

## Palaeoenvironmental reconstruction of the Upper Visean Paprotnia Beds (Bardo Unit, Polish Sudetes) using ichnological and palaeontological data

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In this paper the trace fossil associations and the taphocoenoses from the Upper Visean Paprotnia Beds (Bardo Unit) have been compared. Eleven ichnogenera have been recognized (*Zoophycos*, *Chondrites*, *Protovirgularia*, *Lockeia*, *Palaeophycus*, *Nereites*, *Planolites*, *Altichnus*, *Paleobuprestis*, cf. *Thalassinoides* and ?daedaloid form). A new ichnospecies *Paleobuprestis sudeticus* has been defined herein. It is the oldest wood-boring trace fossil observed in macroscale and the first wood-boring trace fossil preserved on the archaeocalamites stems. Based on ichnodiversity and relative abundance of trace fossils in the investigated strata three ichnoassociations have been distinguished: *Zoophycos–Chondrites–Palaeophycus*, *Palaeophycus–Nereites* and *Paleobuprestis*. Vertical succession of both the taphocoenoses and ichnoassociations reflects the different colonization stages of the substrate and is linked to bathymetric changes in the marine basin from offshore to nearshore conditions in warm climate at low latitude. The Paprotnia profile is a unique record of the Asbian–Brigantian transition.

Key words: palaeoenvironment, trace fossils, ichnoassociations, taphocoenoses, Upper Visean, Sudetes.

### INTRODUCTION

The Paprotnia Beds are one of the lithostratigraphic units in the Middle Mississippian rocks of the Bardo Unit (the central part of the Polish Sudetes) and they are biostratigraphically well-dated. [Haydukiewicz and Muszer \(2002\)](#) recognized five taphocoenoses in the vertical sequence of the Paprotnia section, which differ in the relative frequency of particular taxonomic groups, the size and the state of preservation of specimens. Their studies indicate gradual environmental changes from offshore to onshore conditions. According to [Haydukiewicz and Muszer \(2002\)](#), the Paprotnia Beds represent the shallower facies equivalent of the pelagic *crenistrina* Limestone, which is widespread in the Culm facies of Variscan Europe ([Warnke, 1997](#)). Another interpretation of the environmental deposition of the Paprotnia Beds was presented by [Wajsprych and J drysek \(1994\)](#), who considered that the beds were deposited in the deep sea and the terrigenous material was transported by turbidity currents. They also suggested that most of macrofossils are allochthonous and were redeposited from shallower parts of the basin. [Wajsprych \(1995\)](#) also postulated

a concept of a chemogenic vent-related origin of both the fauna concentrations and the *crenistrina* horizon carbonates.

The usefulness of ichnofossils to the reconstruction of palaeoenvironment is commonly known, because of their *in situ* occurrence. Assemblages of trace fossils are very important in sedimentological analyses, palaeoecology, palaeobathymetry and can also indicate the oxygenation and the salinity of the bottom water (e.g., [Seilacher, 1967](#); [Frey, 1975](#); [Ekdale and Mason, 1988](#); [Frey et al., 1990](#); [Pemberton et al., 1992](#); [Savrdra, 1995, 2007](#); [Bromley, 1996](#); [McIlroy, 2004](#); [Gaillard and Racheboeuf, 2006](#); [Miller, 2007](#); [Buatois and Mángano, 2011](#)). They are also used in biostratigraphy and sequence stratigraphy (e.g., [Miller, 2007](#); [Martin, 2009](#)). Use of trace fossils as ecological indicators in stratigraphic succession provide evidences to the local history reconstruction of environmental change and basin evolution ([Bromley, 1996](#)).

Trace fossils from the Western Polish Sudetes are still poorly known, especially Paleozoic ichnogenera. Mesozoic ichnogenera are rather common in the Middle Triassic and Upper Cretaceous and were described for example by [Jerzykiewicz \(1971\)](#), [Rotnicka \(2005\)](#), [Chrz stek \(2008, 2012\)](#), [Leszczy ski \(2010\)](#), [Chrz stek and Wojewoda \(2011\)](#). In contrast to them, Paleozoic ichnofossils have not been reported except for Permian coprolites ([Roemer, 1857](#)) and Carboniferous *Zoophycos* from the Bardo Unit ([Muszer and Haydukiewicz, 2009, 2010](#)). Recently found trace fossils in the Paprotnia Beds ([Uglik, 2010](#)) allowed the problem of the deposition of the Paprotnia Beds to be resolved.

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The goal of the present study is the description of the discovered ichnotaxa as well as their ichnological characteristics and correlation to the taphocoenoses succession recognized by Haydukiewicz and Muszer (2002). Analysis of these ichnological and palaeontological records is used to create a palaeo-environmental reconstruction of the Paprotnia Beds deposition.

## GEOLOGICAL SETTING

The Paprotnia Beds (an informal lithostratigraphic unit earlier known as the “Paprotnia series” in Polish literature) occur only in the western part of the Bardo Unit of the central Polish Sudetes (Fig. 1). According to the tectonostratigraphic model presented by Wajsprych (1986, 1995) the Bardo Unit is composed of two Paleozoic successions: allochthonous and autochthonous/parautochthonous. The allochthonous succession is represented by large olistoliths of deep marine strata from at least the Upper Ordovician to the Devonian, embedded in Viséan wildflysch (Haydukiewicz, 1990). The autochthonous/parautochthonous succession comprises the Upper Devonian – Mississippian rocks (Wajsprych, 1986, 1995; Haydukiewicz and Muszer, 2002) and was subdivided by Wajsprych (1995) into several informal units: formations and sequences (Fig. 2). The Paprotnia Beds belong to an autochthonous/parautochthonous platform succession. They are included in the lower part of the Winna Góra sequence, whose stratigraphic position is difficult to determine because of the complicated tectonic framework and unexposed contact with neighbouring

units. The scheme of the lithostratigraphic units of this succession is shown on Figure 2 and outlined by Kryza et al. (2008).

The outcrop of these beds is situated about 500 m SE of the Paprotnia Hill (547.3 m a.s.l.), in the road-escarpment between the villages of Czerwiec-zyce and Wojbórz (GPS coordinates E 16°37'29.247). The exposed section of the Paprotnia Beds is 13.7 m thick (Figs. 3 and 4A), but the whole thickness of the lithostratigraphical unit is determined at about 20–25 m (Haydukiewicz and Muszer, 2002). The contact with the underlying sediments is not exposed. The strata dip at 50–60° to the north. In the Paprotnia section three sets of strata can be distinguished: beds 1, beds 2, beds 3 (Fig. 3). The lower part of the Paprotnia section (beds 1) is composed of greenish-grey and grey claystones and mudstones with a few intercalations of thin (up to 3 cm thick) dark grey micritic limestones. These deposits are overlain by dark grey and dark olive mudstones, which are upwards intercalated with thin layers of sandy-mudstones and greywackes as well as six (A–F) bentonite layers and comprise irregularly distributed diagenetic mudstone nodules. The characteristic of the bentonites was presented by August et al. (2003) and Kryza et al. (2007, 2008, 2011). The middle part of the section (beds 2) is composed of sandy-mudstones and greywackes with lenses of dark grey organodetrital limestones (up to 40 cm thick), which abundance distinctly decreases upwards. In the upper part of beds 2 several organodetrital laminae with crushed shells and individual columnals of crinoids occur. The upper part of the section (beds 3) comprises greywackes containing sandy and mudstone intercalations. The sediments pass gradually to the polymictic conglomerates of the Wilcza Beds (Figs. 2 and 3).

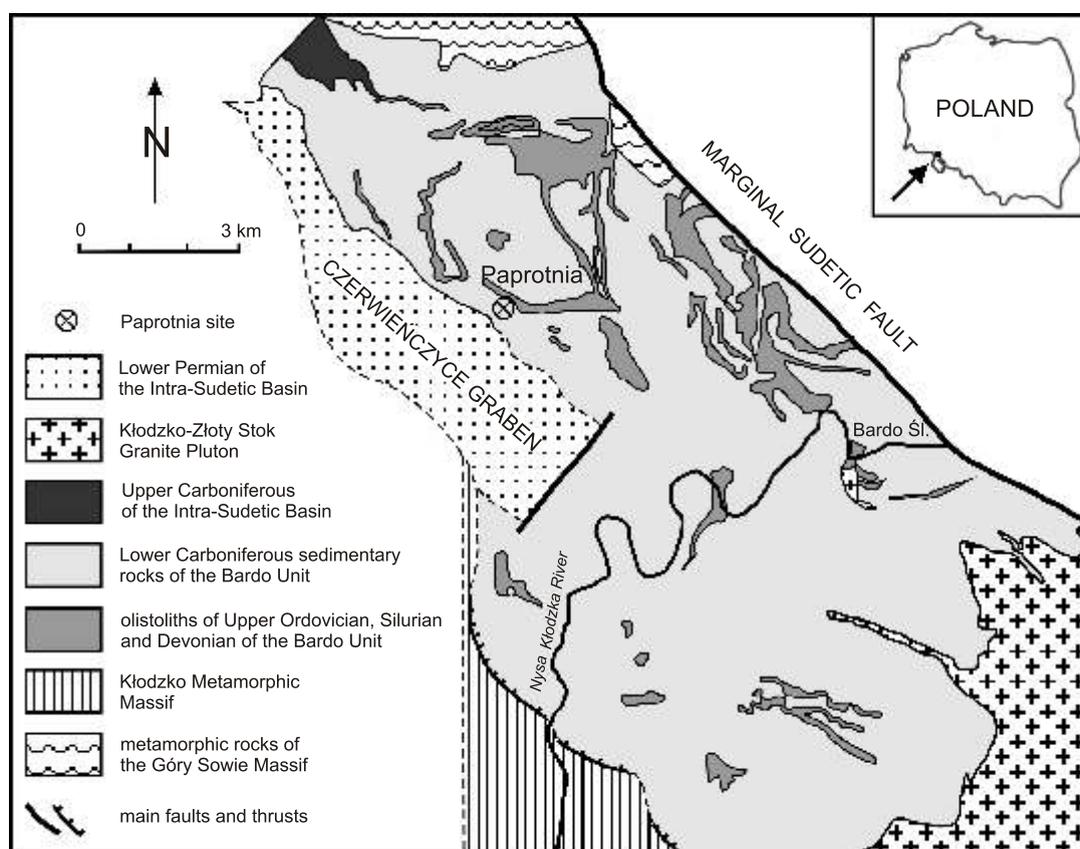


Fig. 1. Location of the Paprotnia site on the simplified geological map of the Bardo Unit (after Oberc, 1957 and Haydukiewicz, 2002; modified)

