper Emsian strata are exposed (Czarnocki, 1919; Walczowski, 1968). The Placoderm Sandstone sequence is formed of quartzitic sandstones, and sandy mudstones interbedded with green and cherry-red clays and greywackes. The sandstones are generally white, locally with a yellowish or reddish tinge with cavities left by weathered-out clays. On the top of the Placoderm Sandstone lie red, grey, and brown shales (upper Emsian) with intercalations of greywacke, claystone and weakly cohesive sandstone (Walczowski, 1968). In some places cross-bedding, wave ripples and rain imprints were found, indicating shallow-water and emergent conditions. Additionally, all remains found were broken, suggesting significant transport before deposition (Walczowski, 1968), is inferred also by Czarnocki (1919) from the terrigenous nature of the sediments. Vertebrate remains are loosely dispersed in a 0.3 metre interval. The exposure is located in a stream valley and the bone-bearing unit occurs in a generally muddy part of the section.

The Kopiec site consists in an inactive quarry located near Iwaniska city, ~60 km south-east of Kielce. Geologically, the site lies on the closure of the Ujazd syncline. The succession exposed at Kopiec is similar to that in a well-known borehole at Haliszka where the most complete profile of the Emsian is represented. Tarnowska (1967) identified five units based on organic remains and lithological changes: (1) lower sandstone, (2) lower sandstone-mudstone, (3) lower sandstone with placoderm remains, (4) mudstone-sandstone and (5) upper sandstone. The whole succession is ~126 m thick. At Kopiec the last upper two units of the succession are eroded (Tarnowska, 1976). The third unit, the upper Emsian Placoderm Sandstone, is developed as coarse-grained sandstones >2 m thick, light grey with thin interbeds of siltstone and clay, the total thickness of the available section exceeding 30 m (Samsonowicz, 1929). Vertebrate remains are abundant in a 5–10 cm thick interval within a thicker (~1.5–2 m) sandstone bed which overlies a muddy layer. Despite its thinness, the bone-bearing unit is as fossil-rich as at Dębska Wola or Podłazie.

Table 2

Relative abundances of vertebrate remains (identified specimens only) on the surfaces of Placoderm Sandstone samples from the Holy Cross Mountains

	Łysogóry region				
	Barcza	Bukowa Góra	Grzegorzowice	Podole	Average [%]
Placoderms	18	16	9	13	14
Chondrichthyans	0	0	0	4	1
Acanthodians	48	23	34	29	33.5
Osteichthyans	7	4	8	12	7.75
Agnathans	27	57	49	42	43.75
TOTAL	%	%	%	%	

	Kielce region					
	Dębska Wola	Podłazie	Bieliny	Masłowiec	Kopiec	Average [%]
Placoderms	33	22	28	25	16	24.8
Chondrichthyans	0	3	2	1	0	1.2
Acanthodians	17	21	26	30	17	22.2
Osteichthyans	28	24	15	22	62	30.2
Agnathans	22	30	29	22	5	21.6
TOTAL	100%	%	%	%	%	

Table 3

Pearson correlation between the Kielce and Łysogóry regions showing the strength of the linear relationship between the two

	Number of vertebrate remains observed on the surfaces of samples of Placoderm Sandstone		Relative abundances of vertebrate remains on the surfaces of samples of Placoderm Sandstone	
	Kielce Region	Łysogóry Region	Kielce region (average %)	Łysogóry region (average %)
Placoderms	297	51	24.8	14
Chondrichthyans	23	5	1.2	1
Acanthodians	255	121	22.2	33.5
Osteichthyans	320	30	30.2	7.75
Agnathans	312	162	21.6	43.75
Pearson Correlation Coefficient	0.53		0.34	

ŁYSOGÓRY REGION

At Barcza Mountain three quarries were distinguished: Northern, Eastern and Southern (Urban, 1980; Wróblewski, 2000; Fijałkowska-Mader and Malec, 2018). Czarnocki (1919) first described the sequence in the Barcza region and observed three characteristic units: Old Red Sandstone, Placoderm Sandstone and Spirifer Sandstone. Later, Czarnocki (1936) constructed a lithological profile in which he distinguished successively the Klonów Beds, the Barcza Beds, the Spirifer sandstones, the Skolithic sandstones and the Ciosowe Sandstones (Fijałkowska-Mader and Malec, 2018). In the Barcza Beds, Kowalczewski (1971) recognized six lithological units and the placoderm remains were found only in the fifth one. It is composed of medium-, locally thick-bedded sandstones and cherry-coloured quartz siltstones. There are sporadic fine- to medium-grained, light-coloured platy sandstones with frequent cavities left by washed-out clay pebbles.

