Invertebrate trace fossil assemblages from the Lower Hettangian of Sołtyków, Holy Cross Mountains, Poland

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ABSTRACT: Invertebrate trace fossil assemblages from the Hettangian (Early Jurassic) alluvial plain deposits of Sołtyków (Holy Cross Mts, Poland) represent three terrestrial ichnofacies: the Mermia ichnofacies (entirely aquatic), Scoyenia ichnofacies, and Coprinisphaera ichnofacies. They span environments from shallow lacustrine to different subaerial fluvial environments. Bivalve burrows and traces, oligochaetae, insect and crayfishes burrows, plant roots, vertebrate tracks and other types of trace fossils record information on biodiversity and palaeoecological conditions. The Sołtyków ichnoassemblages confirm that terrestrial ichnocoenoses were quite diversified, chiefly a result of a changing water table and food availability. Diversity of trace fossils was supported by the strongly mosaic character of local environments. Bivalve burrows are very diversified, and several ichnogenera have been distinguished. Trace fossil producers as well as functional, taphonomic and preservational aspects of ichnofossils are discussed. The following ichnotaxa have been recognized: *Lockeia siliquaria* James, 1879; *L. amygdaloides* (Seilacher, 1953); *L. czarnockii* (Karaszewski, 1974); *Scalichnus* isp.; *Scoyenia* isp.; *Spongeliomorpha* isp.; *Spongeliomorpha carlsbergi* (Bromley and Asgaard, 1979); *Cruziana problematica* (Schindewolf, 1921); cf. *Cruziana* isp.; *Rusophycus* isp.; *Diplichnites* isp.; cf. *Kouphichnium* sp.; *Planolites* isp.; *Palaeophycus* isp.; *Cochlichnus* isp.; cf. *Helminthoidichnites* isp.; cf. *Xylonichnus* isp., and *Linckichnus terebrans* Schlirf, 2006. Various structures attributed to arthropod burrows (vertical to subvertical tunnels), chambered insect nests of Pallichnidae affinity or other nests with septa, earthworm burrows as well as enigmatic radial chambers, likely made by crayfishes, are illustrated. The new bivalve dwelling ichnotaxon *Calceoformites uchmani* igen. et isp. n. is described.

INTRODUCTION

Invertebrate trace fossils have been recognized in the Early Jurassic deposits of the Holy Cross Mountains, representing various fluvial, lacustrine, and marginal-marine environments (Karaszewski 1962, 1971, 1974; Pieńkowski 1985, 2004a). During field work in 2000-2006 in the northern part of the Holy Cross Mountains, well preserved invertebrate trace fossil assemblages were identified in the Lower Hettangian terrestrial Zagaje Formation excavated at the Sołtyków dinosaur tracksite (Figs 1, 2). The Sołtyków exposure (Fig. 3) is an old, long abandoned clay pit. Sołtyków is a well-known site with a rich footprint assemblage of dinosaurs and other tetrapods (for review see Gierliński *et al.*

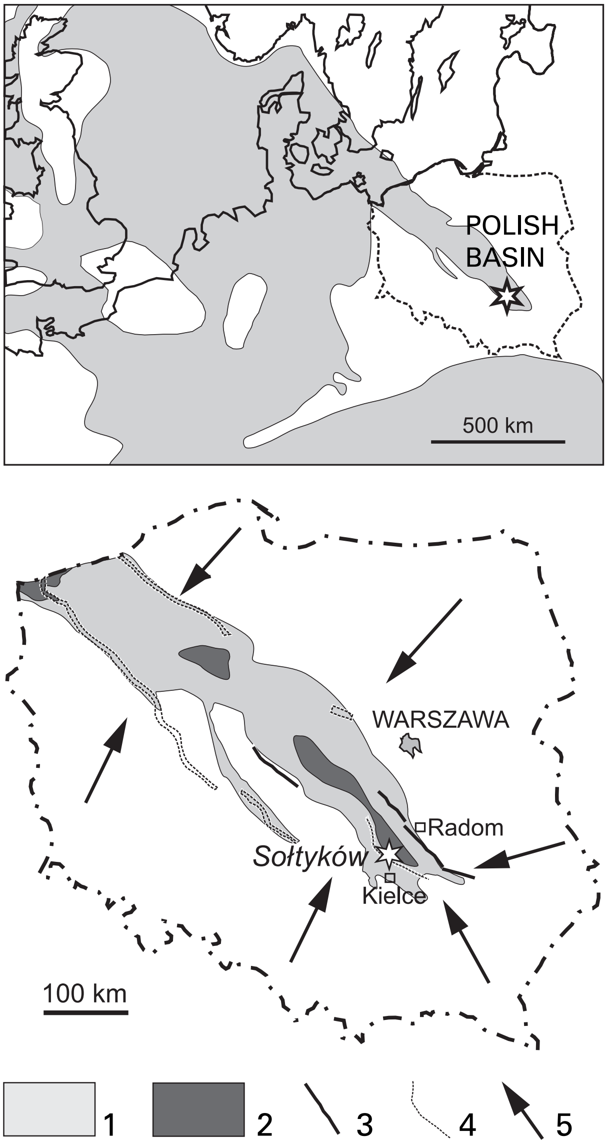

Fig. 1. Hettangian basins of Poland and the rest of Europe and location of Sołtyków outcrop, source areas left in blank: 1 – dominance of alluvial deposits; 2 – dominance of lacustrine deposits; 3 – main syn-sedimentary faults; 4 – other syn-sedimentary troughs and faults; 5 – main directions of sediment transport.

2004). A dinosaur nesting site was also described (Pieńkowski 1998) which resulted in a discussion of the problem (Sabath *et al*. 1999; Pieńkowski 1999). Recently, the Sołtyków exposure has been declared a nature reserve.

Preliminary notes about these trace fossils were published by Gierliński *et al*. (2004) and Pieńkowski (2004a, b), but until now the remainder of the invertebrate ichnofauna has not been documented in detail. Pieńkowski and Niedźwiedzki (2006) briefly reported on the invertebrate trace fossils from Sołtyków, but the presence of some trace fossils bearing a superficial (*cf*. Hasiotis 2002) similarity to such ichnotaxa as *Coprinisphaera, Celliforma*, *Conostichus* and *Conichnus* has not been confirmed. The Sołtyków outcrop reveals highly diverse, rich and well-preserved invertebrate trace fossil assemblages representing domichnia, equillibrichnia, fugichnia, repichnia, fodinichnia and callichnia in the lacustrine and fluvial environments of the Zagaje Formation. A detailed sedimentological interpretation of the Sołtyków site was given by Pieńkowski (2004a).

In the last twenty years, our knowledge of terrestrial (nonmarine, freshwater) invertebrate paleoichnology has greatly increased. Seilacher (1967) was the first to define the terrestrial Scoyenia ichnofacies. Bromley and Asgaard (1979) made a classic study of an extensive ichnofauna from the Late Triassic deposits of Greenland. Later on, Smith *et al*. (1993) proposed the Termitichnus ichnofacies (Coprinisphaera ichnofacies according to Genise *et al*. 2000) as a subset of the Scoyenia ichnofacies. Subsequently, Buatois and Mángano (1995) and Buatois *et al*. (2002) proposed the Mermia ichnofacies for trace fossil assemblages of subaqueous lacustrine environments, and Genise *et al*. (2000) defined the Coprinisphaera ichnofacies for insect trace fossil associations in paleosols. Buatois *et al*. (2002) and Gillette *et al*. (2003) proposed a scheme for terrestrial ichnoassociations, with three ichnofacies: Scoyenia, Mermia, and Coprinisphaera. Buatois *et al*. (2002) limited the Scoyenia ichnofacies to dry environments. Lawfield and Pickerill (2006) addressed the problem of the Scoyenia-Mermia ichnofacies transition.

The purpose of this paper is (1) to describe systematically the trace fossils, and (2) to recognize the ichnofacies (*i.e.* to relate the ichnotaxa to the various depositional environments) from the continental Zagaje Formation at Sołtyków.

The invertebrate trace fossils described are housed in and have been catalogued by the Geological Museum of the Polish Geological Institute in Warsaw (collection prefix Muz. PIG).

GEOLOGICAL SETTING AND PALAEOENVIRONMENTAL BACKGROUND

The Sołtyków exposure is known as a classical outcrop of alluvial-lacustrine deposits (Pieńkowski and Gierliński 1987; Pieńkowski 2004a, b), with a prominent lacustrine package in the middle part

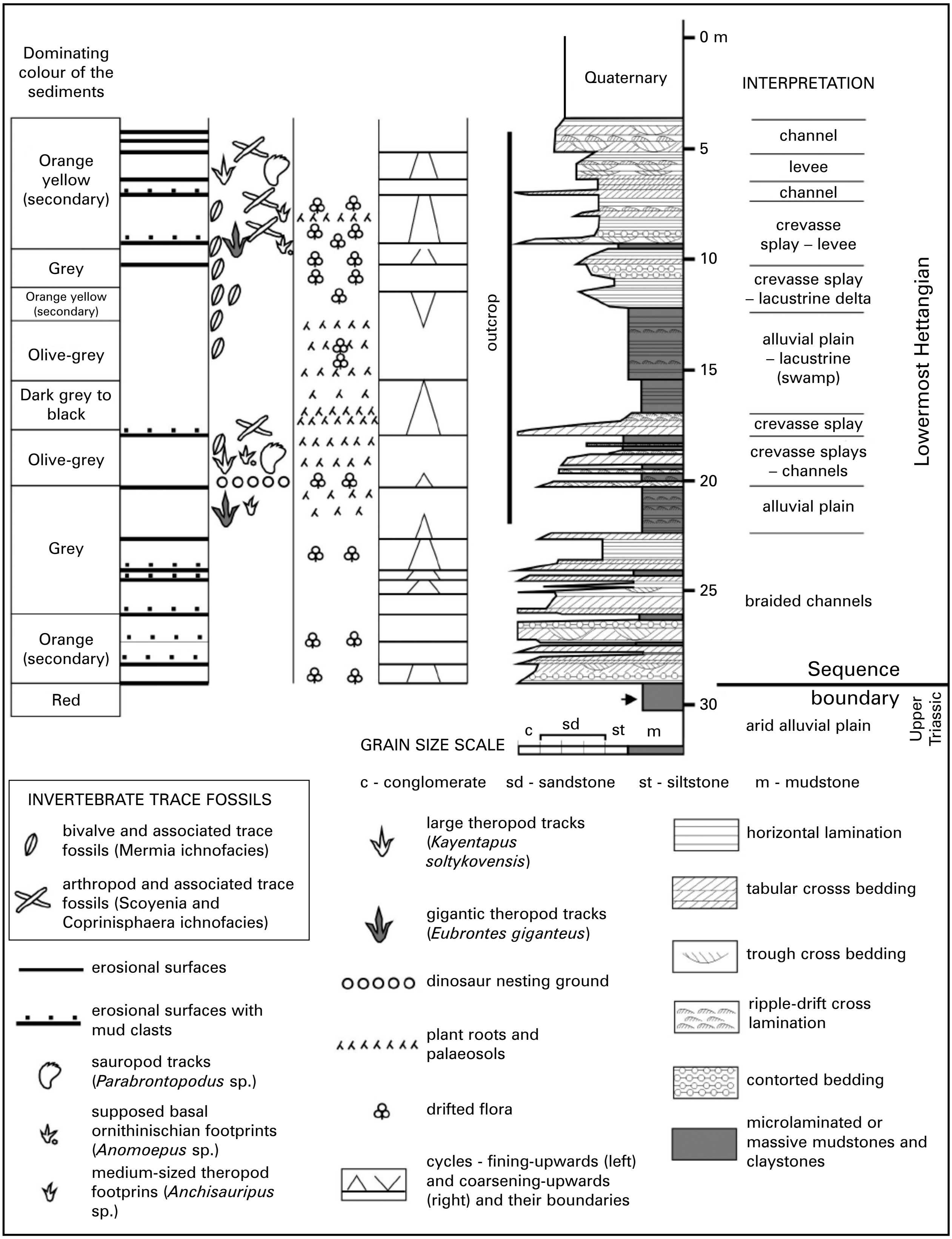

Fig. 2. Lithology of the Sołtyków outcrop and its position in the Sołtyków borehole with sedimentological interpretation and location of invertebrate trace fossils.