stage	British stages	Biostratigraphy	Lithostratigraphy			
			N	S		
VISEAN	Brigantian	V3c	Goniatites - Go	γ	WŁÓCZEK SEQUENCE	
					ORZECH SEQUENCE	?
					SREBRNA GÓRA FORMATION	WILCZA BEDS
	Asbian	V3b	α	δ	WINNA GÓRA SEQUENCE	PAPROTNIA BEDS ?
					WOJBÓRZ SEQUENCE	
	Holkerian	V3a	Ammonellipsites ( <i>Pericyclus</i> ) - Pe	γ		
	Arundian	V2a	V2b	β		
	Chadian	V1a	V1b	γ		
TOURNAISIAN	Courseyan	Tn3	Ammonellipsites ( <i>Pericyclus</i> ) - Pe	β		
					Tn2	
					Tn1b	
FAMENNIAN			<i>Gattendorfia</i>	α	GOŁOGŁOWY FORMATION	
					WAPNICA FORMATION	

Fig. 2. Generalized stratigraphic scheme of the autochthonous/parautochthonous succession of the Bardo Unit (according to Wajsprych, 1995, simplified and modified) correlated with the British Isles stratigraphy based on Harland et al. (1989)

The Paprotnia Beds contain a very rich fossil assemblage dominated by articulate brachiopods, corals (mainly colonial rugosa) and foraminifers, with less frequent cephalopods (goniatids and nautiloids), crinoids, bryozoan colonies, bivalves, gastropods, trilobites, ostracods and flora (Buch, 1839; Schmidt, 1925; Paeckelmann, 1930, 1931; Kühne, 1930; Górecka, 1958; Górecka and Mamet, 1970; Fedorowski, 1971; Haydukiewicz and Muszer, 2002, 2004; Kryza et al., 2008), that allow to assign the deposits to the ammonoid *Goniatites crenistria* Zone (Goα), which corresponds to the Asbian regional substage of the Upper Visean (V3b) (Fig. 2). The late Asbian age was supported by the SHRIMP zircon age of  $334 \pm 3$  Ma obtained for the bentonite layer A from the beds 1 of the Paprotnia section (Kryza et al., 2007, 2008, 2011). Recently, Górecka-Nowak and Muszer (2011) distinguished two miospore biozones in the section: *Tripartites vetustus*–*Rotaspora fracta* (VF) Biozone in the beds 1 and 2 and the *Cingulizonates capistratus* (Cc) Sub-biozone, the lower part of the *C. capistratus*–*Bellisporos nitidus* (CN) Biozone in the beds 3 (Fig. 3). The palynological results indicate that rocks of the Paprotnia section should be assigned to the Upper Asbian and Brigantian (Figs. 2 and 3).

## MATERIAL AND METHODS

Trace fossils described in this study were found during fieldwork mainly between 2008 and 2011 and a few recently found in 2012. The general morphology and orientation of the trace fossils were recorded in the outcrop and 122 samples were collected. The stratigraphic position of the trace fossils was also recorded and observations of the degree of bioturbation and degree of trace fossils density have been made. Several rock samples were cut and the ichnofabric was observed on polished surfaces using a *Nikon SMZ-2T* microscope. Almost all described specimens (with exception of field specimens) are housed at the collections of the Institute of Geological Sciences, Wrocław University (catalogue numbers ING/P-1 to ING/P-38, P1-01a to P1-27).

## SYSTEMATIC ICHNOLOGY

Sediments of the Paprotnia Beds contain relatively moderately differentiated assemblage of trace fossils. Their occur-





Fig. 4A, B – outcrop of the Paprotnia Beds

GPS coordinates N 50°31'57.6"; E 16°37'27.26"; B – outcrop photograph with specimen of *Zoophycos* on the lower bedding surface of the Paprotnia Beds studied only in the field (beds 1); hammer is 24 cm long

ture (Fig. 5D). This trace fossil from the Paprotnia Beds was described in detail and illustrated by Muszer and Haydukiewicz (2009, 2010). Specimens of *Zoophycos* are well-preserved but unfortunately incomplete because of the fragile host mudstones. Most measurements of these trace fossils are difficult because many specimens crosscut each other. There are some helical forms, which have only downward wrapped axial parts (Fig. 6B). The spreiten have a simple morphology comparable to the morphotype A as described by Olivero (2003).

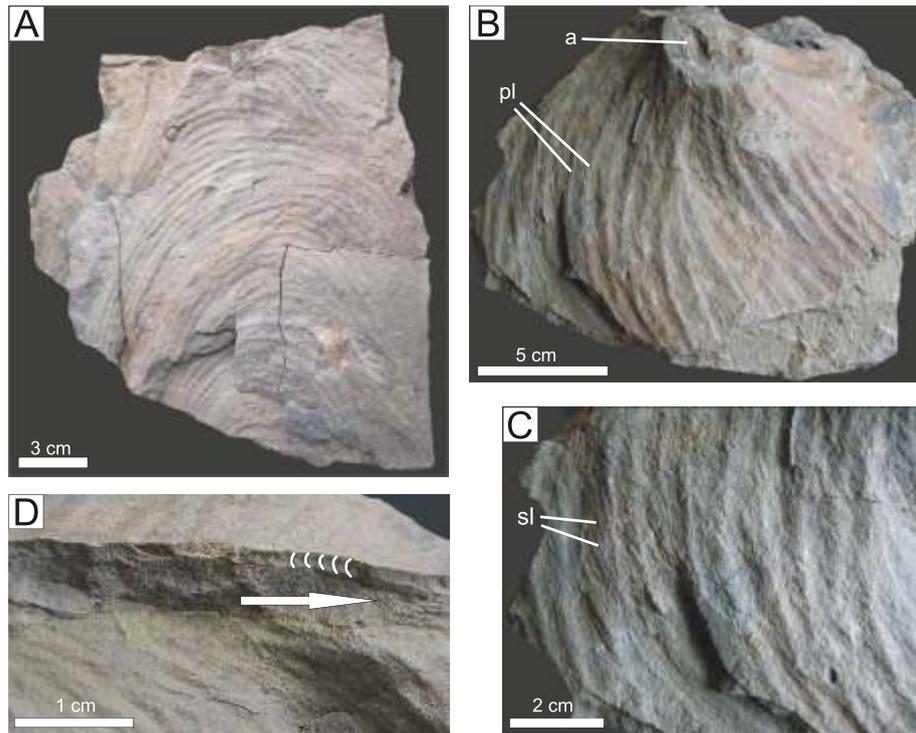
Muszer and Haydukiewicz (2009) recognized two morphotypes A1 and A2, which differ by the presence of secondary lamellae, the size of specimens and main characteristics. Morphotype A1 comprises the larger forms (length between 110 and 160 mm) mostly with secondary lamellae (Figs. 5, 6A, C, D), while morphotype A2 (Fig. 6B, C, E, F) includes smaller forms (length of up to 70 mm) without secondary lamellae. The width of marginal tubes is from 1–2 mm in morphotype A2 to 3–5 mm in morphotype A1. The minimal heights of the individual helical structures range from about 14 mm (morphotype A2) to about 20–35 mm (morphotype A1). The fragmentarily pre-

served marginal tubes are 1–2 mm (morphotype A2) to 3–5 mm (morphotype A1) wide. The distance between two subsequent lamellae is also different in both morphotypes. It ranges from 1–2 mm (A2) to 3–7 mm (A1). The diameter of axial tunnel varies from 12–24 mm (morphotype A2) to usually 19–30 mm (morphotype A1) and only in one specimen of morphotype A1 is 5 mm. The both morphotypes A1 and A2 occur in the same horizon. The acute angle between primary lamellae and secondary lamellae varies from 10° to nearly 30°. The studied specimens lack pellets in the spreite.

The unique complete specimen (morphotype A1), which was studied in the field, is a horizontal, U-shaped lobe (Fig. 4B), which is 260 mm long and 160 mm wide. Its marginal tube is 3 mm in diameter. The distance between two subsequent primary lamellae ranges from 3 to 8 mm. Any secondary lamellae have been observed in this specimen.

**R e m a r k s.** – *Zoophycos* from the Paprotnia Beds clearly corresponds to the constructional model of Gaillard and Olivero (1993). It is similar to Tournaisian forms from Belgium (Gaillard et al., 1999), whose secondary lamellae are not visible, and to the Lower Devonian specimens from Bolivia (Gaillard and Racheboeuf, 2006), though mostly smaller. The distance between two subsequent primary lamellae and the size of axial tunnel are very comparable to those from the middle Pennsylvanian *Zoophycos* of Nova Scotia (McIlroy and Falcon-Lang, 2006). The Paprotnia forms and the Lower Carboniferous Japanese specimens (Kotake, 1997) have similar an acute angle between the major and minor lamella.