At Barcza, >30 m of the Emsian terrigenous Barcza Beds are visible. These are represented by sandstones and mudstones with interlayers of tuffite in the upper part (Król et al., 2021). The upper part of the Barcza Beds is built of mudstones and sandstones, usually up to several tens of centimetres, but locally to a few metres thick, and in their lower part being light and dark grey. The mudstone shows horizontal lamination. In the middle part, Malec (2001) observed an 8.5 m bed of cherry-brown mudstones. The topmost parts of the exposed section are represented by grey-green, fine-grained and horizontally laminated sandstones and mudstones (Czarnocki, 1936; Malec, 2001). The section represents a lagoonal environment similar to that at Bukowa Góra though these localities were not connected (Kowalczewski, 1971). Vertebrate remains are dispersed in a 1–1.5 m interval. Most of the specimens analysed were collected from the dump, but their source horizon is precisely located and corroborated by Fijałkowska-Mader and Malec (2018).

Bukowa Góra includes an active sandstone quarry located ~20 km north-east of Kielce. In the quarry there are three exposed formations: the Zagórze Formation, the Bukowa Mountain Shale Formation and the Kapkazy Formation, which together represent a transgressive trend with a stack of barred shorelines. Our material was taken from the Zagórze Formation (a >200 m thick succession inclined at an angle of 40° to the N–NNE) where mostly white, yellow, red, locally pebbly, laminated sandstones (usually 2–5 m thick) and less consolidated, bedded, dark grey, green, and reddish sandstone/mudstone heterolithic deposits (between several centimetres and 5 m thick) are dominant (Szulczewski and Porębski, 2008). The strata were deposited in a high-energy environment in a marine nearshore zone or river (Czarnocki, 1936; Łobanowski, 1971; Szulczewski, 1995; Fijałkowska-Mader and Malec, 2013, 2018; Urban, 2020). Based on brachiopods, the Zagórze Formation was assigned to the late Emsian, whereas microspores indicate the middle Emsian (Malec, 1990, 2001; Fijałkowska-Mader et al., 1997). Vertebrate remains occur in the so-called “Spirifer Sandstone”, a brachiopod-bearing tempestite. This is the only case in the Holy Cross Mountains where vertebrates co-occur with invertebrates. The horizon analysed for statistical purposes is ~1 m thick.

The Grzegorzowice-Skały section is located ~8 km NE of Nowa Słupia. The section exposes strata from upper Emsian to lower Givetian age, and is represented by marine sandstones, shales, marls, limestone and dolostone with conodonts, corals, crinoids, brachiopods, ostracods, trilobites and acritarchs (Pajchlowa, 1957; Masorz, 2014). These are assigned to the Grzegorzowice Formation which occurs between the terrigenous deposits of the Zagórze Formation (terrigenous-marine deposits with placoderm remains) of upper Emsian and the Eifelian of the Wojciechowice Formation. It was deposited in a very shallow water environment with dolomite deposition (Malec, 2005). The bone-bearing breccia is exposed in the section by the Dobruchna River. Vertebrate remains are scarce within this ~1 m thin interval.

The easternmost site is Podole near Opatów, ~60 km east of Kielce. Emsian strata are represented here as quartzitic sandstones and mudstones belonging to the “Barcza series”. These rocks form an anticline with claystone and mudstone in the hinge and quartzitic grey sandstones in the limbs (Czarnocki, 1919; Samsonowicz, 1934; Romanek, 1994). The sandstone sequence comprises mutually overlapping units of thick- and medium-layered quartzitic sandstone, with 3–6 cm thick intercalations of green tuffaceous claystone. The sandstone contains irregular spaces of various size filled with green mudstone (Romanek, 1994). Additionally, Samsonowicz (1934) indicated the presence of several 30 cm-thick conglomeratic sandstones and conglomerates built of well-rounded quartz pebbles up to 2 cm in diameter cemented with quartzitic sandstone in the Podole region. Vertebrate remains occur here in a 20 cm thick interval and are dispersed in a coarse-grained sandstone.