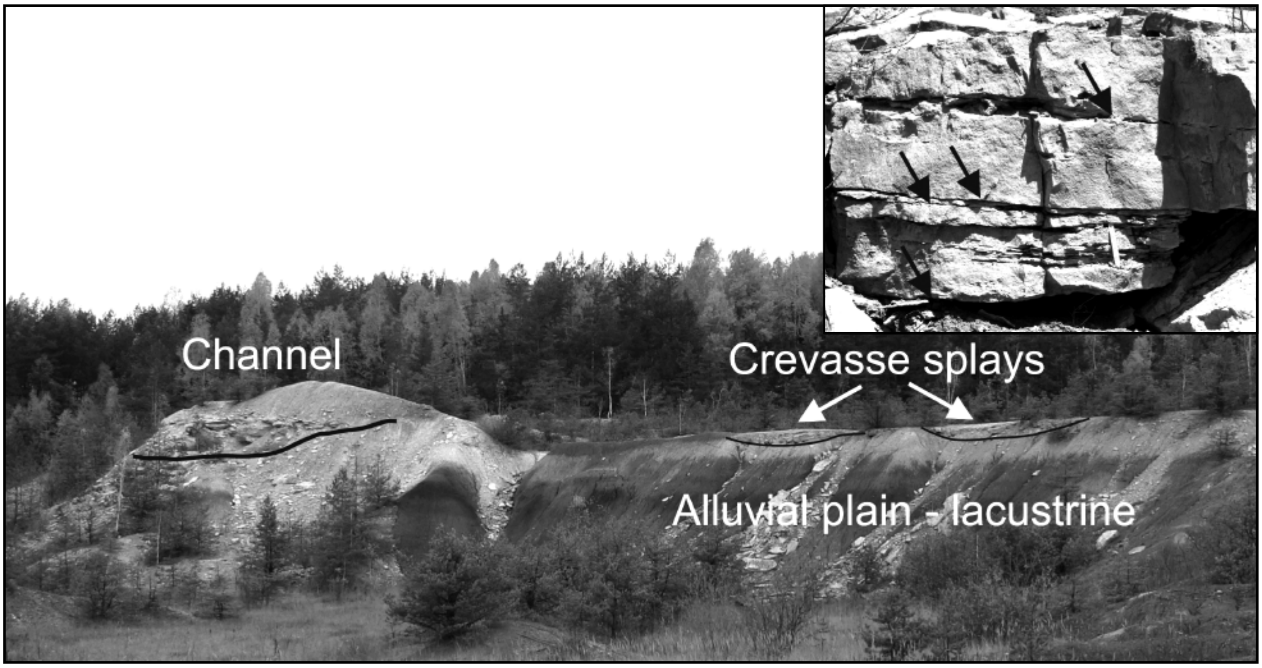

Fig. 3. Sołtyków outcrop revealing alluvial plain-lacustrine mudstones and channel/crevasse splay sandstones (arrowed). Meandering channel depositional subenvironment (main channel, on the left) is represented by medium- to poorly sorted, trough- cross bedded, laterally accreted sandstone lithofacies. Crevasse splay depositional subenvironment (often underlying the meandering channels) are of both type 1 (sharply based) and type 2 (progradational) crevasses. Inset: multi-stage infilling of the crevasse splay (type 1) channel with reactivation surfaces (arrowed). The crevasse splays provided an excellent environment for development and preservation of numerous trace fossils, including bivalve burrows.

of the present-day outcrop and channel/crevasse deposits in its upper part (Figs 2, 3). Floral remains point to an earliest Jurassic (Hettangian = Lias alpha 1-2) age (Wcisło-Luraniec 1991; Ziaja 2006), and the sequence stratigraphic correlation (Pieńkowski 2004a, b) allows one to narrow its age to the Early Hettangian (Planorbis Chron). The Sołtyków exposure fits the avulsion-controlled (crevassing-anastomosing) fluvial sedimentation model (Farrel 2001). However, some features such as laterally-accreted bedding point also to the presence of high-sinuosity/meandering streams (Pieńkowski 2004a). Miall (1977) distinguished four principal types of river, recognisable on the basis of plan-view morphology: braided, meandering, straight and anastomosing. The types of river are controlled by such chief factors as: water discharge, sediment load, channel slope and type of vegetation. Anastomosing/avulsion patterns of an interconnected network of low-sinuosity channels occur where contemporaneous branches of a single river weave around permanent, commonly vegetated, islands or disconnected segments of floodplain (Miall 1996). Anastomosing/avulsion patterns are most common on extremely low-gradient alluvial plains, where stream power is low and the banks consist of muddy, cohesive sediment or are highly vegetated (Nanson and Croke 1992; Emery and Myers 1996). The Sołtyków exposure (Figs 2, 3) comprises a mixed meandering/anastomosing alluvial plain with a channel depositional subenvironment (medium- to poorly sorted, trough- cross bedded, laterally accreted sandstone lithofacies) with, underlying both, type 1 (sharply based, with the sudden incursion of sediment-laden water and sediment transport perpendicular to the main channel) and type 2 (unconfined flow with the basinward progradation of a minor mouth bar/crevasse channel couplet) crevasses – Farrel (2001). Crevasse splays developed at local breaches in the levees which funnelled the flow from the channel during the flood, and provided conduits for suspended- and bed-load sediment dispersal into near-channel (often sub-aquatic – lacustrine) portions of the floodplain (Galloway and Hobday 1996). Crevasse splays in Sołtyków are typical sedimentary “garbage piles”, accumulating large amounts of plant debris and mud clasts. They differ from the associated channel subenvironment deposits in their smaller grain sizes and unit thicknesses. According to the avulsion model (Farrel 2001), an initial avulsion stage is accomplished predominantly by the development of crevasse splay complexes which cause the enlargement of new channels and abandonment of old ones. Channelised crevasse splays show a multistage infilling with reactivation surfaces (Fig. 3). This indicates that the local breaches in the levees occupied the same position for a longer time, funnelling the flow in much the same place during many flood events. The fact that the type 2 crevasses appear in the middle part of the section indicates a growing aggradational/avulsion tendency associated with a much higher water table (Aslan and Autin 1999). Fine bed-load to suspended load sediment was deposited in the floodplain as “overbank” sediments during floods and as “normal” sedimentation in the lacustrine environment. It should be noted that Aslan and Autin (1999) believe that avulsion, rather than simple overbank deposition, contributes to the construction of fine-grained floodplains to a greater degree than is generally recognised. The most frequent overbank/lacustrine lithofacies at Sołtyków is represented by dark, organic-rich, laminated mudstones. Mudstones are dark-grey to black, laminated or of a massive appearance, with numerous plant roots. The crevasse splay subenvironment was particularly favourable for preservation of dinosaur footprints (Pieńkowski and Gierliński 1987, 1999; Gierliński *et al.* 2001) Also invertebrate burrows are concentrated mostly in crevasse splay deposits, and to lesser extent in floodplain deposits and levee deposits (the latter are not very common in Sołtyków due to the low preservational potential of levee deposits being prone to subsequent erosion).

Palaeosols are both of the podzol and gleysol type (see Arndorff 1993). The relatively thick and distinct package of lacustrine deposits in the middle part of the Sołtyków outcrop points to some permanency of the lake/swamp area, with an entirely gleysol type of palaeosol. Plant fossils in the Sołtyków exposure are very abundant and well preserved. The list of plants includes *Neocalamites*, matoniacean, osmundacean and other indeterminate ferns, as well as pteridosperms, benettitaleans and conifers (Reymanówna 1991; Wcisło-Luraniec 1991). Other fossils that occur in Sołtyków are represented by unionid freshwater bivalves, insect remains (Wegierek and Zherikhin 1997), the fresh-water ostracode *Darwinula* sp., and scales of palaeoniscid fishes. Poorly preserved conchostracan carapaces were also found in the lacustrine mudstones.

SYSTEMATIC PALAEOICHNOLOGY

Resting traces (cubichnia)

Lockeia James, 1879. Attributed to bivalves.

Lockeia siliquaria James, 1879

DESCRIPTION: Hypichnial (positive hyporelief), almond-shaped trace with pointed terminations, from 0.2 to 10 mm long, 2-4 mm wide, and 2-6 mm high. Rare in Sołtyków locality.

Lockeia amygdaloides (Seilacher, 1953)
(=*Pelecypodichnus amygdaloides* Seilacher, 1953 – younger synonym, Maples and West 1989),
Fig. 4: 1; Fig. 5: 2-3; Figs 6, 7.

DESCRIPTION: Hypichnial (positive hyporelief), almond-shaped, relatively shallow (semi-relief) traces with sharp or oblong endings, from 5 to 20 mm long, 2-9 mm wide, and 2-6 mm high. In vertical cross-sections rounded or V-shaped. Changing regularity of traces is associated with the type of sediment in which they were preserved.

REMARKS: According to Seilacher (1953), Osgood (1970) and Bromley (1996) these forms represent the resting traces of bivalves. They can occur in large aggregates (Fig. 4). Occasionally, traces within such agglomerations show a preferred orientation, probably parallel to the palaeocurrent direction (Fig. 4: 2; Fig. 6), which is associated with locomotion of the burrowing animal. It should be noted that *Lenticraterion bohdanowiczi* Karaszewski, 1971 from the Early Jurassic sediments in Gielniów, Poland (Karaszewski 1971) clearly corresponds to *Lockeia amygdaloides* (Seilacher, 1953).

Lockeia czarnockii (Karaszewski, 1974)
[=*Umbonichnus czarnockii*; described by
Karaszewski (1974), revised at the generic level
by Pieńkowski (1985) as a younger synonym of
Lockeia James, 1879 (=*Pelecypodichnus*
Seilacher, 1953)] (Fig. 5: 1)

DESCRIPTION: Hypichnial (positive hyporelief), high, drop-shaped, asymmetric traces with strongly convex semi-relief. One termination is strongly convex, whereas the opposite termination merges with the sole of the sandstone bed.

