



***Ptychoplasma conica* isp. nov. — a new bivalve locomotion trace fossil from the Lower Jurassic (Hettangian) alluvial sediments of Sołtyków, Holy Cross Mountains, Poland**

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A new locomotion (repichnion) trace fossil, *Ptychoplasma conica* isp. nov., which is composed of chains of hypichnial mounds, is described from Hettangian alluvial sediments in Central Poland. Its occurrence is limited to amalgamated crevasse sandstones. The trace fossil is associated with freshwater bivalves belonging probably to Unionidae. This trace fossil reflects rhythmic (?diurnal) movement of the tracemaker in accordance with the direction of flow in the crevasse channel, where the forward movement took place in the shallow part of a sandstone layer and was interrupted by resting episodes in deeper sediment layer along the mud-sand interface. Episodic flood events forced bivalves to produce escape structures, moving from deeper (previous) to upper (later) levels of lateral movements. Some vertical burrows with bivalve body fossils preserved at the bottom suggest a taphonomic burial. *P. conica* ranges from Late Triassic to Hettangian.

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INTRODUCTION

Bivalves are common tracemakers both in marine and non-marine fossil and recent environments. One of the commonest of bivalve trace fossils is *Lockeia* James, 1879, which is a resting trace (cubichnion), preserved mostly as amygdaloid hypichnial mounds. No less common is *Protovirgularia* M'Coy, 1850, a locomotion (repichnion) trail, preserved mostly as hypichnial ridges with chevron ribs (e.g., Seilacher and Seilacher, 1994; Mángano *et al.*, 1998). The chevron ribs are traces of a bivalve's cleft foot, which is anchored in the sediment during locomotion (e.g., Seilacher and Seilacher, 1994). Much less is known about locomotion trace fossils related to bivalves having a non-cleft (wedge) foot. These belong to the ichnogenus *Ptychoplasma* Fenton and Fenton, 1937, which is typified by *Ptychoplasma excelsa* Fenton and Fenton, 1937 from the Carboniferous of Texas. This trace fossil is almost unknown. Häntzschel (1975, p. W187) placed it among "Unrec-

ognized and Unrecognizable Genera", mostly because its type material was not available for him. The material was examined by Rindsberg (pers. comm., 2007), who described some trace fossils from the Carboniferous of Alabama under this ichnogenus (Rindsberg, 1994). It is recognized that *Hostynichnium* Pli ka et Sirá ova, 1989 and *Tuberculichnus vagans* Ksi kiewicz, 1977 belong to this ichnogenus (Mikuláš, Rindsberg and Uchman, submitted).

All of the hitherto known ichnotaxa occur in marine environments. In this paper, we describe a new ichnospecies of *Ptychoplasma*, which was found in non-marine Early Jurassic (Hettangian) sediments at Sołtyków in Central Poland. Its morphological features are different from known *Ptychoplasma* ichnospecies, but share the same principles of a locomotive, undulating trail.

Invertebrate trace fossils from Sołtyków, including those produced by bivalves, have been extensively described by Pie kowski and Nied wiedzki (2009). However, one of these ichnofossils needs new definition and detailed behavioural characteristics, which is the aim of the present paper.

GEOLOGICAL SETTING

The Sołtyków exposure is an old, long-abandoned clay pit. This exposure became known as a classic outcrop of Early Jurassic alluvial plain deposits, belonging to the continental Zagaje Formation and the lowermost Jurassic depositional sequence I (Pie kowski and Gierli ski, 1987; Pie kowski, 1998, 2004; Figs. 1–3). Plant remains (Wcisło-Luraniec, 1991; Ziaja, 2006) point to the Hettangian (Lias alpha 1-2), and the sequence stratigraphic correlation (Pie kowski, 2004) allows its age range to be narrowed to the Early Hettangian (*Planorbis* chron — or the earlier, up to date still informal, *Tilmanni* chron). Recently, the conchostracan *Bulbilimnadia killiani* Kozur et Weems 2005, was found at Sołtyków, pointing to the earliest Hettangian (H. Kozur, pers. comm., 2009). The plant fossils and palaeosol levels are very abundant in Sołtyków. The list of plants includes *Neocalamites*, the matoniacean, osmundacean and other indeterminate ferns, as well as pteridosperms, benettitaleans and conifers (Wcisło-Luraniec, 1991; Ziaja, 2006). Other fossils that occur in Sołtyków are represented by a unionid freshwater bivalve assemblage, insect remains (Wegierek and Zherikhin, 1997), freshwater ostracodes, scales of palaeoniscid fish and the above-mentioned conchostracans. The Sołtyków exposure is a well known Early Jurassic tracksite with numerous dinosaur footprints, mainly left by theropods and sauropods, and early mammalian footprints (Pie kowski and Gierli ski, 1987; Gierli ski and Pie kowski, 1999; Gierli ski *et al.*, 2001, 2004). A dinosaur nesting ground has also been described (Pie kowski, 1998). Recently, the Sołtyków exposure has been declared a natural reserve.