*Zoophycos* is a complex burrow system, which was described from marine sediments from Precambrian to Recent (Crimes, 1987; Uchman, 1998). Traditional interpretations place *Zoophycos* within Seilacher's ethologic category fodinichnia (Seilacher, 1986) and include structures produced by endobenthic deposit feeders (Miller and D'Alberto, 2001). It has been also considered as reflecting bacterial farming (Bromley, 1991; Fu and Werner, 1995). In addition, Bromley (1991) proposed three alternative models to explain the downward transport of surface material (the refuse-dump, the cache and the gardening). Recently, the test made by Löwemark et al. (2007) allows to reject the gardening hypothesis in favour of a cache model. Uchman (1995) proposed the term "Zoophycos group" to include all the trace fossils that share some common morphological characteristics of *Zoophycos*. This ichnogenus was described from diverse range of sediments and very wide range of palaeoenvironments from infralittoral to abyssal (e.g., Osgood and Szmuc, 1972; Frey et al., 1990; Leuschner et al., 2002; Olivero, 2007) and even in glacial marine environment (Bhattacharya and Bhattacharya, 2007; Gong et al., 2008). The bathymetric range of this ichnotaxon has increased since the Jurassic (Ekdale and Bromley, 1984; Seilacher, 1986; Bottjer et al., 1988; Kotake, 1989, 1997; Miller, 1991; Bromley, 1996; Olivero, 2003; Wetzel et al., 2007; Knaust, 2009). Paleozoic *Zoophycos* was commonly recognized from shallow-water deposits (Osgood and Szmuc, 1972; Yurewicz, 1977; Frey and Pemberton, 1984; Miller, 1991; Ekdale and Lewis, 1991), but also occur in deeper marine environments (e.g., Burton and Link, 1991; Gaillard et al., 1999; Zapletal and Pek, 1999; Mikuláš et al., 2004; Gaillard and Racheboeuf, 2006). This ichnogenus is usually related to most often dysoxic environments and with low physical energy (e.g., Olivero, 2003; Mikuláš et al., 2004; Buatois and Mángano, 2011).



**Fig. 5. *Zoophycos* isp. – morphotype A1**

**A** – fragment of *Zoophycos* isp. (sample P1/12a/II); **B, C** – spirally coiled structure of *Zoophycos* isp. (sample ING/P-3), a – axial tunnel, pl – primary lamellae, sl – secondary lamellae; **D** – cross-sectional view of *Zoophycos* lamina with menisci (the sections of the primary lamellae – marked by white lines) indicating the direction of the structure extension (sample P1/15/I)

#### Ichnogenus *Chondrites* von Sternberg, 1833

##### *Chondrites* isp.

Fig. 7A–C

**Material and occurrence.** – Several fragments of specimens exposed in cross-sections and on the bedding surface (samples P1/12b/2, ING/P-28). The Paprotnia Beds (mudstones in the upper part of beds 1 – medium abundance).

**Description.** – Partially preserved complex tunnels, branching at sharp angles. The diameter of the tunnels ranges 1–3 mm. They are mostly horizontal or slightly angled to the bedding surface. Branching pattern resembles a dendritic network, which in cross-section appears as deep grey, elliptical or circular spots and tubes. Filling is darker and more fine grained than the host rock. Tunnels are up to 87 mm long and runs parallel to the bedding surface. Rarely they show a dichotomous Y-shaped ends on the polished surface (Fig. 7A, B), which is similar to *Pilichnus*, but *Pilichnus* have much thinner branched strings (Uchman, 1999; Mikuláš et al., 2004).

**Remarks.** – *Chondrites* was classified as a feeding structure (fodinichnion) produced by a so far unknown infaunal deposit-feeder (e.g., Seilacher, 2007), but the prevailing present interpretation is a chemichnion (e.g., Bromley, 1996; Mikuláš, 2006; Rodríguez-Tovar et al., 2010). Depending on various factors like feeding or fill style, two main tracemaker hypotheses were proposed: chemosymbiotic organism living at the aerobic/anaerobic interface (Seilacher, 1990; Fu, 1991; Rodríguez-Tovar and Uchman, 2004) or surface deposit-feeder backfilling the burrows with faecal material (Kotake, 1991; Rodríguez-Tovar and Uchman, 2004). *Chondrites* was found in

sediments from the Tommotian (Crimes, 1992) to Holocene (Löwemark et al., 2004) and represents high variety of ecological conditions: highly oxic (Wetzel, 1991) or oxygen depleted sediments and rich or poor in organic matter (Wetzel and Uchman, 2001). However, in most reported cases, *Chondrites* occurs in low energy environments (Seilacher, 2007) and substrate poor in oxygen in pore waters (e.g., Tyszk, 1994).

#### Ichnogenus *Palaeophycus* Hall, 1847

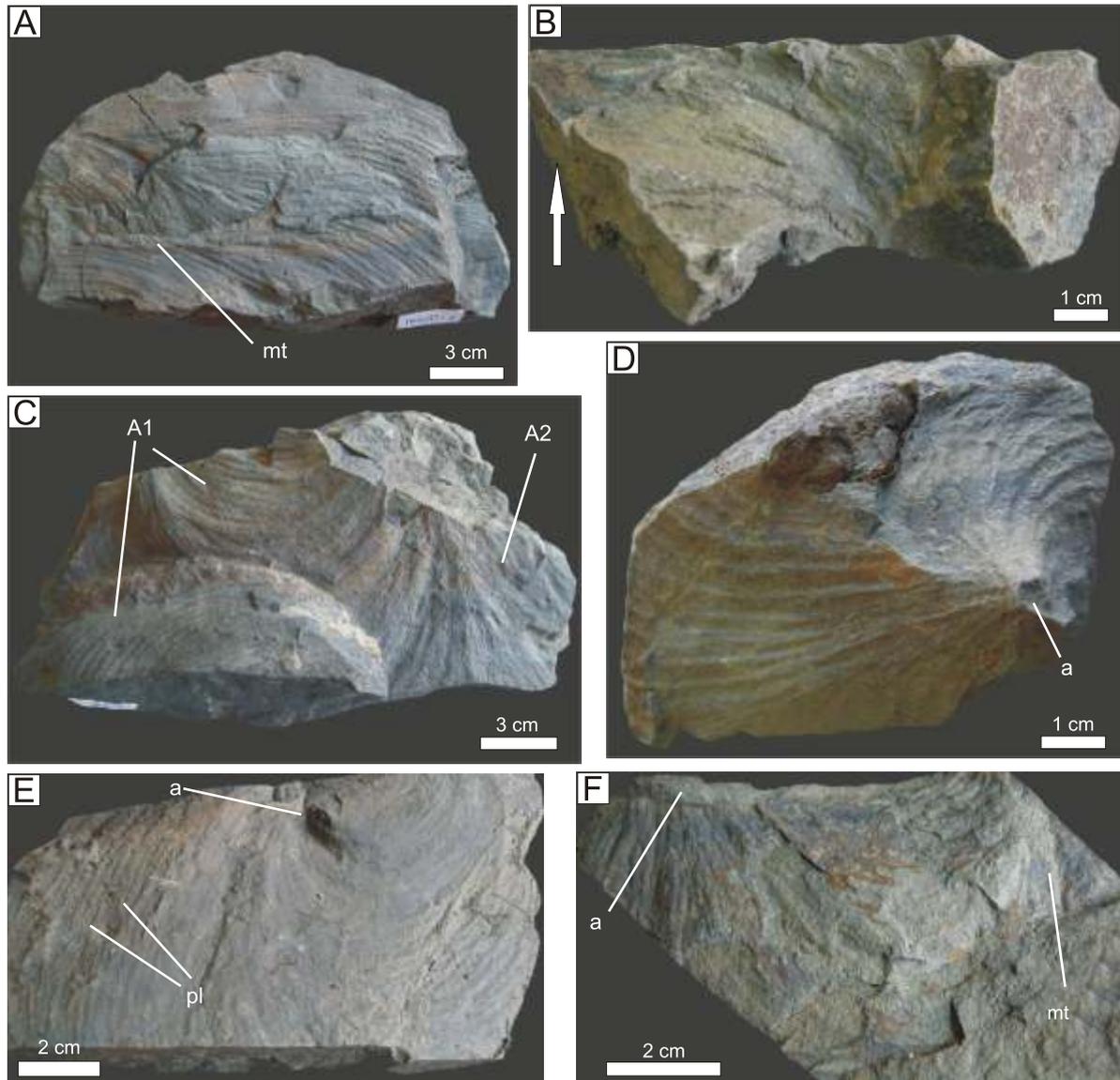
##### *Palaeophycus* isp.

Fig. 8A–D

**Material and occurrence.** – Several dozen specimens (samples P1/12b/1, P1/15b/1, P1/15b, P1/21). The Paprotnia Beds (mudstones in the upper part of beds 1 – medium abundance; greywackes of beds 2 – very common).

**Description.** – Cylindrical, simple or branched (Y-shaped branchings), straight to gently curved tunnels parallel or inclined to bedding plane, 2–4 mm in diameter, at least up to 154 mm long. Walls smooth, non-ornamented, occasionally thinly lined with clay, filled with the same material as the surrounding rock. Some specimens run just on the surface of *Zoophycos* structures (Fig. 8C). Many specimens crosscut each other (Fig. 8A, C).

**Remarks.** – *Palaeophycus* is considered as an eurybathic trace fossil and is found in the wide range of marine and freshwater environments from Precambrian to Recent (Pember-ton and Frey, 1982). It is interpreted as a domichnion of suspension feeders or predators, which filling is passive (Pember-ton and Frey, 1982). For detailed discussion of this ichnogenus see also Keighley and Pickerill (1995).