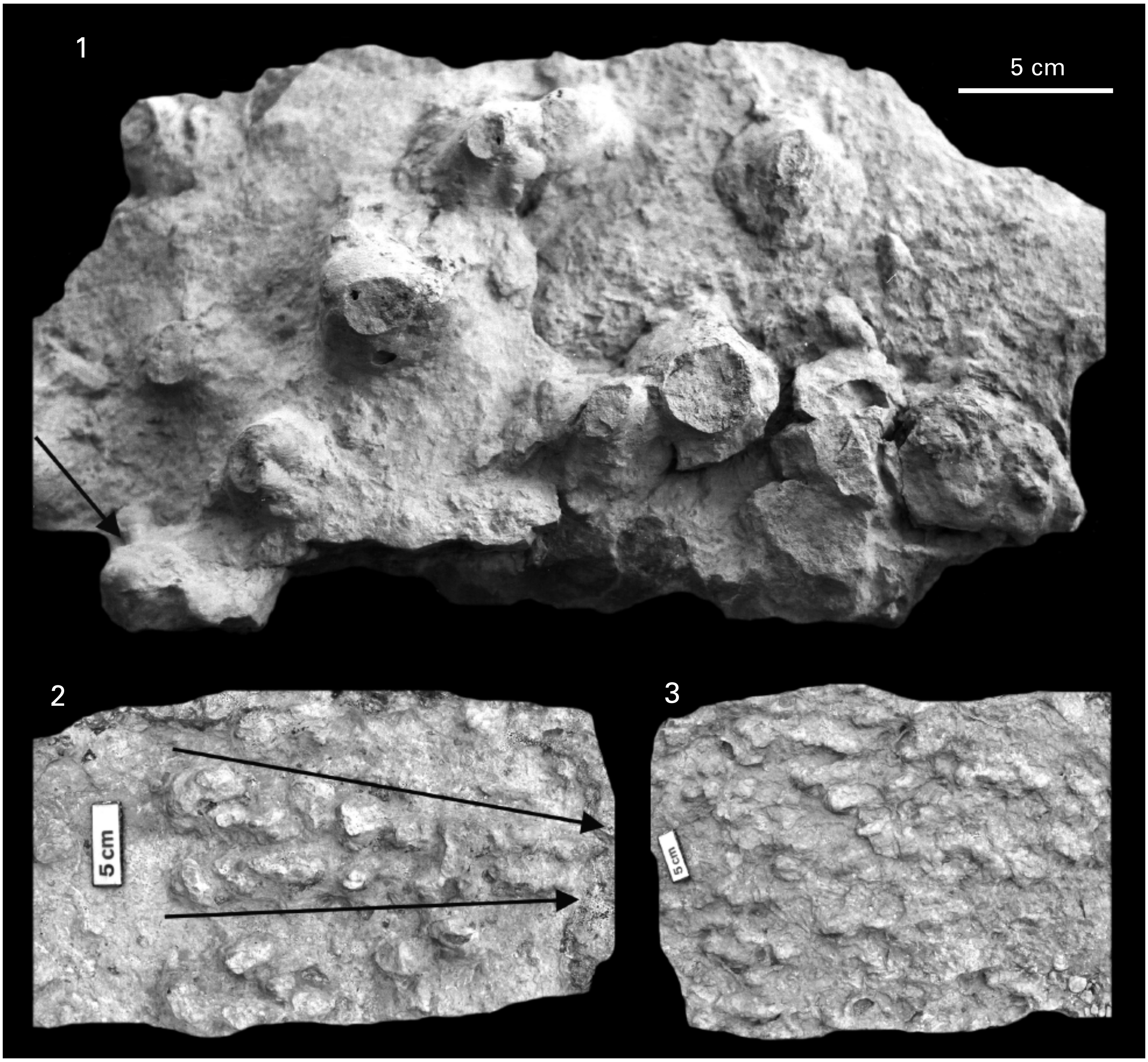

Fig. 4. Bivalve dwelling/resting structures: 1 – various dwelling/resting burrows produced by bivalves subsequently to flood/depositional events. Note drop-shaped *Lockeia czarnockii* (Karaszewski, 1975) and almond-shaped *Lockeia amygdaloides* (Seilacher, 1953) and other bivalve trace fossils, arrowed – the form similar to *Conostichus broadheadi* Lesquereux, 1880 – for detail see Fig. 9: 2; also *Calceoformites uchmani* ichnog. ichnosp. nov., not visible on the photo, occurs on this surface. Bivalve burrows are preserved as positive hyporeliefs on the sole of crevasse splay sandstone. Note two stages of fluvial erosion and subsequent deposition: a deeper stage to the left and a next, shallower stage of erosion to the right. In this case bivalve burrows represent post-depositional trace fossils, trace makers adjusted to erosion/new depositional surfaces, producing meniscate or structureless infillings of the burrows. MUZ.PGI.80.VI.35; 2 – aligned *Lockeia* isp. burrows (arrows) preserved as positive hyporeliefs on the sole of crevasse splay sandstone. Alignment of bivalve burrows/resting tracks is roughly parallel to the palaeocurrent direction. Field photograph; 3 – *Lockeia* isp. burrows preserved as positive hyporeliefs on the sole of crevasse splay sandstone. Field photograph.

REMARKS: The form is much larger (50-80 mm long) than *Lockeia amygdaloides*. Similarly to *Lockeia amygdaloides* these forms can occur in large aggregates, occasionally reflecting the preferred orientation parallel to the palaeocurrent direction, which is associated with locomotion of the animal. Infilling is usually structureless, but meniscate infilling indicating vertical movement of the bivalve was also noted.

Ichnogenus *Rusophycus* Hall, 1952

Rusophycus isp.

DESCRIPTION: Hypichnial, short, bilobate, coffee-bean shaped forms with deep median furrow, transversely wrinkled with striae. Generally, width equals 50-70% of length.

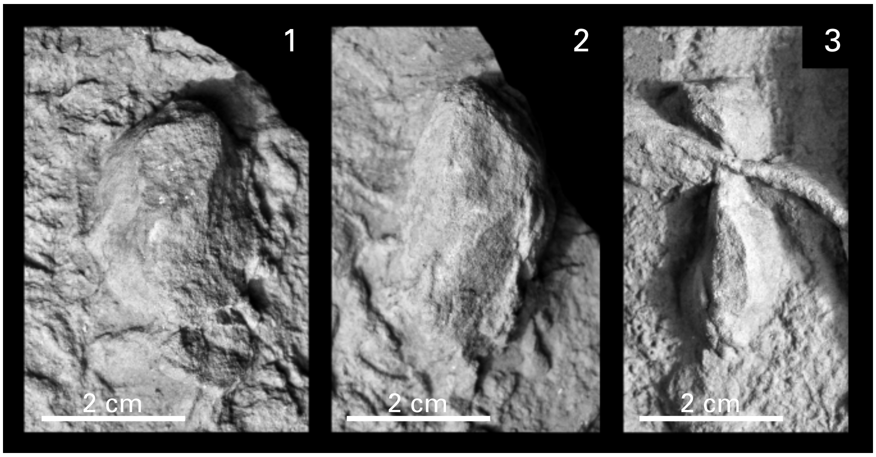

Fig. 5. Bivalve resting tracks: 1 – *Lockeia czarnockii* (Karaszewski, 1974), MUZ PGI 80.VI.122, note asymmetric, drop-like shape of the resting trace; 2-3 – *Lockeia amygdaloides*, MUZ PGI 80.VI.122.

REMARKS: Rare at Sołtyków. Originally assigned to resting tracks of trilobites, later regarded also as resting tracks of other arthropods, including freshwater ones (Bromley and Asgaard 1979).

Traces of adaptation to sediment (equilibrichnia)

Ichnogenus *Calceoformites* igen. n.

TYPE ICHNOSPECIES: *Calceoformites uchmani* isp. n. (Fig. 8: 1-5)

DIAGNOSIS: Clog-shaped hypichnial protrusions occurring on the soles of sandstone beds (positive hyporelief), average size: 30 mm long, 15 mm wide, 30 mm deep. In vertical section they show concave-upward, meniscate infillings (Fig. 8: 4).

GENERIC NAME DERIVATION: after latin *calceo* – wooden shoe (=clog), which resembles the shape of this trace fossil.

REMARKS: a new trace fossil, previously unknown in the literature.

Calceoformites uchmani isp. n.
(Fig. 8: 1-5)

DERIVATION OF THE SPECIES NAME: In honour of Alfred Uchman, our friend and worldwide-known researcher on invertebrate trace fossils.

MATERIAL: Three specimens on two slabs: MUZ PGI 80.VI.121 A and B (two specimens including holotype – MUZ PGI 80.VI.121A – Fig. 8: 1, 2, 5; and paratype – Fig. 8: 3, 4, respectively) and Muz. PGI 80.VI.35 (one specimen); a few field observations. All specimens are stored in the Museum of the Polish Geological Institute in Warsaw.

TYPE LOCALITY: Sołtyków near Stąporków, Holy Cross Mountains, Poland.

TYPE HORIZON: Zagaje Formation, Lower Hettangian (Early Jurassic).

DIAGNOSIS: Clog-shaped protrusions occurring on the soles of sandstone beds (positive hyporelief), average size: 30 mm long, 15 mm wide, 30 mm deep. In vertical section they show concave-upward, meniscate infillings (Fig. 8: 4).

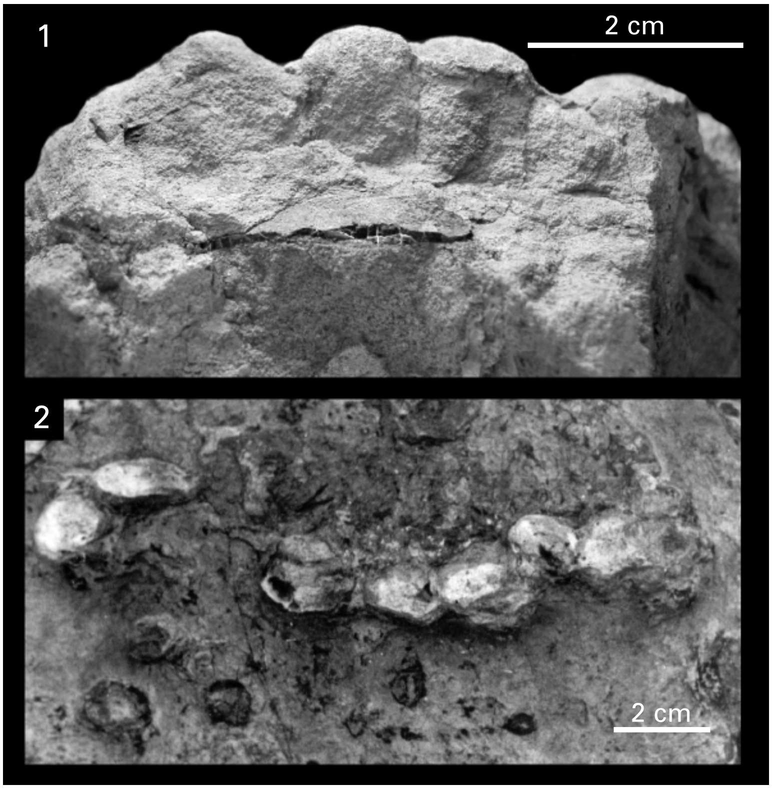

Fig. 6. Bivalve resting and locomotion tracks: 1 – *Lockeia amygdaloides* forming a line of serial positive hyporeliefs, MUZ PGI 80.VI.123; 2 – *Lockeia amygdaloides* arranged in a line of serial burrows. Field photograph.