According to Miall (1977) and his plan-view morphology classification, the types of rivers are controlled chiefly by water discharge, sediment load, channel slope, and type of vegetation. Based on that principle, four types of rivers were distinguished: braided, meandering, straight and anastomosing. Anastomosing/avulsion patterns are most common on very low-gradient alluvial plains, where rate of flow is low and banks consist of muddy, cohesive sediment or are highly vegetated (Nanson and Croke, 1992; Emery and Myers, 1996). A relatively thick and individualized package of lacustrine deposits (dark grey to black, laminated or of massive mudstones with plant-root horizons associated with distal crevasse intercalations (Figs. 2 and 3) points to some permanency of the lake/swamp area during deposition of the sediments and to a low-gradient, low-energy alluvial plain. Likely, fine bed-load to suspended-load sediment was deposited in the floodplain as “overbank” sediments during floods and as a “normal” sedimentation in a 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 generally recognised. The fact that the type 2 crevasse (delta-like) appears in the middle part of the section (Fig. 2) indicates a growing aggradational/avulsion tendency, associated with a much higher water table (Aslan and Autin, 1999). The depth of this lake environment can be estimated at 0 to a few metres, judging

from the common plant roots and stems, particularly those of horsetails (which might have grown under shallow water) and traces of swimming theropod dinosaurs scratching the bottom (Gierli ski *et al.*, 2004). This points to a water depth of about 2 m, judging from a length of legs of *Dilophosaurus*, the alleged producer of these trace fossils.

On the other hand, the presence of individualized channel deposits with laterally-accreted bedding in sandstones and associated crevasse splays point to the existence of periods of more intense drainage and higher energy of currents. Generally, the Sołtyków exposure fits the mixed character between an avulsion-controlled (crevassing-anastomosing) fluvial sedimentation model (Farrel, 2001) and a meandering model with the presence of high-sinuosity/meandering streams (Pie kowski, 2004).

Importantly, channel lithofacies (medium to poorly sorted, trough-cross bedded, laterally accreted sandstone) are commonly underlain by 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). This points to importance of crevassing (= flooding) processes in initiating new courses of channels, which is particularly characteristic of the anastomosing pattern. According to the avulsion model (Farrel, 2001), an initial avulsion stage is accomplished predominantly by the development of crevasse splay complexes that cause the enlargement of new channels and abandonment of old ones. Crevasse splays developed at the 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 at Sołtyków are typical sedimentary “garbage piles”, accumulating rapidly large amounts of plant debris and mud clasts. They differ from the associated channel subenvironment deposits in having smaller grain sizes and unit thicknesses. Channelised crevasse splays show a multistage infilling with reactivation surfaces (Fig. 3), which indicates that the local breaches in the levees occupied the same position for some time, funnelling the flow in much the same place during many flood events.

Crevasse splay subenvironment was particularly favourable for preservation of the dinosaur footprints (Pie kowski and Gierli ski, 1987; Gierli ski and Pie kowski, 1999; Gierli ski *et al.*, 2001). Invertebrate burrows (Pie kowski and Nied wiedzki, 2009) concentrate mostly also in crevasse splay deposits, and to a lesser extent in floodplain deposits and levee deposits; the latter are not very common at Sołtyków because levee deposits are prone to subsequent erosion. Non-marine trace fossils have been recently described by Pie kowski and Nied wiedzki (2009) and they comprise forms belonging to the *Coprinisphaera*, *Scoyenia* and *Mermia* ichnofacies (using of the term *Coprinisphaera* ichnofacies for this section and for Jurassic deposits in general, however, is a matter of debate). Bivalve trace fossils have been also described in that paper, although the peculiar bivalve locomotion trail described herein needs more detailed characterization.