RESULTS AND DISCUSSION

Among 2115 elements observed and counted on the surfaces of Placoderm Sandstone blocks of different sizes according to their accessibility at exposure (Table 1), 1576 were identified as vertebrate fragments. They could be assigned to one of the following vertebrate groups: placoderms, chondrichthyans, acanthodians, osteichthyans, and agnathans. In each locality no less than 84 such fragments were observed, which gives a good basis for statistical analysis and comparison of the faunal assemblages. The largest number of specimens (679) was identified at Podłazie, because of the longest and most intense exploration of that site.

Environmental preferences assigned to groups of early/lower vertebrates found in the bone-bearing breccia (based on Janvier, 1996; Benton, 2014) point to a mixed character of their assemblages. This likely resulted from a high-energy environment during the redeposition and final deposition of faunal remains coming from different ecological niches. Acanthodians that have been identified in the Placoderm Sandstone were fishes that lived in the open sea (Burrow and Szrek, 2018), but placoderms had a wide range of environmental tolerance and in the Early Devonian they occupied mainly marginal-marine, or even brackish environments, such as lagoons or flooded river valleys (see Denison, 1978; Janvier, 1996) together with heterostracan agnathans. Thus, the assemblages recorded in the Placoderm Sandstone contain forms that were transported from the open marine realm (acanthodians, chondrichthyans) and mixed with those that lived in a marginal-marine environment (placoderms and sarcopterygians).

Although in all the sections studied all vertebrate groups are present (except chondrichthyans, which are generally very rarely found and are represented only by small, barely identifiable pieces of fin spine), a clear differentiation of the relative abundances can be observed (Table 2; diagrams in Fig. 2). The Łysogóry sections are characterized by a smaller amount of shallow water (Szrek and Dupret, 2017) placoderms (14% on average) and osteichthyans (~8%), but a higher content of open marine acanthodians (~33%) in comparison to the Kielce region (25, 30 and 22%, respectively). This result is consistent with the general agreement regarding the offshore character of the deposits in the northern part of the Holy Cross Mountains (Szulczewski, 1995). However, the large relative abundance of ostracoderms (mainly heterostracans 44%), in the Łysogóry region, compared with only ~22% in the Kielce region, is surprising. There is also a significant difference in the results between the easternmost Kopiec locality and the four other sites of the Kielce region. In the latter, the content of osteichthyans oscillates around 20%, while at Kopiec it exceeds 60%. This may be a record of local environmental phenomena such as marine currents or a river mouth which influenced the vertebrate composition and/or segregation. The result of a Pearson calculation at 0.53 points to a strong correlation despite nominal differences. The same calculation with percentage data indicates moderate correlation at 0.34 of Pearson correlation coefficient. In both cases this correlation is positive, which means that as the amount of vertebrate remains in the Kielce region increases, those in the Łysogóry region will also see an increase.

The taxonomic composition of vertebrate remains in the Holy Cross Mountains, with all the major Early Devonian vertebrate groups well-represented, and despite its local and regional variations, reflects the situation described from upper Emsian localities across Laurussia (Szrek and Dupret, 2017). The possible dispersal routes of arthrodirans, porolepiforms and actinopterygians were discussed by Schultze and Cumbaa (2017) and show open marine connections between the northern localities of Poland and those that were near the central and southern parts of Baltica during its collision with Laurentia (Mark-Kurik et al., 2013). Notably, the sarcopterygian genus *Heimenia* directly connects the Anderson River Emsian fauna (Northwest Territories, Canada) with the Baltic and Holy Cross Mountains contemporaneous localities. Mondéjar-Fernández and Clément (2012) noted that the migration must have ended before the closure of open marine links. The presence of *Heimenia* in the Holy Cross Mountains was first suggested by Ørvig (1969) based on the material described by Kulczycki (1960) and corroborated by Wilk et al. (2020). The rest of the fauna does not reflect such direct systematic affinities (see Szrek and Dupret, 2017), and is characterised as transitional between Baltica and western Europe.

CONCLUSIONS

Quantitative and qualitative analysis of vertebrate remains exposed on the surfaces of siliciclastic bone-bearing breccia from the Early Devonian (Emsian) of the Placoderm Sandstone from the Holy Cross Mountains in Poland, produced significant although not unexpected results. The high relative abundances of acanthodians and relatively low content of placoderms and sarcopterygian osteichthyans in the four sections of the northern Łysogóry region (in comparison to contrasting results for the five sections from the southern Kielce region) generally supports the earlier assumptions of offshore conditions in the north and marginal-marine in the south. The rather counterintuitive high content of armoured agnathans in the Łysogóry region needs further investigation.

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