**Fig. 6. *Zoophycos* isp. – morphotype A1 and A2**

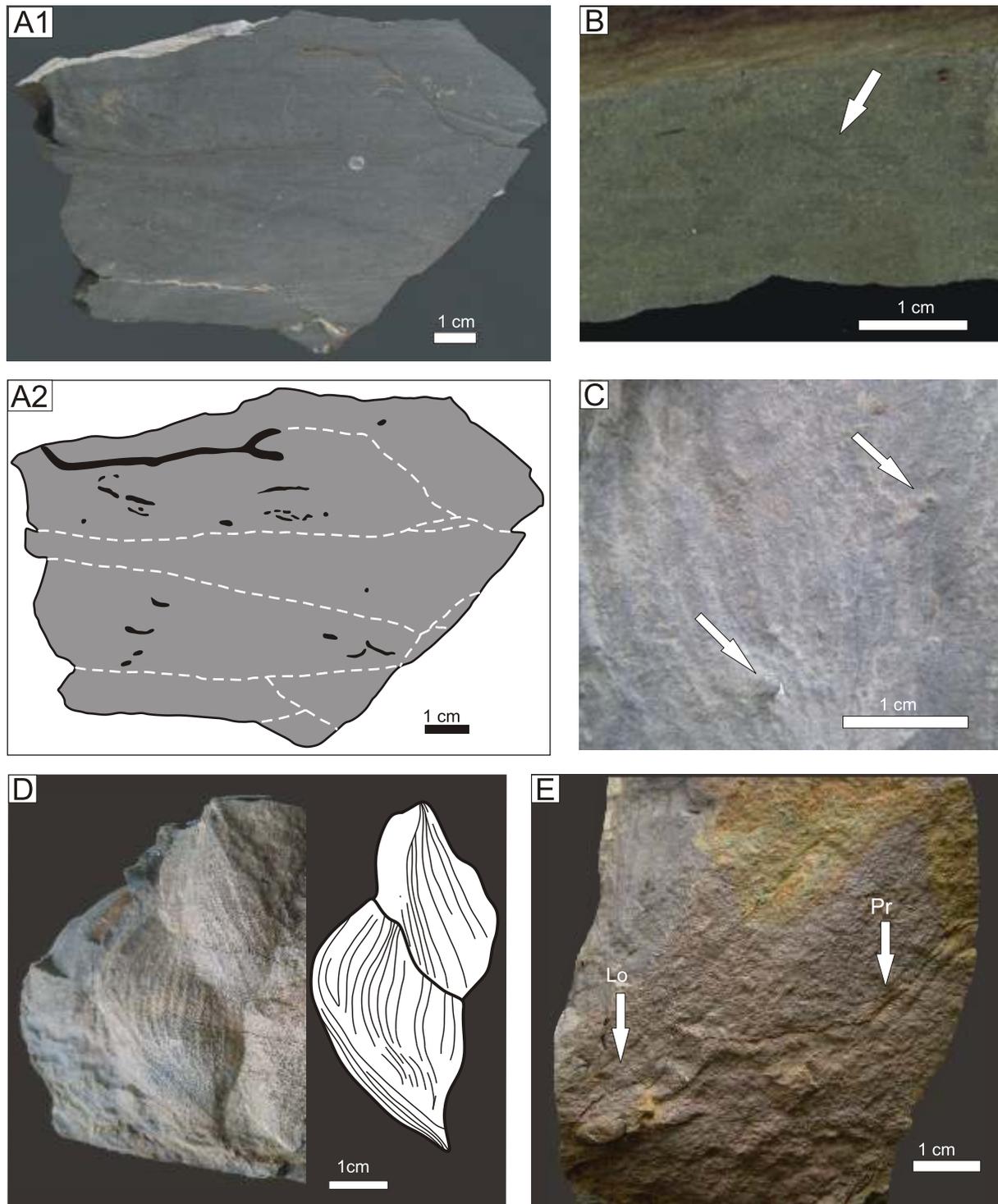
A – morphotype A1 (sample ING/P-1); B – orientation of the *Zoophycos* structure (morphotype A2) to the bedding surface; arrow marks the direction of the top of bed (sample P1/14d); C – morphotype A1 and A2 (sample P1/15b); D – morphotype A1 (sample ING/P-35); E – morphotype A2 (sample ING/P-23); F – morphotype A2 (sample ING/P-25); a – axial tunnel, mt – marginal tube, pl – primary lamellae

?daedaloid form  
Fig. 7D

**Material and occurrence.** – One specimen (sample ING/P-36). The Paprotnia Beds (mudstones in the upper part of beds 1). The sample was collected from a talus material and its occurrence is coincidental with very common abundance of *Zoophycos*.

**Description.** – Complex, three-dimensional, vertical to bedding spreite structure of helicoidal shape, composed of two distinct whorls. The external structure of whorls is individually striated. The set of striations runs sigmoidal or archwise across the face of each whorl. The height of whole structure is 35.4 mm and the width ranges from 7 to 13.9 mm for both whorls respectively.

**Remarks.** – Seeing that the sample was found in the debris material, the original orientation and direction of construction of the burrow (upward or downward) is impossible to determine. Proper identification of the trace is problematic due to its limited similarities with other ichnogenera. The morphologic features of the described specimen are best suited for the enigmatic highspired spreite trace fossil generally assigned by Seilacher (2007: p. 112, pl. 39) to “daedaloid burrows” group. However, that giant specimen was found only in the Upper Jurassic pelagic limestones of southern France. Thus, both age and facies are not compatible with those of the Paprotnia Beds. In overall appearance the held specimen resembles the Lower Ordovician *Daedalus desglandi* (Rouault, 1850) (Seilacher, 2007: p. 126, pl. 44), but is much smaller, not so high and tightly coiled, and again represents different age. In vertical view the inner, spiral part of *Dictyodora liebeana* (Geinitz, 1867) may



**Fig. 7.** *Chondrites* isp., ?daedaloid form, *Protovirgularia* isp. and *Lockeia* isp.

*Chondrites* isp. on the polished surface of sample P1/12/2 in photograph (A1 – dark tunnels) and line drawing (A2 – black colour); B – *Chondrites* isp. on the polished surface of sample ING/P-28; C – the ends of tunnels of *Chondrites* isp. on the surface of *Zoophycos* structure indicated by arrows, sample P1/15c; D – ?daedaloid form and outline, sample ING/P-36; E – *Protovirgularia* isp. (Pr) with visible arcuate curved segments and *Lockeia* isp. (Lo), sample P1/12a/IV

show some similarities with the described structure. *D. liebeana* is known from the Lower Carboniferous Culm facies of the Europe (Benton, 1982; Lehotský et al., 2002; Mikuláš et al., 2004) and Minorca Island (Orr et al., 1996; Llompert and Wieczorek, 1997). Nonetheless, the specimen from the Paprotnia Beds differs from *D. liebeana* in several distinctive features: (1) it lacks visible in bedding plane top view meandering band, (2) it has

different than “Tannenbaum-Typ” shape of the coil (*sensu* Zimmermann, 1893; Benton, 1982), and (3) occurs in shallow marine deposits, not in the deep-sea turbidite sediments. It is possible that the described specimen could represent the upper axial part of *Zoophycos*, but it does not have a distinct marginal tube. The precise identification of the trace maker has significant limitations, but judging by the helicospiral shape, external

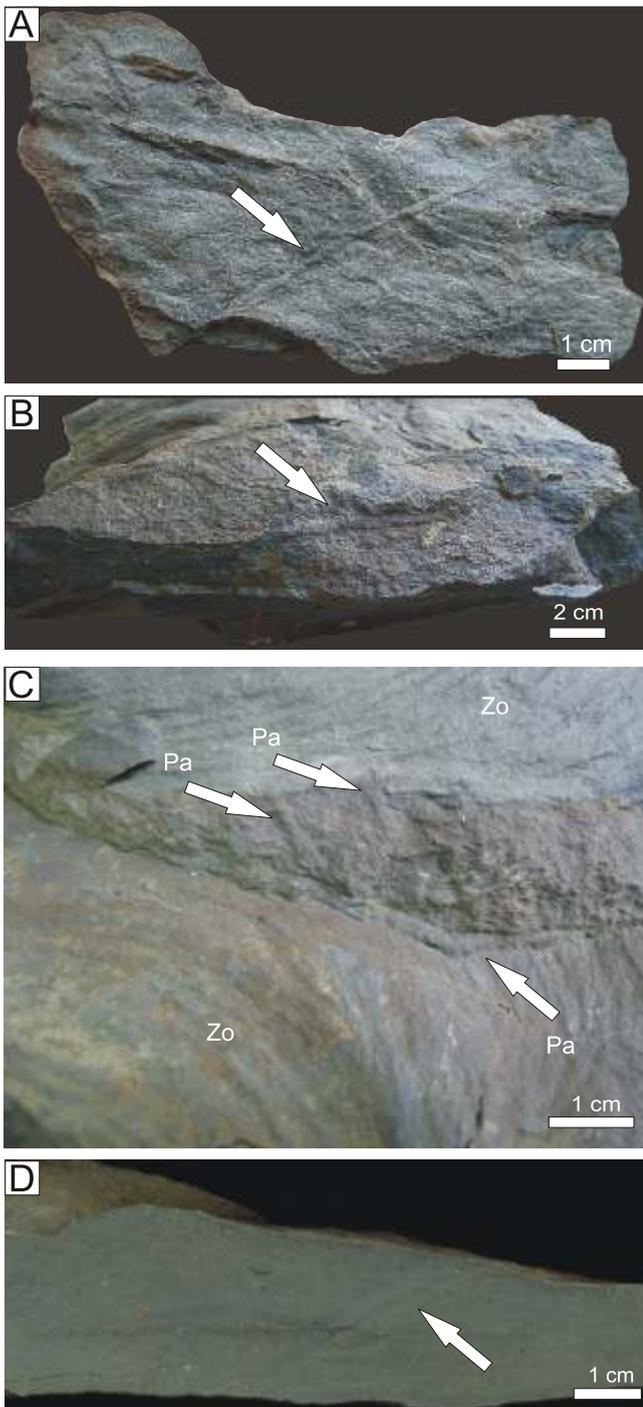


Fig. 8. *Palaeophycus* isp.

A – sample P1/21; B – sample P1/15b; C – *Palaeophycus* – Pa on the surface of *Zoophycos* – Zo and inclined to the surface, sample P1/15b; D – specimen on the polished surface of sample ING/P-2; arrows indicates the trace fossils

striations and vertical propagation of the burrow it is proposed that the trace is a feeding structure (fodinichnion) of a worm-like animal.

Ichnogenus *Protovirgularia* McCoy, 1850  
*Protovirgularia* isp.  
 Fig. 7E

**Material and occurrence.** – One specimen (sample P1/12a/IV). The Paprotnia Beds (mudstones in the upper part of beds 1).