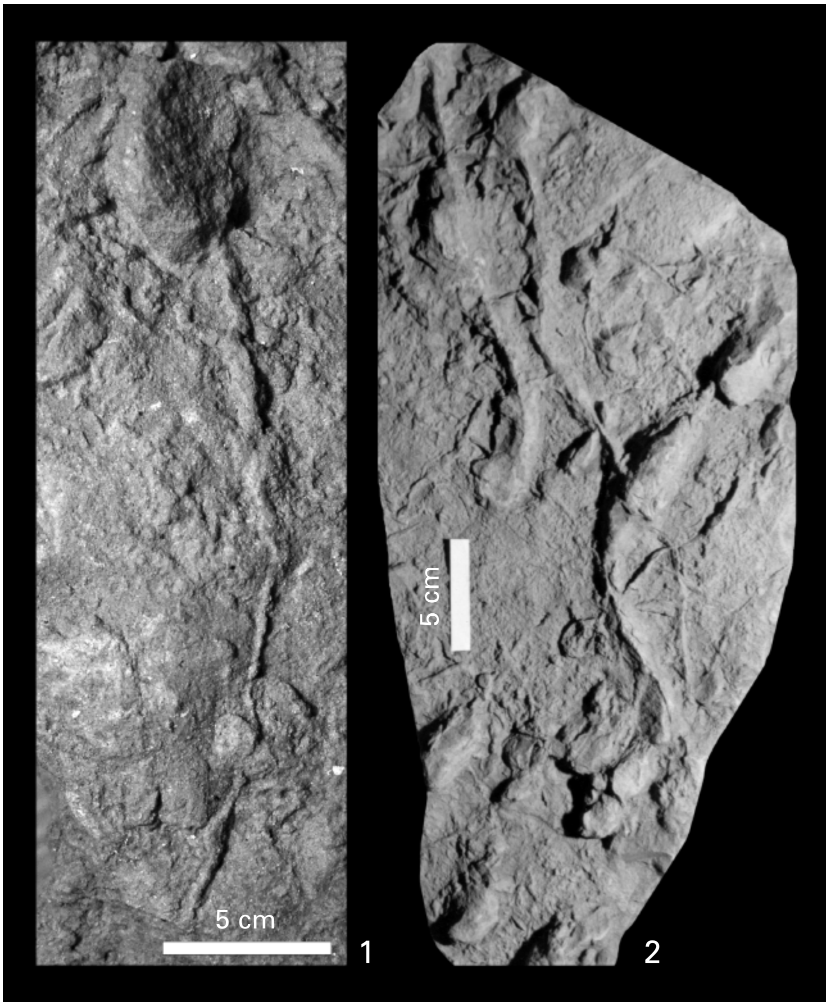

Fig. 7. Bivalve locomotion trails and resting tracks: 1 – bivalve locomotion trail ending with *Lockeia amygdaloides* resting trace, field photo; 2 – winding bivalve locomotion trails ending with *Lockeia amygdaloides* resting traces, MUZ PGI 80.VI.122.

REMARKS: In one case, an articulated unionacean bivalve fossil in life position has been found in the burrow, which identifies the trace makers. The main, oblong part of the trace fossil represents the cast of the bivalve's shell, while the "heel-like" protrusion at the end of the burrow represents the cast of the bivalve's protruding foot. The end of the heel-like protrusion may be formed into the shape of an additional small bump. These features indicate that the animal tried to adapt to newly deposited sediment. Similar forms have never been described previously in the literature. The trace fossil represents a repetitive structure, known from several separate specimens. This form is very distinctive, and the morphological departure from *Lockeia* isp. is considerable enough to justify creation of a new ichnogenus and ichnospecies.

Dwelling structures (domichnia)

Indeterminate conical structures

DESCRIPTION: Medium to large conical, vertical burrows, 35 mm diameter, up to 50 mm long, with almond-shaped termination. Infilling is usually structureless, but in places they show faint meniscate infilling. Preserved either as hypichnial or endichnial forms, usually endichnial burrows passing into hypichnial structures. Superficially, they bear some resemblance to *Conichnus* Myanill, 1966 or *Conostichus* Lesquereux, 1878, but they lack either a regular conical shape (*Conichnus*) or a characteristic apical disc (*Conostichus* – for discussion see Pemberton *et al*. 1988).

REMARKS: One specimen (Fig. 9: 2) showing a peculiar protrusion at the end of the burrow (representing the cast of the bivalve's protruding foot), closely resembles *Conostichus broadheadi* Lesquereux, 1880 because of the well-developed longitudinal fluting and the presence of a relatively narrow and short apical disc, which does not display prominent septation (Pemberton *et al*. 1988, fig. 3: A, B). However, because only one specimen of this structure was found in the Sołtyków exposure, one can not prove if this trace fossil occurs as an articulate, repetitive structure or if it represents just a random aggregation of structures. Moreover, this ichnotaxon was previously reported only from marine facies (Pemberton *et al*. 1988) and is unknown from other terrestrial settings. Until more specimens are found, one should refrain from confirming the presence of this ichnospecies in the Sołtyków trace fossil assemblages.

Associated with *Lockeia*, these forms show transitional stages to *Lockeia* and thus they all are interpreted as bivalve dwelling structures.

Escape/dwelling structures (fugichnia/domichnia)

Ichnogenus *Scalichnus* Hanken, Bromley and Thomsen, 2001

Scalichnus isp. (Fig. 9: 1)

DESCRIPTION: Endichnial/hypichnial, large, vertical, sack-like structures, up to 200 mm long, 20-30 mm in diameter, oval in cross section, retrusive, filled with sand. Infilling is usually structureless, but in longer forms one can observe meniscate arrangement of infilling lamina, particularly in the lower part of the structure (Fig. 9: 1). Differs from *Scalichnus phiale* described by Hanken *et al.* (2001) in smaller size and relatively inconspicuous clay lining. Similarly to Hanken *et al.* (2001) we interpret this form as a dwelling/escape structure of mud-dwelling bivalves.

Locomotion trails (repichnia)

Straight to winding, linear trails (Fig. 7: 1, 2)

DESCRIPTION: Three morphotypes of these hypichnial, rarely epichnial trails, showing different sizes and shapes, were found at the Sołtyków locality. They differ in vertical cross section, representing either irregular, interrupted half-tubes (Fig. 7: 1) or triangular ridges passing gradually into typical *Lockeia amygdaloides* (Fig. 7: 2).

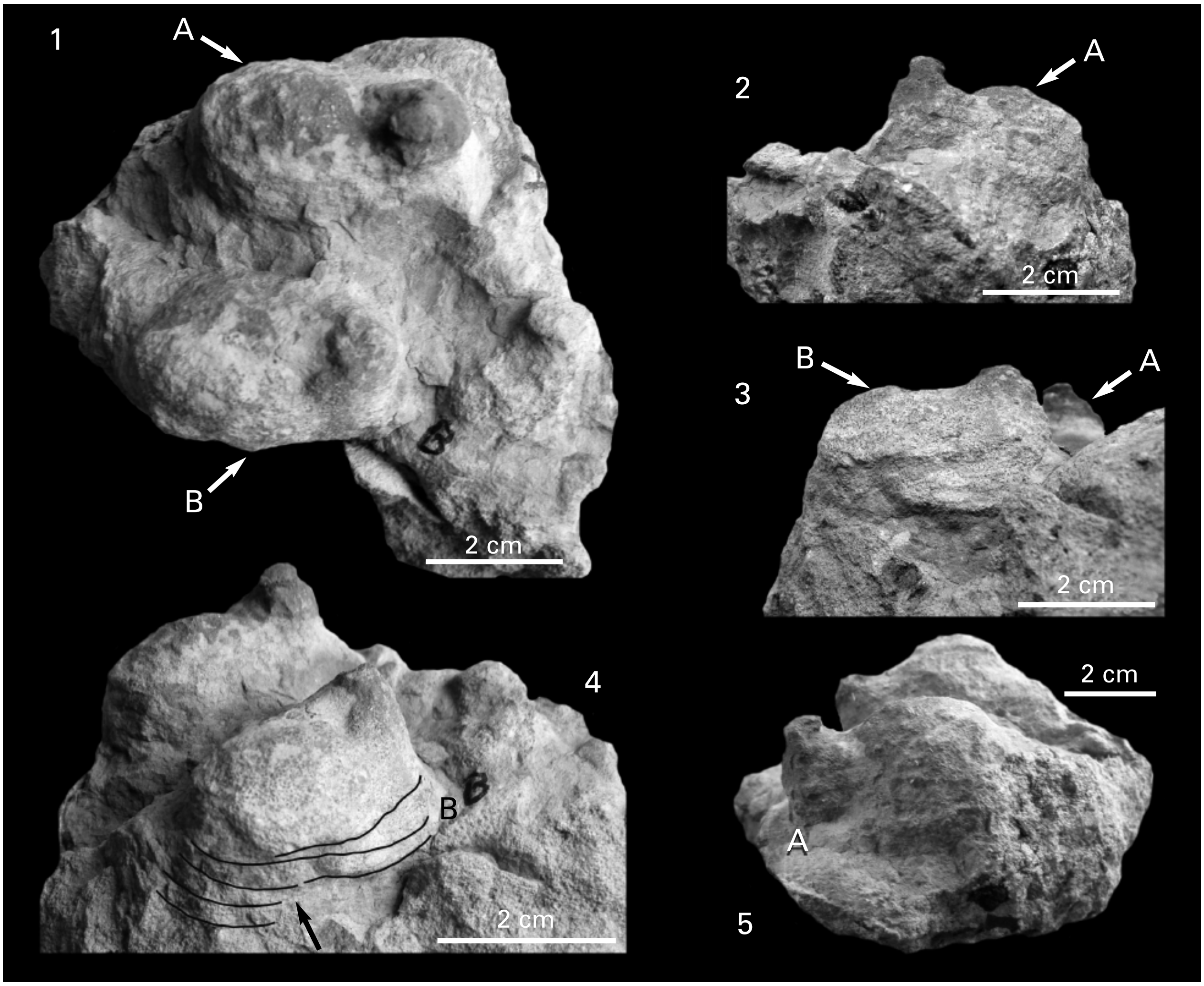

Fig. 8. Bivalve dwelling/resting structure *Calceoformites uchmani* igen. n. et isp. n., MUZ PGI 80.VI.121A (holotype) and MUZ PGI 80.VI.121B (paratype), note clog-shaped burrow with oblong impression of a shell and heel-like (with or without additional bump on top) trace representing foot protrusion: 1 – holotype (A) and paratype (B), positive hyporelief on the sole of sandstone, plane view; 2 – side view showing the small bump at the end of the trace of the foot protrusion ("heel"); 3 – paratype, side view, note meniscate infilling; 4 – oblique view of the paratype (in the front) with the meniscate infilling (arrowed); 5 – oblique view of the holotype in the front and paratype in the background.