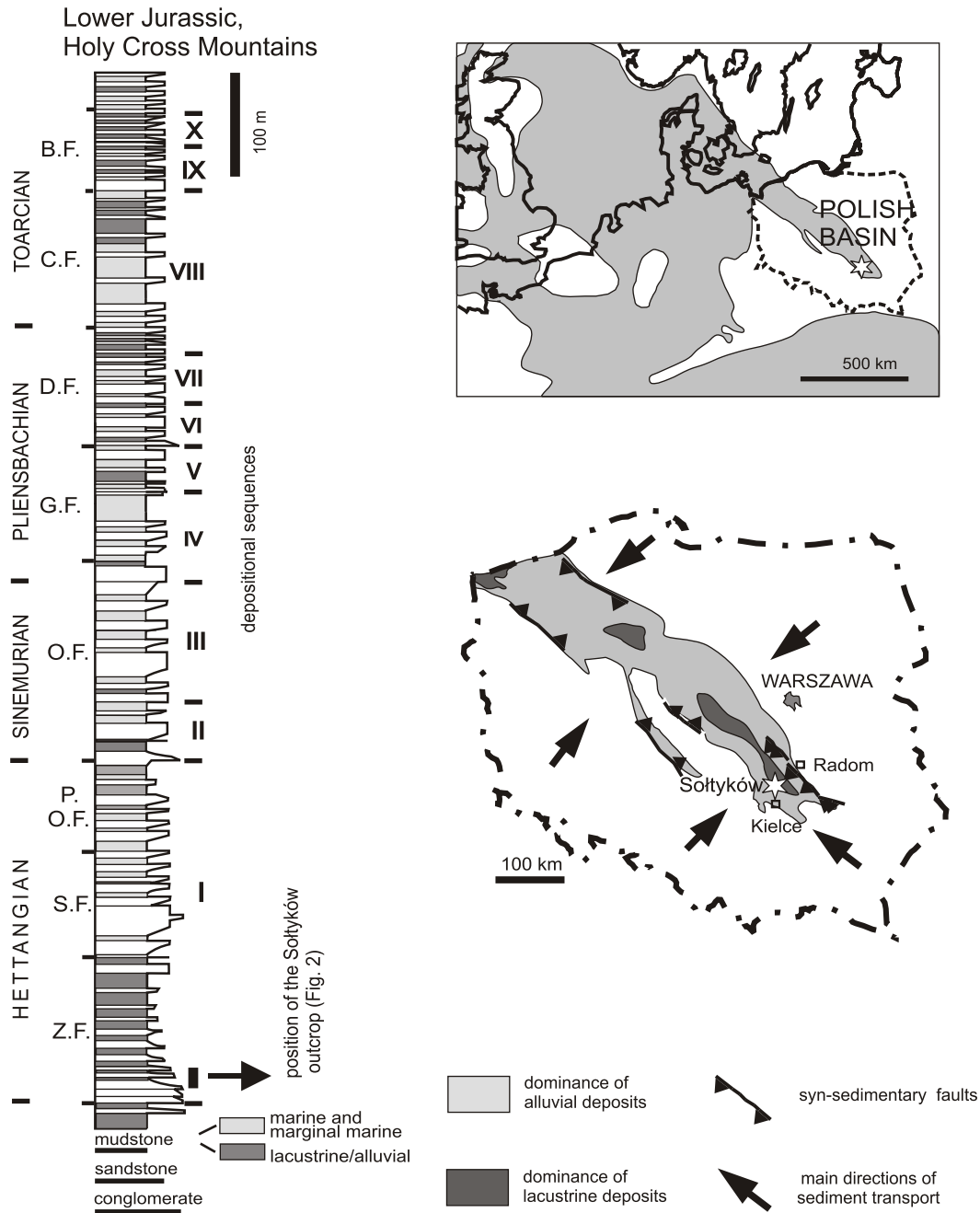


Fig. 1. Hettangian basins of Poland and NW Europe with synthetic profile of the Lower Jurassic in the Holy Cross Mountains region and location of the Sołtyków outcrop