**Description.** – Slightly undulating, unbranched, horizontal trail. Its length reaches 57.5 mm and width 3.5 mm. Internal structure consists of arcuate curved and chevron-like segments, highlighted by ribs. The ribs are unevenly spaced about 1–4 mm apart. No visible median ridge. The burrow is filled with sediment of the same type as the surrounding rock and terminated by *Lockeia* isp. (Fig. 7E).

**Remarks.** – This trace fossil reveals some similarities to *Protovirgularia rugosa* (Miller and Dyer, 1878), but it differs by predominance of arcuate curved segments over chevron-like ones. *Protovirgularia* isp. is classified as a locomotion trail of a deposit-feeding (repichnion) bivalve (Seilacher, 2007). It is known from various marine and freshwater deposits from the Arenig to Miocene (Uchman, 1998; Uchman and Gądzicki, 2006).

Ichnogenus *Lockeia* James, 1879  
*Lockeia* isp.  
 Fig. 7E

**Material and occurrence.** – One specimen (sample P1/12a/IV). The Paprotnia Beds (mudstones in the upper part of beds 1).

**Description.** – Elongated, single, almond-shaped mound preserved as a convex hyporelief, with smooth margin and a bit vague terminations. The trace is 7.5 mm long and 3 mm wide (Fig. 7E). It is closely associated with *Protovirgularia* isp.

**Remarks.** – *Lockeia* is interpreted as a bivalve resting trace (cubichnion; Seilacher, 2007). These traces occur in sediments representing a wide range of marine and freshwater environments since the Ediacaran (Abbassi, 2007).

Ichnogenus *Nereites* MacLeay, 1839  
*Nereites missouriensis* (Weller, 1899)  
 Fig. 9B, C

See Uchman (1995) for a detailed synonymy, supplemented here by the following:

- 1998 *Nereites missouriensis* (Weller); Głuszek, p. 534, fig. 13A, B.
- 2004 *Nereites missouriensis* (Weller); Mikuláš, Lehotský and Bábek, p. 85, pl. 7, fig. 1.
- 2009 *Nereites missouriensis* (Weller); Hoffmann, Paszkowski, Uchman and Szulc, fig. 20B, C.
- 2009 *Nereites missouriensis* (Weller); Olivero, Medina and López, p. 65, fig. 4a.
- 2012 *Nereites missouriensis* (Weller); Joseph, Patel and Bhatt, p. 205, pl. IV, 1.

**Material and occurrence.** – Several dozen of specimens (samples P1/23, ING/P-13b). The Paprotnia Beds (mudstones in beds 2 – medium abundance; sandy mudstones in the lower part of beds 3).

**Description.** – Horizontal, irregularly curved, winding and unbranched, meandering traces. The burrows are shallow and curve in all directions. The filling is formed by dark fine-grained material, mostly structureless, partially poorly meniscate and different than the host rock. The traces are surrounded by about 1 mm thick zone of reworked sediments, which is usually coarser than the host rock. The maximum preserved length of the trace is 55 mm and the width of the trace (without zone of reworked sediments) ranges from 3 to 6 mm.

**Remarks.** – The trace fossil *Nereites* has been described from many occurrences ranging from the Late Precambrian (Crimes, 1987) to the Miocene (Uchman, 1995; Hu et al., 1998) or possibly Quaternary (Ekdale and Lewis, 1991). *Nereites missouriensis* (Weller) has been interpreted as the internal meandering grazing trails (pascichnion) (Seilacher and

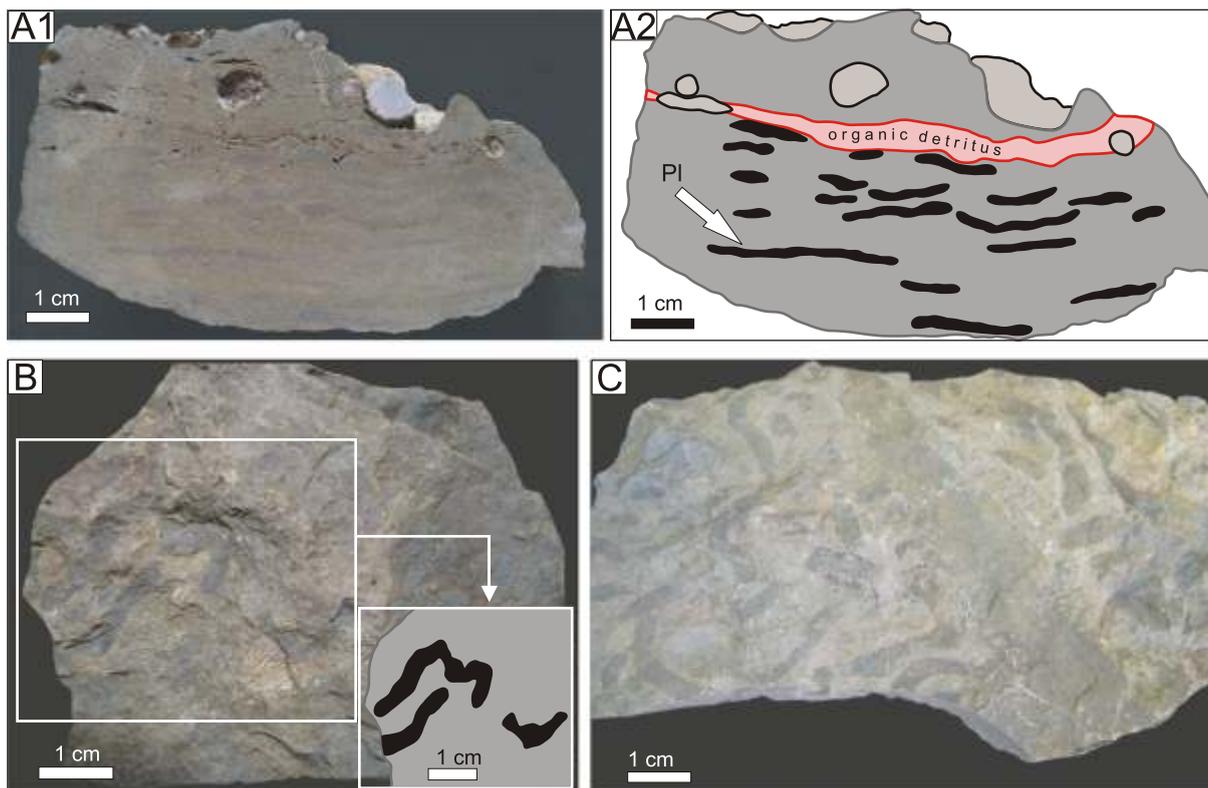


Fig. 9. *Planolites* isp. and *Nereites missouriensis* (Weller)

A1, A2 – *Planolites* isp. on the polished surface of sample P1/20d in the photograph of (A1) and line drawing (A2);  
 B, C – *Nereites missouriensis* (Weller) on the bedding surface (B – sample P1/23, C – sample ING/P-13b)

Meischner, 1965; Seilacher, 1986). The suggested possible producers were wormlike deposit-feeders or other organisms such as molluscs, arthropods, or holothuroids (e.g., Häntzschel, 1975; Głuszek, 1998; Mángano et al., 2000; Joseph et al., 2012 and references therein). *N. missouriensis* is a eurybathic form and a typical component of the *Nereites* ichnosubfacies, which is distributed in distal flysch facies (e.g., Uchman, 2007; Olivero et al., 2009; Joseph et al., 2012). However, these trace fossils also occur in other environments, such as tidal flats (Mángano et al., 2000), shallow-marine deposits (e.g., Crimes and Anderson, 1985) and freshwater lakes (Wetzel, 2002). Modern *Nereites* is restricted to the upper oxygenated sediment interval and is absent in anoxic sediments (Wetzel, 2002).

Ichnogenus *Planolites* Nicholson, 1873  
*Planolites* isp.  
 Fig. 9A1, A2

**Material and occurrence.** – Several specimens (sample P1/20d). The Paprotnia Beds (sandy mudstones in the middle part of beds 2 – medium abundance).

**Description.** – Straight or sinuous, unlined and unbranched, horizontal burrows, filled with material different than the host rock (Pemberton and Frey, 1982). The filling is finer grained than the host rock, dark grey and structureless. In cross-section the ichnogenus is cylindrical or ellipsoidal in outline. Their diameters vary from 2 to 3 mm. The longest measured tunnel is 35 mm long.

**Remarks.** – *Planolites* belongs to the group of eurybathic traces and is found in sediments of various marine and

freshwater environments, from the Precambrian to Recent (Pemberton and Frey, 1982). This ichnogenus is described as a facies-crossing form (Pemberton and Frey, 1982; Rodríguez-Tovar and Uchman, 2004). It is usually interpreted as a pasichnion structure produced by polyphyletic vermiform deposit feeders, which actively backfilled the burrows (Pemberton and Frey, 1982; Keighley and Pickerill, 1995; Rodríguez-Tovar and Uchman, 2004).

Ichnogenus *Altichnus* Bromley and Hanken, 1991  
*Altichnus* isp.  
 Fig. 10A

**Material and occurrence.** – One specimen (sample P1/22). The Paprotnia Beds (greywackes in the upper part of beds 2).

**Description.** – Straight, unbranched, almost vertical funnel-shaped tube. Diameter of the structure decreases from 11 mm at the opening to 2 mm at the bottom. Along the tube there are two visible widenings (Fig. 10A). Maximum observed length is 48 mm.

**Remarks.** – *Altichnus* is classified as a dwelling burrow of a suspension feeder (Gaillard and Racheboeuf, 2006). This trace is characteristic for marine shallow water environments since the Early Cambrian (Bromley and Hanken, 1991). The conical widenings of the tube of the specimen from the Paprotnia Beds probably reflects growing of their creators or may be the result of adjusting to the deposition of sediments (equilibrium traces). Given the ability to adapt to environmental changes, *Altichnus* tracemakers were probably opportunistic organisms (Gaillard and Racheboeuf, 2006).