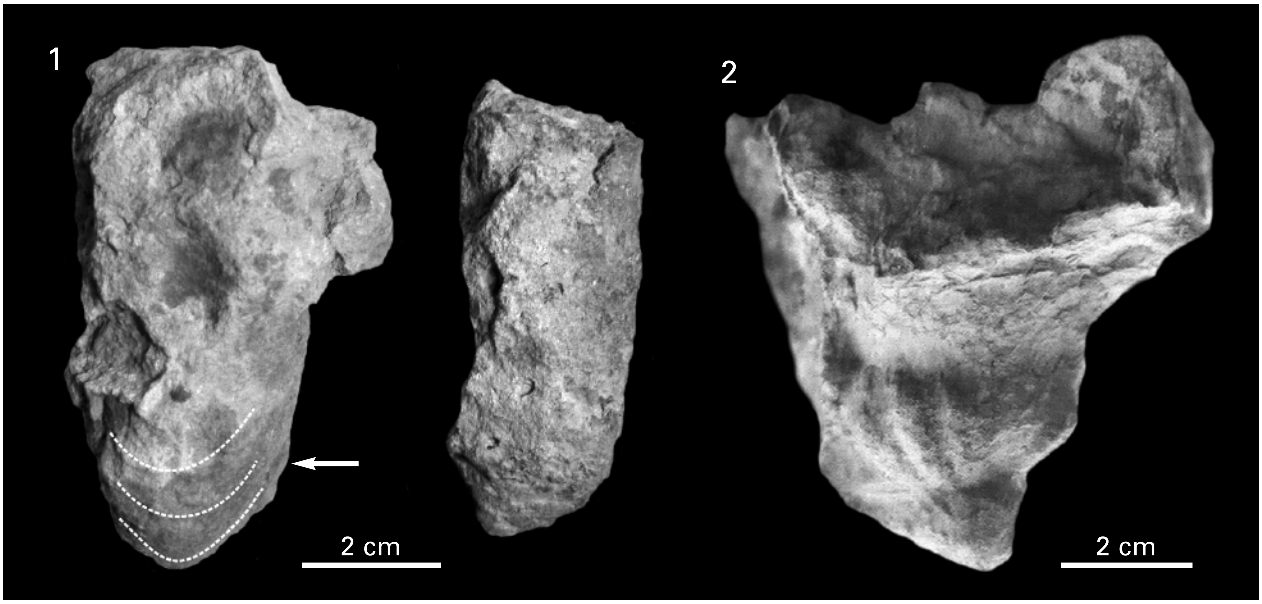

Fig. 9. Bivalve escape and dwelling structures: 1 – *Scalichnus* isp. Escape structure of a bivalve with faint meniscate infilling, MUZ PGI 80.VI.124; 2 – bivalve burrow resembling *Conostichus broadheadi* Lesquereux, 1880, note well-developed longitudinal fluting and presence of relatively narrow and short apical disc, which does not display prominent septation, MUZ.PGI.80.VI.35.

REMARKS: Such morphological variation is probably associated with different locomotion behaviour of the bivalves and with different types of sediment. Chain-like arrangements of *Lockeia* are occasionally associated with the trails, pointing to the same trace makers (bivalves) of these trace fossils. Extant unionoid bivalves are generally sluggish animals, spending most of their lifetime partially or totally buried in the sediment (Piechocki and Dyduch-Falniowska 1993). Traces of their locomotion can be observed in the oral zone of lakes and rivers. They become mobile due to change of their habitat, for example during droughts or seasonal weather fluctuations; they also become dispersed during floods (Piechocki and Dyduch-Falniowska 1993) producing sets of aligned resting forms, like those at Sołtyków (Figs 4: 2; 6).

Ichnogenus *Cruziana* d'Orbigny, 1842

Cruziana problematica (Schindewolf, 1921)
(Fig. 10: 1)

DESCRIPTION: Small (2-10 mm wide), hypichnial, elongate bilobate trace fossil covered by transverse striae. Morphology varies according to depth of burrowing of the trace maker. Occasionally, only a faint pair of hypichnial ridges is visible.

REMARKS: Bromley and Asgaard (1972, 1979) attributed these traces to fresh-water arthropods. Originated by simple ploughing using all or only anterior appendages. Pollard (1985) interpreted *Cruziana problematica* as notostraca locomotion trails.

cf. *Cruziana* isp.

DESCRIPTION: Medium (15-20 mm wide), hypichnial, bilobate trace fossil, without apparent ornamentation, which differentiates these forms from *Cruziana*. Rare at Sołtyków. The two specimens were found in crevasse splay deposits, associated with a podzol type of palaeosol.

REMARKS: Similar trace fossils are usually interpreted as locomotion trails of arthropods (Glaessner 1957; Trewin 1976), most probably insects or crustaceans. The lack of transverse striae is probably a preservational feature.

Ichnogenus *Diplichnites* Dawson, 1873

Diplichnites isp. (Fig. 10: 6)

DESCRIPTION: Hypichnial trackway (15-20 mm wide) consisting of two parallel rows of fine ridges, obliquely oriented to trace axis. Originally interpreted as locomotion trails of trilobites scratching the bottom, latter extended to other arthropods, including non-marine ones (Bromley and Asgaard 1979).

REMARKS: Trace fossil rare in Sołtyków locality (3 specimens), and were found in crevasse splay deposits.

Ichnogenus *Kouphichnium* Nopcsa, 1923

cf. *Kouphichnium* isp.

DESCRIPTION: They are represented by small V-shaped, hypichnial marks (positive hyporelief, about 4-6 mm long) showing either chaotic or slightly linear orientation.

REMARKS: At Sołtyków, two specimens similar to *Kouphichnium* have been found. *Kouphichnium* is usually regarded as the locomotion trails of limuloids (Xiphosura) or similar-shaped crustaceans (Hasiotis and Demko 1996). They could be left by representatives of the Malacostraca. Usually, *Kouphichnium* occurs in brackish-marine or marine sediments (Goldring and Seilacher 1971; Romano and Whyte 1987, 1990). In the Lower Jurassic of Poland, *Kuophichnium* was identified also in brackish-marine sediments (Pieńkowski 1980, 1985), but more recently it has been found also in lacustrine/fluvial environments (Hasiotis and Demko 1996; Romano and Whyte 2003).

Ichnogenus *Cochlichnus* Hitchcock, 1858

Cochlichnus isp.

DESCRIPTION: Hypichnial, sinusoidal, horizontal trails (positive hyporelief) about 1-3 mm wide.

REMARKS: Interpreted as locomotion trails of molluscs, arthropod larvae or nematodes.

Feeding/locomotion burrows (fodinichnia)

Ichnogenus *Scoyenia* White, 1929

Scoyenia isp. (Fig. 10: 3)

DESCRIPTION: Endichnial/hypichnial, linear, slender burrows with rope-like sculpture (usually not well visible) and variable diameter (5 to 15 mm), stuffed with sediment (sometimes showing inconspicuous meniscate pattern), parallel or oblique to bedding surfaces, often crossing each other. *Scoyenia* occurs in bunches of several to twenty individual burrows. Occasionally it occurs on different overlapping levels.

REMARKS: *Scoyenia* is attributed to arthopods, possibly beetles (Coleoptera) or similar entomofauna (Ratcliffe and Fagerstrom 1980). Similar forms were described by Hasiotis and Bown (1992) and Hasiotis and Demko (1996) from the Late Jurassic Morrison Formation (Colorado, USA). It is worth mentioning that body fossils of Coleoptera were found at Sołtyków (Wegierek and Zherikhin 1997). The burrows occur in sediments attributed to fluvial channel and crevasse splay facies. They are associated with well-aerated palaeosols (podzol type), plant roots being filled with sediment and not containing much coaly organic matter.

Ichnogenus *Spongeliomorpha* de Saporta, 1887

Spongeliomorpha isp. (Fig. 10: 2, 5)

DESCRIPTION: Endichnial, thick (diameter variable, 20-50 mm), elongate (at least 200 mm long), cylindrical, often branching burrows, horizontal or oblique to bedding surfaces. Surface covered with network of various scratchmark casts (similar to those described by Hasiotis and Mitchell 1993).

REMARKS: Structures similar to *Spongeliomorpha* isp. are interpreted as arthropod burrows by Hasiotis and Demko (1996) in the Upper Jurassic Morrison Formation, Salt Wash Member. For taxonomic discussion of *Spongeliomorpha* see Schlirf (2000). At Sołtyków, four specimens of *Spongeliomorpha* have been found, and they occur in crevasse splay deposits, rarely in alluvial plain deposits.

Spongeliomorpha carlsbergi
(Bromley and Asgaard, 1979) Schlirf, 2000

DESCRIPTION: Endichnial, individual cylindrical trace fossils that may exhibit T- or Y-branching. Described as *Steinichnus carlsbergi* by Bromley and Asgaard (1979), regarded by Metz (1993) and Schlirf (2000) as a junior synonym of *Spongeliomorpha*. This ichnospecies shows more pronounced scratchmark casts than other *Spongeliomorpha*.

REMARKS: According to Kennedy (1967) and Hasiotis (2002), these burrows represent the locomotion and, most likely, deposit-feeding behaviour of mud-dwelling beetles (Coleoptera). *Spongeliomorpha carlsbergi* is connected with levee or crevasse splay deposits.