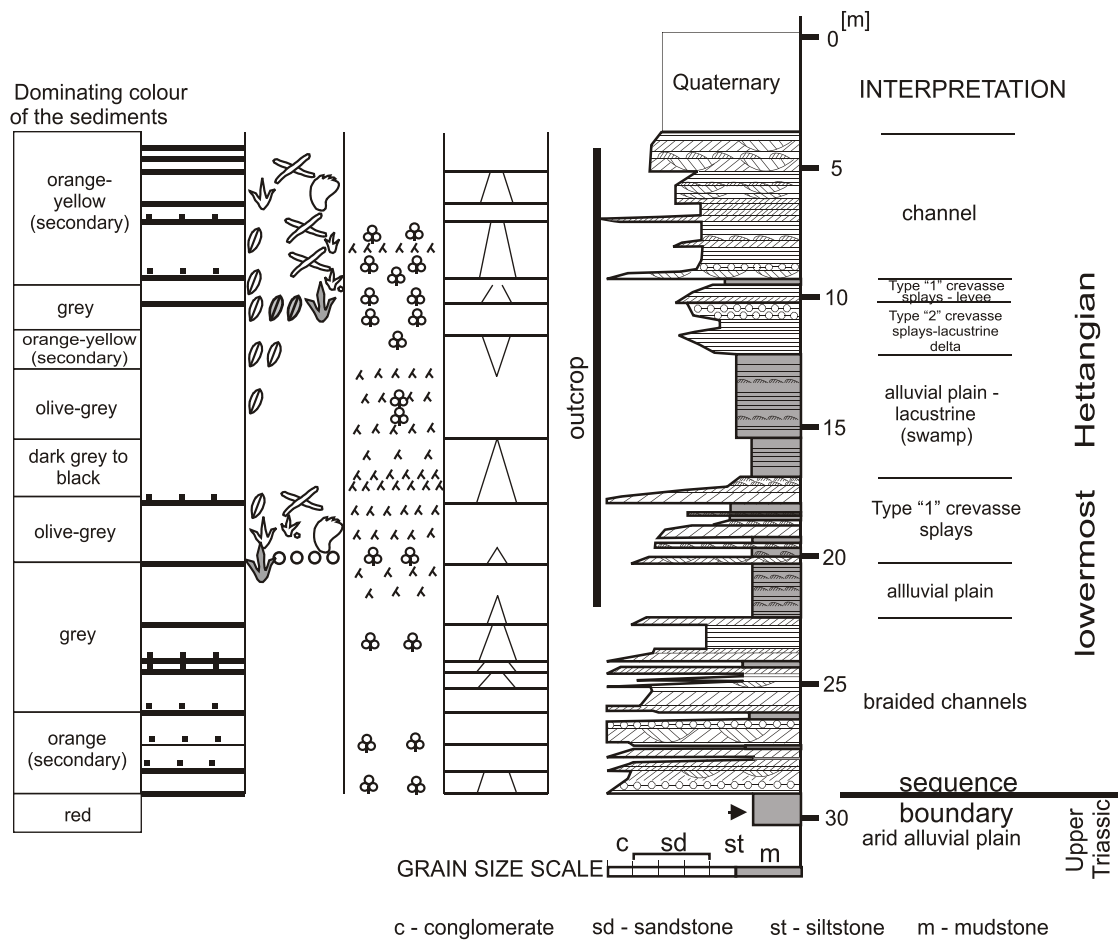
Lithoformations: Z.F. — Zagaje Fm., S.F. — Skłoby Fm., P.O.F. — Przysucha Ore-Bearing Fm., O.F. — Ostrowiec Fm., G.F. — Gielniów Fm., D.F. — Drzewica Fm., C.F. — Ciechocinek Fm., B.F. — Borucice Fm.; source areas left blank; after Pie kowski, 2004 (simplified)

SYSTEMATIC PART

Ichnogenus *Ptychoplasma* Fenton and Fenton, 1937
 Type ichnospecies *Ptychoplasma excelsa*
 Fenton and Fenton, 1937

D i a g n o s i s. — In hypichnial aspect, nearly smooth, undulating, continuous to discontinuous subhorizontal ridges that display a characteristically amygdaloid, carinate or blocky cross-section, little or no chevron sculpture, and commonly a straight, winding, irregularly meandering or looping course (Mikuláš, Rindsberg and Uchman, submitted).

R e m a r k s. — *Ptychoplasma* differs from *Protovirgularia* M Coy, 1850 by its undulatory relief and only local, faint chevron ribs, if present at all. *Lockeia* James, 1879 is limited only to single mounds.



INVERTEBRATE TRACE FOSSILS

- bivalve and associated trace fossils (*Mermia* ichnofacies)
- Ptychoplasma conica*
- arthropod and associated trace fossils (*Scoyenia* and *Coprinisphaera* ichnofacies)

- erosional surfaces
- erosional surfaces with mud clasts
- sauropod tracks (*Parabrontopodus* isp.)
- supposed basal ornithischian footprints (*Anomoepus* isp.)
- medium-sized theropod footprints (*Anchisauripus* isp.)