**Fig. 10.** *Altichnus* isp., cf. *Thalassinoides* isp. and *Paleobuprestis sudeticus* isp. nov.

**A** – *Altichnus* isp. (sample P1/22), arrows show the widening of the tube; **B** – cf. *Thalassinoides* isp. on the bedding surface (sample ING/P-37); **C** – cf. *Thalassinoides* isp. on the polished surface (sample ING/P-37), arrows show the trace fossils; **D–F** – *Paleobuprestis sudeticus* isp. nov. (D, E – holotype – sample P1/24 a; one side is distinctly more bored than the other; F – sample P1/24b)

Ichngenus *Paleobuprestis* Häntzschel, 1962

**Description.** – Circular and elliptical borings and channels (diameter 2–10 mm) under bark of conifer fossil wood, recognizable all around tree and resembling work of Recent buprestids (after Häntzschel, 1962; Hasiotis 2004).

**Remarks.** – *Paleobuprestis* was first described by Walker (1938) as channels under the bark of *Araucarioxylon arizonicum* from the Triassic of Petrified Forest National Monument in Arizona (USA). According to Häntzschel (1975) the stratigraphical range of this ichnogenus is restricted to Triassic, but Hasiotis (2004) cited it also from the Upper Jurassic Morrison

Formation (USA). *Paleobuprestis* isp. has been also found in the Upper Cretaceous Price River Canyon (Hasiotis et al., 1994).

*Paleobuprestis sudeticus* isp. nov.

Fig. 10D–F

**H o l o t y p e.** – Sample P1/24a (Fig. 10D, E), repository: Department of Stratigraphic Geology, Institute of Geological Sciences, Wrocław University.

**T y p e l o c a l i t y.** – The Paprotnia Beds, the Bardo Unit, Sudetes, Poland.

**T y p e h o r i z o n.** – The Paprotnia Beds, beds 3.

**D e r i v a t i o n o f t h e n a m e.** – The ichnospecies name refers to Sudetes, where it was discovered.

**M a t e r i a l a n d o c c u r r e n c e.** – Over a dozen of specimens (samples: P1/24a, P1/24b, P1/24c). The Paprotnia Beds (greywackes in the middle and upper part of the beds 3 – medium abundance).

**D i a g n o s i s.** – Mostly straight or slightly curved, shallow and narrow channels without raised bands occurring on the casts of archaeocalamites stumps.

**D e s c r i p t i o n.** – Simple or branching, variably preserved channels closely associated with the casts of *Archaeocalamites* sp. stumps. Channels are often straight or slightly curved and preserved as a negative epirelief. They cross the stumps in various directions. Most of them run perpendicular or obliquely to the imprints of the *Archaeocalamites* vascular system. Channels are shallow (depth less than 1 mm) and without filling. Their diameter varies from 2 to 4 mm and length is up to 35 mm. Some traces are visible as single circular holes on the surface of the sample (Fig. 10E). This trace fossil is recognizable all around the stump, but it is worth noting that one side of the stump is distinctly more bored than the other (see Fig. 10D, E). Described channels are very similar to effect of work of Recent buprestid beetles (see Hüntzschel, 1975; Hasiotis, 2004).

**R e m a r k s.** – *Paleobuprestis sudeticus* isp. nov. differs from the other *Paleobuprestis* ichnospecies by substrate (wood material), course and size of the channels. In contrast to the other *Paleobuprestis* ichnospecies, which have been described only from conifer wood, *Paleobuprestis sudeticus* occurs on the surface of external molds of archaeocalamites. It should be emphasized that the wood material of archaeocalamites was certainly different than conifers. Unfortunately, the wood material is not preserved. *Paleobuprestis sudeticus* is very similar to *Paleobuprestis minima* Walker, 1938, but it differs by a lack of raised bands. Additionally, none of the traces completely encircled the stem. They have also slightly larger diameter. From *Paleobuprestis maxima* Walker, 1938 the specimens from the Paprotnia Beds differ in displaying much more tortuous course and also have a considerably smaller diameter.

The channels are considered as combined feeding and reproductive behaviour of adult and larval beetles of the family Buprestidae (fodinichnia, calichnia). Genise (1995) proposed the term xylichnia as a name for wood borings. These trace fossils are characteristic for terrestrial, wooded environments (Belayeva et al., 2002). *Paleobuprestis* has been described only from the Mesozoic (Walker, 1938; Hüntzschel, 1975; Hasiotis et al., 1994; Hasiotis, 2004). In light of the presented data, the specimens from the Paprotnia Beds are the oldest record of *Paleobuprestis*.

The wood borings from the Paprotnia Beds have probably been made in dead wood, but before advanced decay as the stems do not show signs of tissue response to plant wounding (feeding scars). The criteria used to recognize herbivory from detritivory in the fossil record were proposed by Labandeira (1998) and are poorly applicable in case of sediment-cast spec-

imens. According to this author, detritivory is the dominant feeding form of arthropods in Paleozoic terrestrial environments.

The oldest wood borings observed in microscale (under scanning microscope) are known from the Visean (Brigantian) fossil charcoal of gymnosperms from East Kirkton (Scotland) (Rolfe et al., 1990; Scott et al., 1992; Galtier and Scott, 1994) and from *Permnoxylon* (cordaites) petrified wood from the Lower–Middle Pennsylvanian (Cichan and Taylor, 1982). *Paleobuprestis sudeticus* isp. nov. was discovered in the upper Visean (Brigantian) sediments (Fig. 3) and actually is the earliest wood-boring trace fossil observed in macroscale and the first wood-boring trace fossil preserved on the archaeocalamites stems.

Wood borings become common from the Upper Carboniferous (Scott et al., 1992). Most of them are produced by organisms other than insects, especially oribatid mites (Labandeira et al., 1997), but some may have been created by cockroaches or other insects feeding on rotten wood (Scott and Taylor, 1983; Belayeva et al., 2002). The earliest possible beetle borings are in the Permian glossopterids (Grimaldi and Engel, 2005). Most insect borings are recorded from much younger strata – from the Mesozoic and Cenozoic (Genise, 1995). The earliest definitive beetle borings are from the Triassic of Europe and Arizona (Grimaldi and Engel, 2005). In the Mesozoic borings become more diverse, which is connected with the radiation of beetles (Labandeira, 2001).

Ichnogenus *Thalassinoides* Ehrenberg, 1944

cf. *Thalassinoides* isp.

Fig. 10B, C

**M a t e r i a l a n d o c c u r r e n c e.** – One specimen (sample ING/P-37). The sample was collected from a talus material of beds 3, the Paprotnia Beds (greywackes – rare).

**D e s c r i p t i o n.** – Horizontal, branching burrow system consisting of slightly flattened (Fig. 10C), unlined and smooth-walled components of variable size. The diameter of the tunnels varies from 8.8 to 16.3 mm in the irregularly swelled areas between and at branching points. The tunnel's fill is greywacke, homogeneous and structureless. The burrows display Y-shaped bifurcations and are preserved in a positive epirelief.

**R e m a r k s.** – The specimen was collected from a talus material, and it cannot be excluded that it constitutes a part of a larger, probably three-dimensional structure. The vertical shafts are not visible as in type F of *Thalassinoides* described by Doyle et al. (2005). Occasionally crossed burrows could give an impression of false branching (Keighley and Pickerill, 1997). Such features limit the categorical assignment of the trace fossil. According to Myrow (1995) and Seilacher (2007), the bulb-shaped dilatation of the tunnels are interpreted as “turnaround” regions of the trace maker. Considering all the characteristics, the described structures remind the most of the ichnogenus *Thalassinoides* Ehrenberg.

*Thalassinoides* is known from various marine environments (Monaco et al., 2012), however, it occurs mainly in shelf and neighbouring deposits (Bromley, 1996) and is commonly considered as an indicator of oxic conditions (Savrdá and Bottjer, 1986; Doyle et al., 2005). This ichnogenus is known since the Cambrian to the present (Myrow, 1995; Ekdale and Bromley, 2003; Sprechmann et al., 2004; Hofmann et al., 2011), but became really widespread during Mesozoic and Cenozoic (Rodríguez-Tovar and Uchman, 2004). The burrows attributed to *Thalassinoides* have been produced mainly by scavenging and deposit-feeding crustaceans (Frey et al., 1984; Ekdale, 1992; Myrow, 1995; Bromley, 1996; Watkins and Coorough, 1997; Uchman, 2007) and are widely interpreted as a fodini-

chnia or less frequently as a domichnia (Rodríguez-Tovar et al., 2010) or agrichnia (Bromley, 1996).

## TRACE FOSSIL ASSOCIATIONS

In the Paprotnia Beds trace fossils are variously distributed (Fig. 3). This is linked both to their frequency and ichnotaxonomic diversity within the section. In the lower and middle parts of beds 1 any trace fossils have been found. The greatest diversity of trace fossils occurs in the upper part of beds 1 and in beds 2, but it distinctly decreases upwards the profile (Figs. 3 and 11). Three ichnoassociations, each identified by the most abundant and common ichnotaxa, have been recognized. According to Gaillard and Racheboeuf (2006) ichnoassociation is a specific interval that probably corresponds to relatively stable environmental conditions.

### ZOOPHYCOS–CHONDRITES–PALAEOPHYCUS ASSOCIATION

This ichnoassociation is typified by high density and moderate diversity of trace fossil assemblages and comprises the following ichnotaxa: *Zoophycos*, *Chondrites*, *Palaeophycus*, ?daedaloid form, *Protovirgularia* and *Lockeia* (Fig. 3). The association has been recognized in the upper part of beds 1. *Zoophycos* is the dominant ichnotaxon and its high and medium abundance defines the range of the described association (Fig. 3). The first *Zoophycos* appears in the mudstone beds interval where no significant changes in lithology are observed. This may suggest that the main factor for their appearance had to be controlled by palaeoecological conditions such as bottom waters, sediment oxygenation and nutrient content. However, the abundance of *Zoophycos* clearly increases just above the main bentonite horizon (E; Fig. 3), and as noted by Haydukiewicz and Muszer (2002) and Muszer and Haydukiewicz (2009) this may have been contributed to the enrichment of bot-

tom waters and sediment with fertilizing substances. In the described part of the profile the lack of significant changes in the morphology of these traces along their vertical range has been observed. As suggested by Olivero (1996), one of the most favorable conditions for the development of such complex structures as *Zoophycos* is a low rate of sedimentation. However, his studies were limited to the Jurassic and Cretaceous forms.