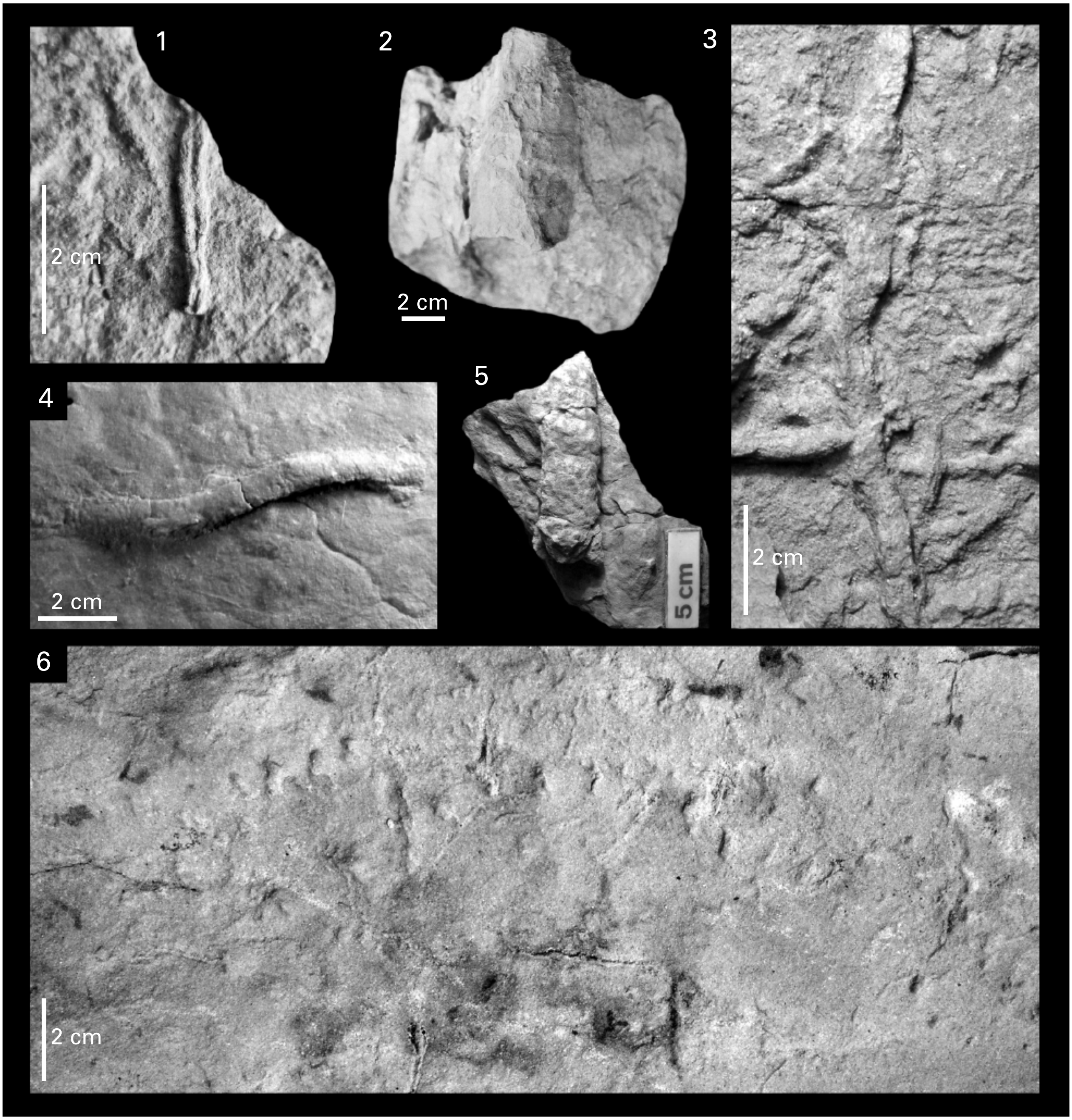

Fig. 10. Arthropod and *incertae sedis* trace fossils: 1 – *Cruziana problematica* (Schindewolf, 1921), note bilobate trails without apparent ornamentation – probably locomotion trails of arthropods, positive hyporelief, MUZ.PGI.80.VI.125; 2 – *Spongeliomorpha* isp., thick, cylindrical, oblique (almost vertical) burrow with network of cast of scratch marks possibly produced by arthropod. To the left – subvertical knob-walled tunnel, showing sometimes meniscate infilling, possibly produced by arthropods (?Coleoptera) or earthworms, MUZ.PGI.80.VI.126; 3 – *Scoyenia* isp., linear, rope-like burrows parallel to bedding surface, arthropod (?beetle) burrows, field photograph; 4 – *Planolites* isp., winding, smooth burrow, horizontal or slightly oblique to bedding plane, MUZ.PGI.80.VI.127; 5 – *Spongeliomorpha* isp., thick, cylindrical, horizontal burrow with knobs and scratch marks, arthropod burrow, MUZ.PGI.80.VI.128; 6 – *Diplichnites* isp., note two parallel rows of fine ridges, obliquely oriented to track axis, an arthropod locomotion trail, positive hyporelief, field photograph.

Ichnogenus *Planolites* Nicholson, 1873

Planolites isp. (Fig. 10: 4)

DESCRIPTION: Tubular, endichnial and hypichnial, unbranched, usually horizontal burrows, 4-12 mm in diameter, circular to elliptical in cross-section, filled with sediment differing from the surrounding host sediment; burrow boundary with surrounding sediment is distinct.

REMARKS: Often they occur in clusters. Burrows tend to overlap one another rather than intersect. *Planolites* isp. is believed to have been formed by a worm-like organism eating its way through the sediment, with the burrow fill representing the material that passed through the organism's alimentary canal – thus the filling of the burrow is active (the major difference between *Palaeophycus* and *Planolites*) – Alpert (1975). At Sołtyków, they are usually associated with crevasse splay or alluvial plain deposits and with palaeosols of the podzol type.

Ichnogenus *Palaeophycus* Hall, 1847

Palaeophycus isp.

DESCRIPTION: Endichnial and hypichnial, horizontal, straight or slightly curved, sporadically branching burrows, oval in cross section. The burrows show a distinct lining. Burrow-infilling usually identical to the host sediment, except that in places the grain size of the fill may be slightly coarser.

REMARKS: Hitherto, several specimens of this ichnogenus have been found in crevasse splay and channel deposits.

Smooth vertical and subvertical branching tunnels

DESCRIPTION: These endichnial, vertical and subvertical, branching tunnels (Fig. 11: 1, 2) usually occur in assemblages; on the horizontal surface one can find a number of outlets (Fig. 11: 4). Internal surface of these tunnels are smooth, there is no evidence of septae or meniscate infillings. Walls of these tunnels show discrete linings. It is not clear if these tunnels might represent parts of more complicated systems.

REMARKS: To some extent they resemble beetle tunnels (beetle body fossils have been found at Sołtyków – Wegierek and Zherikin 1997), but their origin is still not clear. In any case, they are probably insect burrows representing an Early Jurassic stage of the growing role of insects in pedogenic processes.

Knob-walled tunnels

DESCRIPTION: Endichnial, knob-walled, straight to slightly curved, commonly horizontal (Fig. 11: 3-4) occasionally also vertical (Fig. 11: 1, 4), simple, rarely branching tunnels, 7-15 mm wide. The material obtained does not allow one to state whether these tunnels are organised in more complicated systems. The knobby lining (*sensu* Bromley 1996) resembles *Ophiomorpha* isp. (regarded by Schlirf 2000 as a younger synonym of *Spongeliomorpha*).

REMARKS: Because of the pelleted wall (Fig. 11: 1), this type of trace fossil could be left by beetles (Coleoptera), whose body fossils were reported from the Sołtyków locality (Wegierek and Zherikin 1997). However, some tunnels seem to be completely filled with pellets. In that case they are similar to *Edaphichnium* isp., interpreted as earthworm burrows (Hasiotis 2004). Moreover, similar structures (particularly the Y-branched forms – Fig. 11: 1), were described by Bedatou *et al.* (2008) and Genise *et al.* (2008) as burrows made by crayfishes (*Loloichnus* isp.). A faint meniscate filling (Fig. 11: 3) may point either to an oligochaete, crayfish or beetle origin of these structures.

Structures attributed to nesting behaviour (callichnia)

Mace-shaped or irregular ellipsoid chambers

DESCRIPTION: Various endichnial chambers (mace-shaped or irregular spherical/ellipsoid) were found in levee-crevasse splay deposits (Fig. 12: 1, 3). As all these structures were found in a weathered debris pile, the primary orientation in the host sediment is not known. Also, it is not clear whether these chambers formed parts of more complex systems. The chambers show thick, structureless walls (Fig. 12: 1, 3) representing

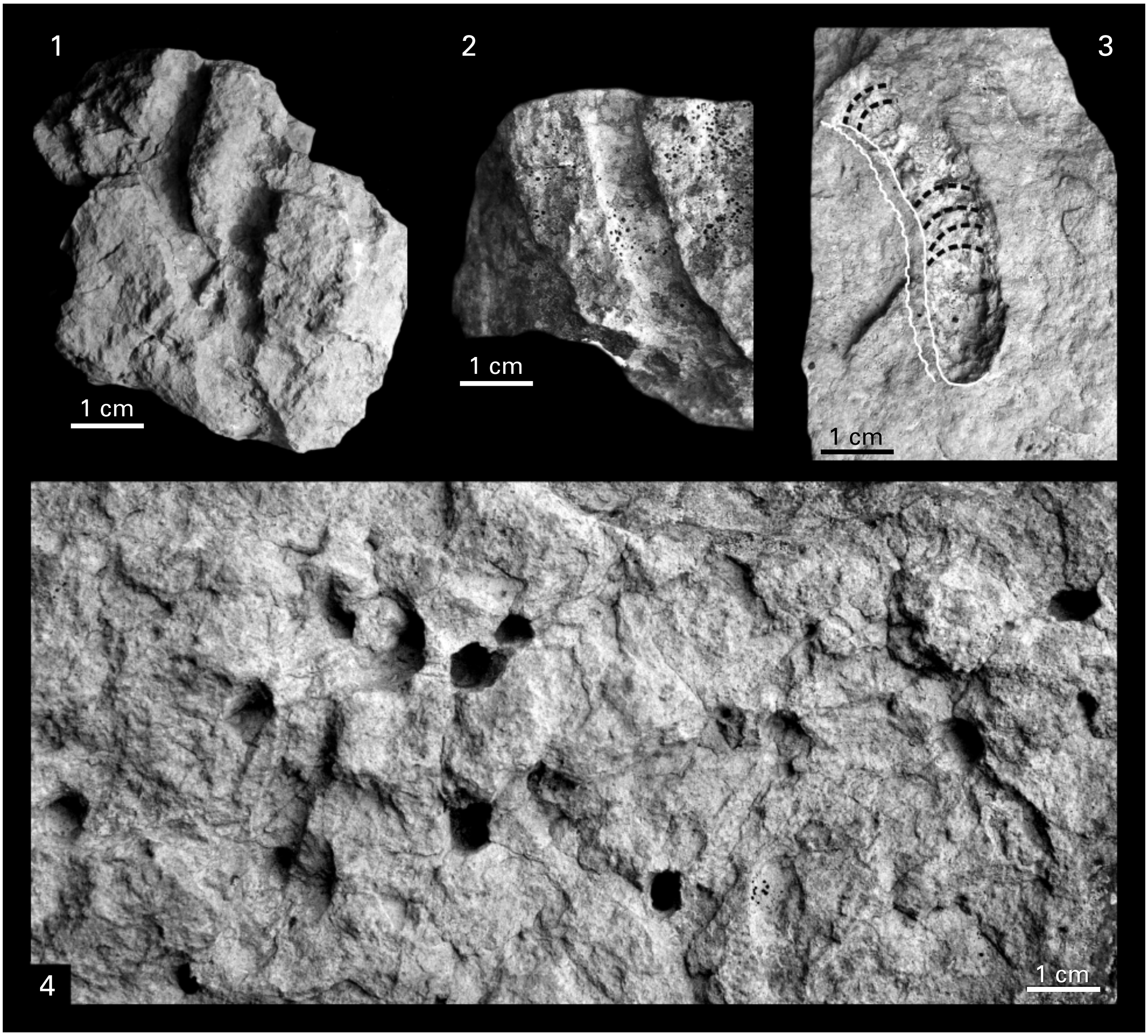

Fig. 11. Various tunnels attributed to arthropods (most probably Coleoptera or crayfishes) or earthworms (knob tunnels): 1 – vertical, Y-branching tunnel with smooth surface and discrete lining, MUZ.PGI.80.VI.129; 2 – oblique tunnel with smooth surface and discrete lining, MUZ.PGI.80.VI.130; 3 – horizontal tunnel with knob walled surface (white line) and faint meniscate infilling (dashed black lines), negative epirelief, MUZ.PGI.80.VI.131; 4 – bedding plane with outlets of vertical/oblique cylindrical tunnels, field photograph.

diagenetic haloes of iron oxides (formerly siderite). Mace-shaped chambers have smooth inner and outer surfaces. The filling is unknown as they were found empty.

A single specimen of an irregular, flattened, ellipsoid chamber with a large cavity occurring in the flat side of the chamber is interesting (Fig. 12: 3). A small cavity can be seen on the opposite flat wall of the chamber. Striatations are visible on the inner wall of the chamber, which may represent impression of meniscate infilling (the infilling was missing when the specimen was found).