*Zoophycos* is closely associated with *Chondrites*, which sporadically crosscuts *Zoophycos* structures (Fig. 7C) and most likely represents the deepest tier. It is difficult to determine the precise penetration depth of *Chondrites*. These trace fossils occur only within mudstones and do not propagate into sandy mudstones. They are limited strictly to the local *Zoophycos* abundance zone. *Zoophycos* and *Chondrites*, as it is widely accepted (e.g., Bromley and Ekdale, 1984; Buatois and Mángano, 2011), penetrate deeply into the substrate in oxygen-depleted sediment, but this does not necessarily indicate poor oxygenation in bottom waters. *Zoophycos* is a prerequisite of somewhat higher oxygen contents in the sediment.

In this ichnoassociation *Palaeophycus* is quite often found. *Zoophycos* is also crossed by *Palaeophycus* at various angles (Fig. 8C) and some *Palaeophycus* run just on the surface of *Zoophycos* structures. It is not inconceivable that the producer of *Zoophycos* and *Palaeophycus* was the same organism (Miller, 2003). In this case, *Zoophycos* would represent feeding structures (fodinichnion), while *Palaeophycus* would represent dwelling structures (domichnion) of the same animal. *Protovirgularia* and *Lockeia* occur rarely and have a very limited vertical distribution (Fig. 3). Also ?daedaloid form is very rare and its vertical range coincides with the local abundance zone of *Zoophycos*.

The spatial relations between the trace fossils of the described ichnoassociation indicate three tiers: the shallowest tier is represented by *Protovirgularia* and *Lockeia* which occur only on the surface of the mudstone beds, deeper include *Palaeophycus*, ?daedaloid form and *Zoophycos* traces, and the deepest tier is characterized by *Chondrites*.

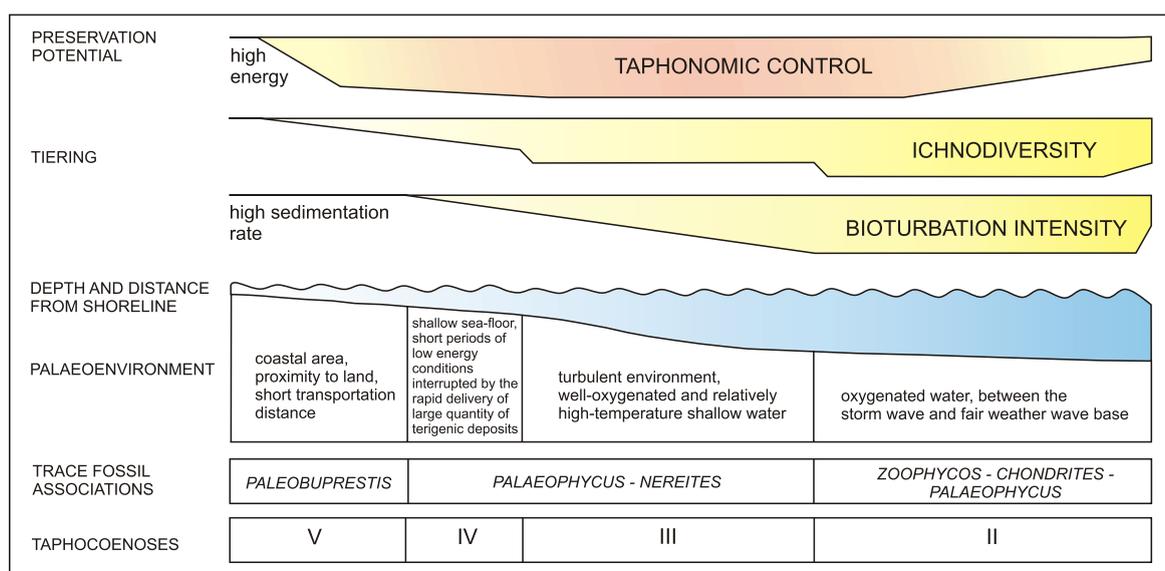


Fig. 11. Diagram of the relationships between ichnofabric trends, controlled by ichnodiversity and bioturbation intensity, bathymetry and ichnoassociations correlated with taphocoenoses (II–V; Haydukiewicz and Muszer, 2002)

Diagram is inspired by fig. 13 of Gaillard and Racheboeuf (2006)

The tracemakers of large and complex structures (*Zoophycos*), may occupy the sediment by the relatively long period of time, and hence they could have a significant impact on the surrounding environment. Through the expansion of their structures they could have controlled the organization and development of the ambient, local ecosystems (Miller, 2003). As a result, the coexisting trace fossils may not represent a large variety and/or large quantities (taphonomic processes should also be taken into account). These relationships seem to be confirmed in the studied association, where *Zoophycos* dominates other traces and that corresponds to the *Zoophycos* ichnofacies in terms of Seilacher (1967, 2007). The *Zoophycos* ichnofacies is most characteristic for quiet-water settings below the storm wave base, particularly in shelf to slope areas (Buatois and Mángano, 2011). As stated in Frey and Seilacher (1980), one of the significant environmental controls of this ichnofacies is a lowered oxygen level associated with abundant organic material.

#### PALAEOPHYCUS–NEREITES ASSOCIATION

This association is characterized by medium density and medium to low diversity of trace fossil assemblages, which consist of *Palaeophycus*, *Nereites missouriensis* (Weller) (Fig. 11), *Zoophycos*, *Planolites* and *Altichnus* (Fig. 3). Disappearance of complex trace fossils and domination of simple, mostly horizontal forms suggest changes in palaeoenvironmental conditions, which are also reflected by changes in lithology. The *Zoophycos* specimens observed in the upper part of beds 2 are rare, clearly smaller and show less regular structure. This corresponds to the change in lithology from mudstones to sandy mudstones and greywackes.

*Palaeophycus* is a dominant ichnotaxon in this association, which occurs most commonly and is present in greywackes. This suggests that its tracemaker colonized the environment with an increased input of clastic material. Due to the very simple construction, it is likely that these traces reflect one single type of behavior of their producers and the structure formation process should have been relatively short (in comparison to the complex *Zoophycos*).

*Planolites* occurs locally only within the sandy mudstones between limestone lenses and its presence corresponds to moderate energetic conditions. As soon as these conditions change to become more turbulent, which is manifested in the presence of organodetrital laminae (crushed shells and individual columnals of crinoids), this ichnotaxon disappears (Fig. 9A1, A2). Only horizontal, small in diameter forms of *Planolites* were found here. Both *Planolites* and *Palaeophycus* represent shallow tiers but they differ in abundance within the described association. The increased density of their traces is confined to irregularly distributed horizons within beds 2, what suggests the presence of recurring changes in palaeoecological conditions.

*Nereites missouriensis* (Weller) abundance is medium to low. This ichnogenus occurs in grey mudstones and sandy mudstones, which are slightly lighter in colour, than others. It may suggest better oxygenated waters and sediments. As evidenced by presence of tortuous traces produced while grazing, it is likely that the sediment was fairly rich in nutrients. The organism does not have to overcome long distances to acquire food.

The appearance of *Altichnus* may suggest faster delivery of the clastic material at the top of the studied ichnoassociation (Fig. 3). The presence of nearly vertical traces could indicate shallow, high-energy environmental conditions. This trace fossil association corresponds to the *Cruziana* ichnofacies (Seila-

cher, 1967, 2007), which occurs from just above the fair-weather wave base to the storm wave base (Buatois and Mángano, 2011).

#### PALEOBUPRESTIS ASSOCIATION

This ichnoassociation is represented by the lowest diversity and low to moderate density of trace fossils assemblage and include only two ichnotaxa: cf. *Thalassinoides* isp. (Fig. 11) and *Paleobuprestis sudeticus* isp. nov. (Fig. 3). In comparison to previous associations, the abundance of distinguished ichnotaxa and intensity of bioturbation considerably decrease. The significant change in the lithology could also be observed – sediments are becoming coarse-grained and consist mainly of greywackes. The association occurs in the middle and upper parts of bed 3.

*Paleobuprestis sudeticus* isp. nov. is closely associated with stems of *Archaeocalamites* sp. and occurs only on the surface of a few percent of the trunk sediment-casts. They were formed on land and then transported to the marine environment probably by a river. The amount of the stem casts with preserved feeding traces could have been modified by processes:

- occurring on the land, also those related to initial adaptation of the trace maker to new food source and modification of feeding mode;
- during transportation phase where the stems were exposed to mechanical damage;
- controlled by stress factors in the marine environment such as sedimentation rate or fossilization processes.

The density of *P. sudeticus* varies from moderate (Fig. 10D) to low (Fig. 10E) within the studied assemblage and within separate stem samples. The irregular, side depending distribution of those traces seems to reflect the stem position in the terrestrial environment. The more intensively bored side could have been more accessible for trace makers. The lack of many clear signs of mechanical damage may suggest short transportation distance. Morphologic features of horsetail stems such as hollow pith area could have prevented the long-term floatation (they could quickly fill with water and sank) and also indicate proximity to land (Haydukiewicz and Muszer, 2002).