REMARKS: These structures (particularly the ellipsoid ones) probably represent excavated chambers, which can be compared to those produced by insects (Genise 2004). The irregular, ellipsoid chamber could be tentatively included to the ichnofamily Pallichnidae (Genise 2004), *i.e.* trace fossils composed of sphaerical, ovoid, hamate, or lunate chambers lacking a constructed wall. Pallichnidae (namely, *Fictovichnus* Johnston, Eberth and Anderson, 1996) have been recorded from Jurassic deposits (Hirsch 1994). Members of the ichnofamily Pallichnidae are interpreted as representing pupation chambers and brood masses of beetles

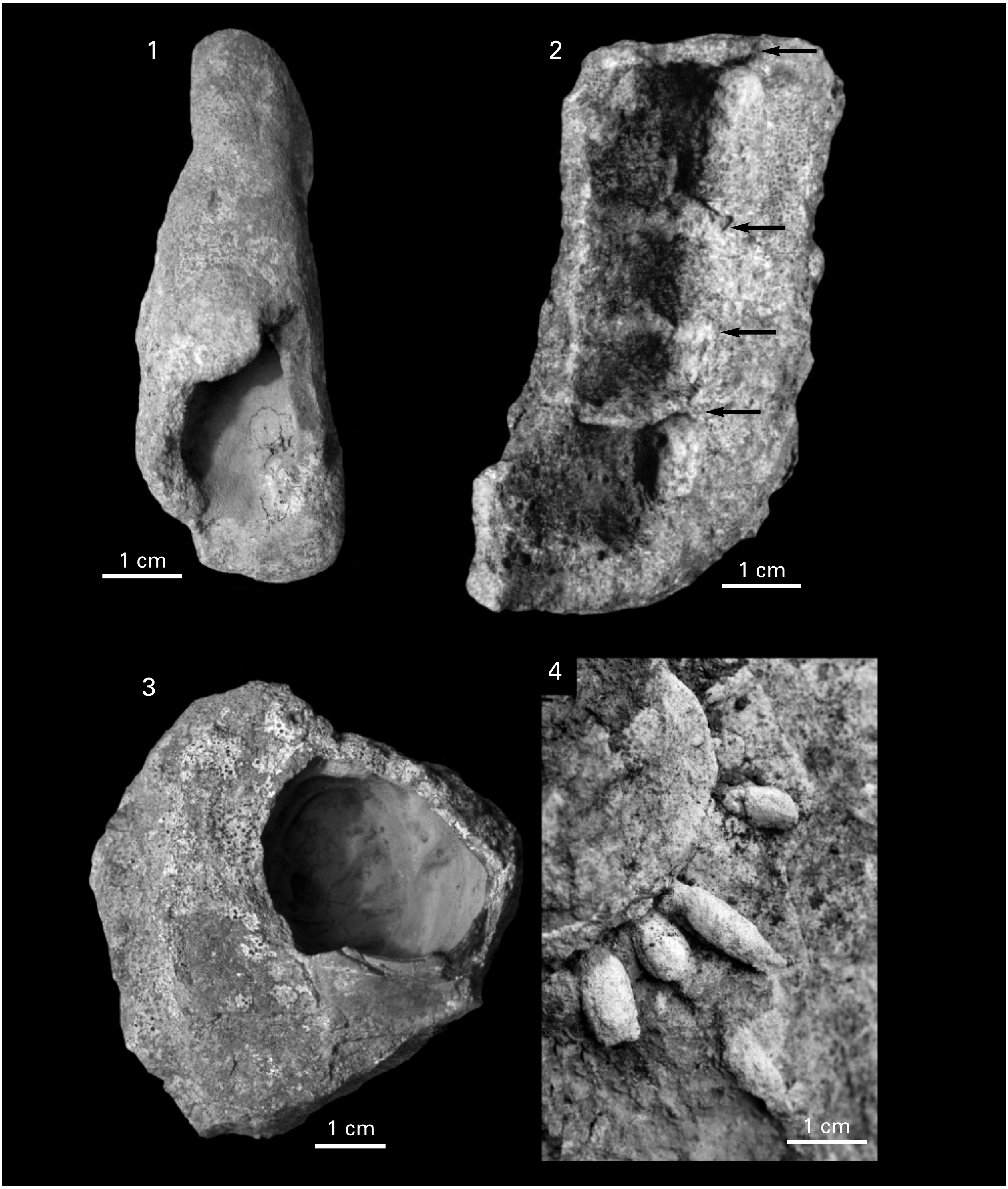

Fig. 12. Various chambered structures attributed to insects, earthworms, crayfishes or unknown animals: 1 – mace-shaped tunnel with smooth surfaces, note thick, structureless walls representing diagenetic haloes of iron oxidises (formerly siderite), MUZ.PGI.80.VI.132; 2 – one of several chambers attached to each other, showing a secondary chamber system of four sub-chambers separated by septa, occurrence of such chambers point to complex architecture of nesting insects (likely cicadas), MUZ.PGI.80.VI.133; 3 – irregular, ellipsoid chamber with thick, structureless walls representing diagenetic haloes of iron oxides (formerly siderite) showing similarity to the ichnofamily Pallichnidae which is attributed to pupation chambers and brood masses of beetles (Genise 2004), similar irregular chambers are also produced by earthworms as aestivation chambers. MUZ.PGI.80.VI.134; 4 – radially-oriented cells around a large, vertical tunnel, single cells are mace-shaped, cell walls are smooth, these structures bear resemblance to those made by crayfishes (*Loloichnus* isp., *Cellicalichnus* isp., *Dagnichnus* isp. – Genise *et al.* 2008; Bedatou *et al.* 2008), although the side chambers lack meniscate infillings, field photograph.

(Genise 2004). Of course, irregular chambers could also be left by other organisms such as earthworms producing their aestivation chambers (Jorge Genise, pers. comm.).

Large nest structures with septa

DESCRIPTION: Endichnial clusters of large (up to 100 mm long and up 40 mm wide), subvertical chambers, occasionally with a series of conspicuous parallel, transverse septa separating these shafts into chambers up to 20 mm high (Fig. 12: 2).

REMARKS: The development of a secondary chamber system within the primary chamber system and the aggregate nature of primary chambers (they are attached to each other) point to the complex architecture of insect constructed chambers (Genise 2004). Such chambers suggest the nesting behaviour of insects (?cicadas; Jorge Genise, pers. comm.). They also show some affinity (in shape and clustering of chambers) to modern wasp (Hymenoptera) nests illustrated by Hasiotis (2002), but attribution of Jurassic trace fossils to modern taxa may be misleading.

Radial chambers around large tunels
(Fig. 12: 4)

DESCRIPTION: Endichnial, radial array of cells around a large, vertical shaft. Single cells are mace-shaped, cell surfaces are smooth, infilling of the cells is structureless.

REMARKS: One possible interpretation is that they represent rhizomes extending from a central stem. However, a plant interpretation is rather unlikely as these structures lack any characteristic plant tissue fabric, so common in all plant remains from Sołtyków. Another possible interpretation involves arthropod (crustacean? spider? insect?) burrows, possibly associated with nesting behaviour (subterranean reproductive nests). Similar structures (although showing side chambers with meniscate infillings) were described by Bedatou *et al.* (2008) and Genise *et al.* (2008) as terrestrial crustacean breeding trace fossils, most likely made by crayfishes. In that case, the radial structures would occur around a pre-existing tunnel. It should be pointed out that any interpretation of this peculiar structure is tentative, as only a single structure was found.

Trace fossils in plant elements (borings and gnawing traces)

Plant destruction for feeding, reproduction or dwelling purposes differs fundamentally from burrowing or boring in sediment or rock. Because plant-insect interactions frequently are very specific, even morphologies already known from the sediment/rock record should be kept separate (Schlirf 2006). Terrestrial woodgrounds commonly contain a variety of distinctive insect borings (Ekdale 1985). Fragments of coniferous trees (pieces of logs and branches) are common in the channel deposits in Sołtyków. The wood borings of Sołtyków are irregular. Large fragments of coniferous wood are very common in the channel and crevasse deposits. Some of these fragments contain borings. Most probably, they represent the activities of wood-boring land animals (for example insect larvae). In the aquatic environment, grazing traces on living stems of sphenophytae or on dead wood occurred; they were produced probably by gastropods, insect larvae or crustaceans.

Ichnogenus *Xylonichnus* Genise, 1995

cf. *Xylonichnus* isp. (Fig. 13: 1)

DESCRIPTION: Cylindrical to irregular, longitudinal borings occurring at different depths in xylem. They are probably interconnected by more or less horizontal tunnels. Length: 10-30 mm; width: 3-10 mm.

REMARKS: Preserved as sandstone infilling in a cast of wood fragment. These borings in the wood were made probably by insect larvae (probably Coleopterans).

Ichnogenus *Linckichnus* Schlirf, 2006

Linckichnus terebrans Schlirf, 2006 (Fig. 13: 2)

DESCRIPTION: Smooth, unbranched, cylindrical (test-tube shaped) borings, with circular openings and oval terminations. Preserved as casts in full relief in a weathered wood fragment. Length: 3-10 mm; width: 3-5 mm.

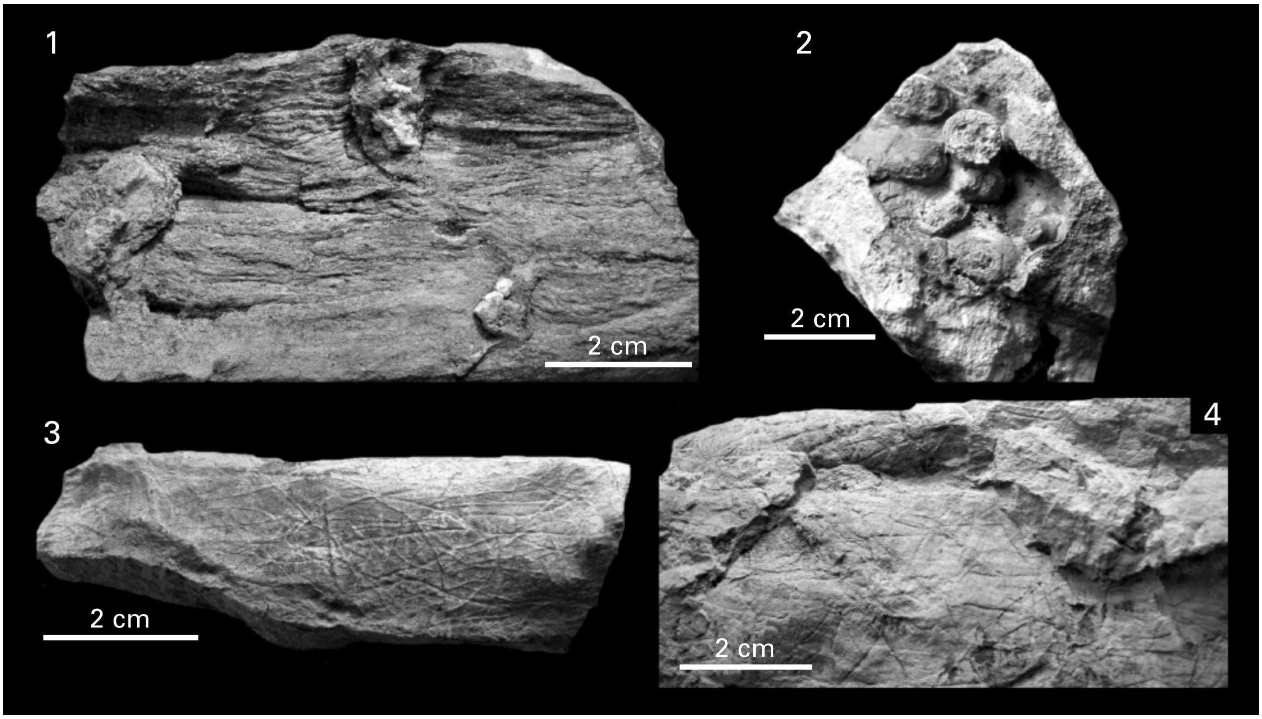

Fig. 13. Trace fossils in plant elements: 1 – *Xylonichnus* isp., cylindrical and irregular, unbranched borings preserved as sandstone infillings in the cast of a wood fragment, MUZ.PGI.80.VI.135; 2 – *Linckichnus terebrans* Schlirf, 2006, smooth, unbranched, test-tube shaped cylindrical borings in a wood fragment preserved as full relief, MUZ.PGI.80.VI.136; 3-4 – cf. *Helminthoidichnites* isp. Linear trace fossils preserved as concave and convex reliefs on stem surfaces (sphenophyte and conifer stems), most probably these structures represent scratch marks on the exposed stems made by insect larvae or gastropods, MUZ.PGI.80.VI.137 and MUZ.PGI.80.VI.138.