The trace fossil cf. *Thalassinoides* isp. is preserved partially and it is difficult to estimate the depth of their bioturbation. The incomplete bioturbation could imply a stress factor which affected the completion of the structure or may suggest erosion of the above laying sediment and latter exhumation of the trace level upon the bedding plane (Doyle et al., 2005). The occurrence of erosion episodes in this environment may explain the development of a local discontinuity or hiatus between the type F *Thalassinoides* bearing beds and the beds deposited above them (Doyle et al., 2005). Furthermore, as it is reported by Górecka-Nowak and Muszer (2011) this part of the Paprotnia section (beds 3) is incomplete (with several hiatuses), what may affect the overall low diversity and density of traces within the described ichnoassociation. The ichnogenus *Thalassinoides* is frequently related to the oxygenated conditions and soft, but fairly cohesive substrates (Bromley, 1996; Buatois and Mángano, 2011).

#### PALAEOENVIRONMENTAL INTERPRETATION

The lithological record and vertical succession of the palaeontological material (taphocoenoses, ichnoassociations) were used to the palaeoenvironmental reconstruction of the

Paprotnia Beds deposition (Figs. 3 and 11). Fossils and trace fossils reflect the different colonization stages of the substrate, which was controlled by bathymetric changes in the marine basin from offshore to nearshore conditions. That conclusion is also supported by the last palynological studies (Górecka-Nowak and Muszer, 2011).

The lowest part of the Paprotnia section (lower part of beds 1; Fig. 3) is composed of claystones and mudstones with rare intercalations of micritic limestone beds. These sediments contain taphocoenosis I (Haydukiewicz and Muszer, 2002), whose main components are cephalopods, small spiriferids, thin-shelled chonetids, productids, gastropods, scarce bivalves and terrestrial plant detritus. Some ostracods, foraminifers, small amounts of calcareous algal detritus and various calcareous tubes and spines (some of them are serpulid and brachiopod remains) occur in this assemblage. Trace fossils were not found. The benthic community is mainly represented by epifaunal suspension and deposit feeders, which inhabited a clayey-muddy soft ground. The low taxonomical diversity of this community, the small size of benthic taxa, the thin shells and lack of bioturbation may indicate the oxygen-deficient bottom waters in mid- or outer shelf conditions. Miospores are very abundant, but often pyritized and poorly preserved (Górecka-Nowak and Muszer, 2011).

The mudstones with bentonite layers and greywacke intercalations from the middle and upper parts of beds 1 contain taphocoenosis II (Haydukiewicz and Muszer, 2002). When compared to the previous taphocoenosis, this one is enriched in solitary rugosa, trilobites, fragments of crinoids and bryozoan colonies, whereas the relative abundance of cephalopods distinctly decreases. Brachiopods are represented by mainly spiriferids, productids and some chonetids. The abundance of foraminifers and ostracods is variable. The deposits also contain calcareous algal remains (palaeoberesellids). Numerous trace fossils (mainly represented by *Zoophycos*) are also present in the upper part of beds 1 and their richness increases vertically. In this part of the profile the association *Zoophycos–Chondrites–Palaeophycus* was recognized (Fig. 3). The progressive increase in species richness in taphocoenosis II, the dominance of epifaunal suspension feeders, and the presence of burrows in the host sediment may be regarded as an evidence of aerobic conditions at the sea-floor. A decrease of the intensity of miospore pyritization and their better state of preservation is distinctly visible (Górecka-Nowak and Muszer, 2011). These sediments were accumulated in the environment located between the storm wave and fair weather wave bases, in oxygenated water, but the dark grey sediments suggests that substrate was probably poor in oxygen in pore waters. The benthic organisms of this taphocoenosis could have existed in an environment with a gradually increasing influx of terrigenous material and bottom water turbulence. The progressive increase of fossils and trace fossils diversity, recorded above the thickest bentonite layer (E), could indicate water fertilization, which could lead to intensification of phytoplankton and zooplankton development.

In the middle part of the Paprotnia section (beds 2), within mudstones and greywackes with lenses of organodetrital limestones, the taphocoenosis III was recognized (Haydukiewicz and Muszer, 2002). The relatively high fossil frequency of particular benthic organisms (corals, brachiopods, polychaetes) and the distinct decrease of cephalopods are characteristic for this taphocoenosis. The coral associations mainly contain various species of *Lithostrotion* and *Diphyphyllum* (Fedorowski, 1971), which formed bushlike and subceroid or ceroid colonies. It is probable that small patches in which corals and algae were abundant were formed during short periods of low clastic inflow.

Almost well-preserved productoid valves (mainly large *Gigantoproductus*) occur in coral-rich calcareous lenses. Chonetids are also common in this taphocoenosis, but the abundance of spiriferids decreases. Some of the organodetrital limestone lenses contain rich calcareous algal remains (Dasycladaceae), ostracods and foraminifers. Recent dasycladales are found exclusively in warm waters, usually at low latitudes (Beadle, 1988) and occur in masses not deeper than 30 m, sporadically exist up to 90 m (Flügel, 1985; Brett et al., 1993). The various kinds of trace fossils are of common occurrence (Fig. 3) and the association *Palaeophycus–Nereites* was recognized in this part of the section. It can be assumed that the organisms of this community lived in turbulent conditions in shallow subtidal sea-floor with moderate to periodically higher energy conditions and well-oxygenated waters. The abundance of corals and dasycladales may indicate a relatively warm-water environment. The calculated seawater temperature was estimated on the basis of the oxygen isotope composition of Early Carboniferous brachiopod shells from a variety of western European locations and is oscillating between 23 and 38°C (Bruckschen and Veizer, 1997).

In the lower part of beds 3 of the Paprotnia section, in the mudstones and greywackes, the taphocoenosis IV was distinguished (Haydukiewicz and Muszer, 2002). It is composed of scarce, diminutive brachiopods, infaunal bivalves, fragments of bryozoans and crinoids. The macrofaunal fossils are usually fragmentarily preserved and associated with foraminifers, ostracods, small gastropods and calcareous algae detritus, which are distributed only in the lower part of the mentioned sedimentary package. The association *Palaeophycus–Nereites* continues until the end of this taphocoenosis. The drastically reduced fossil assemblage, occurring only in the thin mudstones intercalating the greywackes, reflects a renewed settling of the eurytopic organisms only. The low state of preservation of shells, and rare trace fossils point to a high-energy environment of near-shore conditions.

The uppermost part of the Paprotnia section (middle and upper parts of beds 3) is composed of greywackes with mudstones and sandy-mudstone intercalations. These sediments contain the taphocoenosis V, which is represented only by the numerous remains of terrestrial plants (mainly horsetail and lepidodendron stems, fern leaves and seeds). Faunal remains are totally absent. The miospores are well-preserved, not pyritized, but their frequency is extremely low and phytoclasts are numerous (Górecka-Nowak and Muszer, 2011). It should be interpreted as a result of increasing sediment input during accumulation and the shorter distance of their transportation. In this part of the Paprotnia section the *Paleobuprestis* association has been distinguished. The presence of cf. *Thalassinoides* isp. and redeposited *Paleobuprestis* implies a nearshore environment. The listed components of this community suggest a proximity to land and a short transportation distance.

## SUMMARY AND CONCLUSIONS

Eleven, ethologically diversified and dominated by the feeding traces of deposit feeding organisms, ichnotaxa have been described in the Paprotnia Beds. The ichnotaxa occur only in the middle and upper parts of the Paprotnia section (upper part of beds 1, beds 2 and beds 3 – Fig. 3). Among them a new ichnospecies *Paleobuprestis sudeticus* has been created. It is the oldest recorded evidence of wood-boring trace fossil observed in macroscale and the oldest preserved on the archaeocalamites stems.

Based on all of the occurring trace fossils, their frequency and ichnotaxonomic diversity, three associations: *Zoophycos–Chondrites–Palaeophycus*, *Palaeophycus–Nereites* and *Paleobuprestis* have been recognized. The ichnodiversity decreases upward the profile from six ichnotaxa in the *Zoophycos–Chondrites–Palaeophycus* association to two ichnotaxa in the *Paleobuprestis* association. It may be related mainly to changes of environmental conditions and the partial replacement of the complex trace fossils (e.g., *Zoophycos*, *Chondrites*) by mostly simple forms (e.g., *Altichnus*, *Palaeophycus*). The availability of nutrients and the feeding mode of the trace makers seem to have important influence on trace fossil distribution, especially in the *Zoophycos–Chondrites–Palaeophycus* association correlated with taphocoenosis II. *Zoophycos* is the most abundant trace fossil in the Paprotnia section and its concentration is limited to the upper part of beds 1. From the beds 2, upwards the profile, significant changes in the environmental conditions have been observed. It is reflected either in lithology, taphocoenoses and ichnoassociation composition (Fig. 3). *Palaeophycus–Nereites* association is well correlated with taphocoenosis III (the richest benthic assemblage) and with taphocoenosis IV. Availability of food supply does not always imply the increased bioturbation. Despite the relatively high nutrient content (huge amount of organic detritus) in *Paleobuprestis* association (beds 3), water energy and high sedimentation rate were the main factors controlling the trace fossils distribution. The lowest ichnodiversity and bioturbation intensity observed in

the uppermost part of the profile (beds 3) could be additionally explained by the incomplete lithological record, what is confirmed by palynological data (Górecka-Nowak and Muszer, 2011).

The Paprotnia Beds represent a unique record of the Asbian–Brigantian transition. The ichnological data provides the evidence to support the opinion of Haydukiewicz and Muszer (2002) and Górecka-Nowak and Muszer (2011) that deposition of the studied rocks took place in the shallowing marine environment, during the offshore to onshore transition in the warm, probably tropical climate at low latitudes. In the light of performed studies, the palaeoenvironmental interpretation presented by Wajsprych and J drysek (1994) and Wajsprych (1995) is not confirmed.

The beds 1 and the lower part of beds 2, which are assigned to the upper Asbian are a shallower-water equivalent of the pelagic *crenistrina* Limestone (the Culm facies of Variscan Europe). The upper part of the Paprotnia section (the upper part of beds 2 and beds 3) represents incomplete littoral sediments of the Brigantian, and is a record of the European Brigantian third-order regression (Ramsbottom, 1973; George et al., 1976).

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