REMARKS: According to Schlirf (2006), these borings may represent detritivorous habitation dwellings or oviposition structures of insects in already-dead wood.

Ichnogenus *Helminthoidichnites* Fitch, 1850

cf. *Helminthoidichnites* isp. (Fig. 13: 3, 4)

DESCRIPTION: Concave and convex linear reliefs on stem surfaces (sphenophyte and conifer stems). The thin, winding scratches on the surface of plant (mostly *Neocalamites* sp.) stems are 10-50 mm long and 0.5-2 mm wide. Some of these structures show a regular pattern.

REMARKS: Most probably these structures represent surficial scratches (gnawing traces) on the exposed stems made by gastropods, insect larvae or crustaceans.

RELATIONSHIP OF TRACE FOSSIL ASSEMBLAGES WITH LITHOFACIES AND DEPOSITIONAL SUBENVIRONMENTS

The trace fossils from Sołtyków can be preliminarly arranged in certain ichnofacies associated with depositional subenvironments. In some subenvironments, the dominance of certain invertebrate trace makers is obvious – for example in the permanently aquatic (lacustrine) environment bivalves dominate. However, they show conspicuous ethological variety producing resting, locomotion, dwelling and escape structures. The channel subenvironment (main channel) contains a relatively poor ichnoassemblage such as locomotion traces produced by bivalves and other organisms (mostly arthropods). A highly diverse assemblage occurs on the sole of crevasse splay beds, which is largely connected with the food availability and very high preservational potential. This assemblage is dominated by bivalve resting, locomotion and escape structures as well as arthropod-made structures. The occurrence of bivalves in crevasse environment needs to be addressed, because in general individual crevasse splays represent only short flooding events on alluvial plains. However, crevasse splays in the anastomosing/avulsion depositional environment developed on low-gradient alluvial plains and usually entered an aquatic (lacustrine) environment (at least at its lower, distal parts), which was capable of supporting rich bivalve assemblages. Moreover, channelised crevasses at Sołtyków, representing an initial avulsion stage of channel migration, show some permanency (multi stage infilling of the channel – Fig. 3). Crevasse splays provided both large amount of organic debris (food availability) and excellent preservational potential for invertebrate burrows.

Better drained environments such as levees, the upper parts of exposed crevasse splays and the dry alluvial plain were dominated by crustacean (crayfishes) and insect trace fossils. Other forms like those attributed to oligochaetes are relatively rare. Crayfishes and insects played an important role in pedogenesis and some clustered chambers with serial septa (Fig. 12: 2) are clearly insect nests.

It is clear that a key factor controlling the diversity of ichnotaxa was the position of the water table. According to Gillette *et al.* (2003) it is possible to distinguish wet (Mermia), transitional (Scoyenia) and dry (Coprinisphaera) ichnofacies. The concept of the Coprinisphaera ichnofacies (Gillette *et al.* 2003), extended from its previous meaning of a post-Eocene insect ichnofacies associated with grasslands (Genise *et al.* 2000) to one of three universal terrestrial ichnofacies is still under dispute – one of the main reason is that there is a strong correlation between the Coprinisphaera ichnofacies and herbaceous plant communities (Genise *et al.* 2000). Therefore no true *Coprinisphaera* has been recorded from deposits older than Eocene (Laza 2006) – *Coprinisphaera* isp. is a very distinct callichnia structure, representing Scarabaeinae dung beetle behaviour unknown from pre-Eocene deposits, and the whole ichnofamily Coprinisphaeridae does not occur in deposits older than Late Cretaceous (Genise 2004). Applying the traditional concept of ichnofacies introduced by Seilacher (1967) is a complicated matter in terrestrial environments. If a given ichnofacies should be characterized by a dominance of certain behaviour patterns, then the behaviour pattern represented by the ichnofamily Coprinishaeride is unknown from deposits older than the Late Cretaceous and consequently the ichnofacies Coprinisphaera seems to be inadequate for Jurassic deposits. Due to significantly changing character of these ichnofacies through Mesozoic-Cenozoic time, perhaps a series of ichnofacies characteristic of subsequent geological periods would be a better approach. In the meantime we follow the ichnofacies concept of Gillette *et al.* (2003), understanding the conventional character of this subdivision and at the same time, encouraging further discussion on this problem.

DISCUSSION AND CONCLUSIONS

Trace fossils of the Mermia ichnofacies attributed to bivalves are very diversified (6 trace fossil ichnospecies, including the one new ichnospecies). They reflect very diversified behaviour in response to changing environmental conditions. In particular, anastrophic burial during flood events forced bivalves to react and to make traces indicative of different behaviour (digging – dwelling, moving horizontally, resting or vertical escape structures). When the flood-derived sediment layer was relatively thin, the bivalves would rest on more or less the same level, initially producing various forms such as *Lockeia amygdaloides* (Seilacher, 1953); *Lockeia czarnockii* (Karaszewski, 1974) and *Calceoformites uchmani* igen. n., isp. n. Commonly, these hypichnial forms are preserved on the soles of crevasse splay sandstones. After the flood event waned, bivalves could move around producing sets of aligned *Lockeia* and arrays of vertical structures (Fig. 6) with meniscate infilling. *Calceoformites uchmani* igen. n., isp. n. represents a form reflecting the adaptation of the animal to newly deposited sediment (equilibrichnia). If the deposited sediment layer was thick, the bivalves would produce escape structures such as *Scalichnus* isp. When the flood event waned, they tried to get back to the surface producing escape structures with meniscate infillings such as *Scalichnus* (often associated with *Lockeia*). Similar escape structures were described by Reineck (1958) and Thoms and Berg (1985). In some bivalve dwelling and escape structures bivalve body fossils have been found. Such finds indicate that some bivalves were buried by too heavy a column of sediment and they simply could not make their way to the surface. These bivalves probably represent Unionoidea (three distinct forms have been identified). Similarly as today, Unionoidea inhabit alluvial – lacustrine environments and usually occur in assemblages dominated by one species (Piechocki 1969). In the lacustrine environment Unionoidea occur within the littoral zone at a shallow water depth (0.25-5.5 m) and they usually do not form dense assemblages (Widuto and Kompowski 1968; Lewandowski and Stańczykowska 1975). However, in the Sołtyków locality we observed quite common mass aggregations of *Lockeia* (Fig. 4: 2, 3), often more than 100 traces per one square meter. The relatively high rate of subsidence and sedimentation inferred for the Sołtyków locality (Pieńkowski 2004a) makes the supposition that some particular beds could be exposed for bioturbation for a long time unlikely. Thus, the mass aggregations of *Lockeia* are associated rather with a dense population of bivalves. Such gregarious behaviour is observed in extant bivalves either in places with active current action (fluvial environment) or in populations occurring together during the breeding period. Association with currents is an obvious feeding opportunity behaviour. Alingment of *Lockeia* along the current (Figs 4: 2, 3; 6) is quite common at Sołtyków. Also the sediment substrate is important as bivalves avoid some types of sediment, such as the admixture of too coarse sediment (Piechocki 1969; Piechocki and Dyduch-Falniowska 1993). Bivalve dwelling and resting structures have been found in fluvial channel, lacustrine – alluvial plain deposits and most commonly on the soles of crevasse splay beds. Interestingly, some of these forms are pre-depositional, other are post-depositional (in case when the deposited sediment was not too thick, bivalves adapted to a new situation, moving around the same depth, producing arrays of resting tracks; in case when the sediment was too thick, bivalves moved up to attain a new habit producing vertical escape structures with meniscate infilling). The abundant occurrence of bivalve traces in crevasse splay deposits is also related to the much higher preservational potential provided by rapid crevasse deposition.

Insect trace fossils from Jurassic deposits are still insufficiently known, the presence of knob walled tunnels and vertical branching tunnels may point rather to structures made by crayfishes (Bedatou *et al.* 2008; Genise *et al.* 2008), also some structures produced by earthworms could be similar. Ellipsoid chambers also show affinity to insect trace fossils, namely to the Pallichnidae ichnofamily representing pupation chambers of beetles (Genise 2004). Again, one should bear in mind that these structures could be also produced by other organisms, such as earthworms. Particularly intriguing are large associated chambers with serial septa, which can be attributed to the nesting behaviour of insects (possibly cicadas). Nevertheless, the presence of chambered trace fossils of insect nest affinity in the earliest Hettangian is noteworthy. Hemiptera and Coleoptera body fossils have been found at Sołtyków (Wegierek and Zherikhin 1997), but the diversity of the trace fossil assemblages suggests that the Early Hettangian entomofauna of Sołtyków was much more diversified. Insects played an important role in the ecosystem at Sołtyków; they were relatively abundant and their interaction with wood material is proven by the presence of wood borings and gnawing traces, such as cf. *Xylonichnus* isp., *Linckichnus terebrans* and *Helminthoidichnites* isp. Moreover, together with other arthropods, such as crayfishes, they played an important role in the formation of soil. These facts encourage discussion both on the ichnofacies dilemma (such as a Coprinisphaera ichnofacies definition) and the ichnostratigraphy of terrestrial deposits. The Sołtyków outcrop reveals an interesting (because very early) record of some more complex structures which can be attributed to insects (such as associated chambers with serial septa or ellipsoid chambers of Pallichnidae affinity). However, we share the view of Genise (2004) that similarly to the case of Triassic and Jurassic trace fossils from the Chinle and Morrison formations attributed by Hasiotis (2002) to insects, such old finds should be very sound as they would have an impact on the general view on Jurassic and older palaeosols and insect evolution (Retallack 1976, 1980; Genise 2004; Genise *et al.* 2004). According to Bedatou *et al.* (2008) and Genise *et al.* (2008), crayfishes played important role in the formation of Mesozoic soils. At the present stage, we report these preliminary finds in order to encourage further studies and discussion on insect fossil nests in palaeosols older than Cretaceous (for discussion see Genise 2004; Genise *et al.* 2004; Bedatou *et al.* 2008; Genise *et al.* 2008). Certainly, arthropods, particularly crayfishes and insects formed an important element of the food chain in Sołtyków, providing food for other animals like small amphibians, reptiles and mammal-like animals, of which numerous footprints have been found in this locality, particularly in the sediments associated with soil profiles.

Sołtyków ichnoassemblages confirm that terrestrial ichnocoenoses were quite diverse and were chiefly controlled by changes in the water table and food availability. The diversity of the ichnotaxa was enhanced by the strongly mosaic character of the environments.

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