- large theropod tracks (*Kayentapus soltykovensis*)
- gigantic theropod tracks (*Eubrontes giganteus*)
- dinosaur nesting ground
- plant roots and palaeosols
- drifted flora
- cycles - fining-upwards (left) and coarsening-upwards (right) and their boundaries
- horizontal lamination
- tabular cross bedding
- trough cross bedding
- ripple-drift cross lamination
- contorted bedding
- microlaminated or massive mudstones and claystones

Fig. 2. Sedimentological log of the Soltyków outcrop (after Pie kowski 2004, emended) with indication of the crevasse deposits bearing *Ptychoplasma conica* isp. nov.

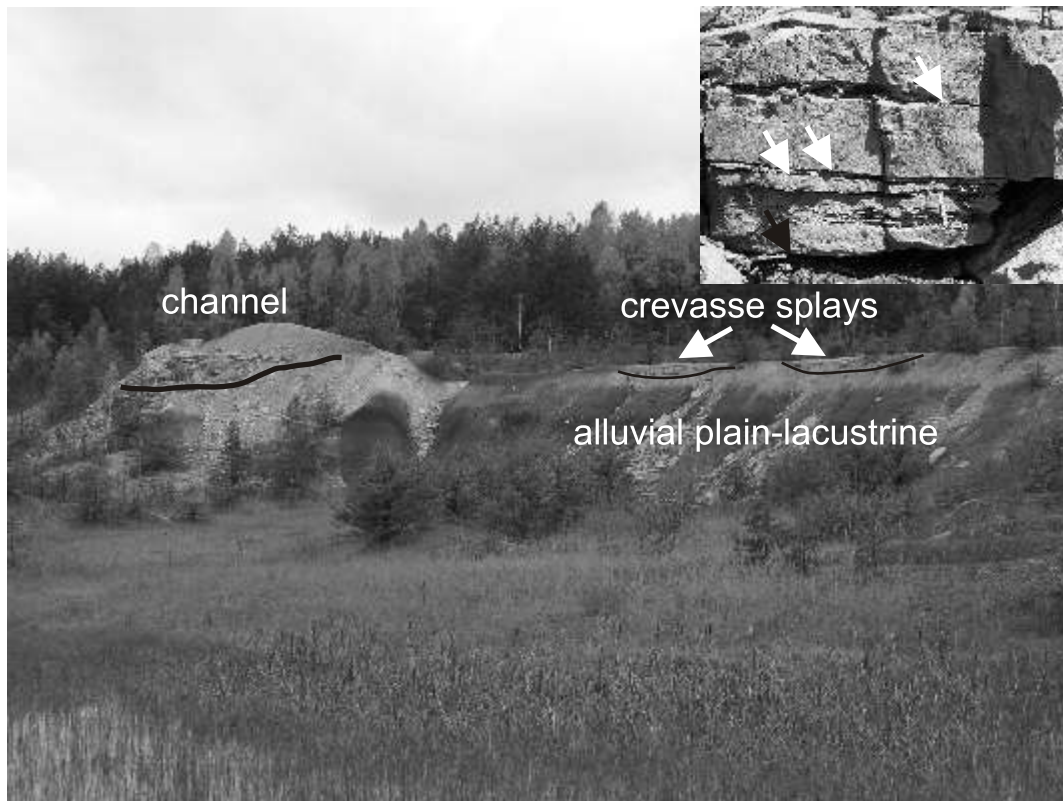


Fig. 3. Sołtyków outcrop revealing alluvial plain-lacustrine mudstones and channel/crevasse splay sandstones (arrowed)

The main meandering channel is visible on the left. Inset: multi-stage sedimentation of the crevasse splay (type 1) with erosional surfaces bounding successive flood events (arrowed); *Ptychoplasma conica* isp. nov. was found in the crevasse splay facies illustrated on this photograph

Ptychoplasma conica isp. nov.
(Figs. 3–6)

1949, einzelige Reihenhöcker-Spur – Linck, 666–669, pl. 8, figs. 1–2.

1955, Unbenannte Kriechspur einer Muschel – Seilacher, fig. 5 (31) [referred to Linck, 1949, pl. 8, fig. 1].

nomen nudum 1994, *Lockeia seriali* n. ichnosp. – Seilacher et Seilacher, 10.

2009, aligned *Lockeia amygdaloides* (Seilacher, 1953) — Pie kowski and Nied wiedzki, 119, fig. 4: 2.

D e r i v a t i o n o f n a m e. — From the overall conical shape of mounds in the chain.

M a t e r i a l a n d h o l o t y p e. — 3 slabs in the Polish Geological Institute-National Research Institute (MUZ PGI 80.VI.139, 80.VI.140, 80.VI.141). The holotype is in the slab MUZ PGI 80.VI.139 (cut into four pieces A, B, C, D — pieces A and B is the holotype). The same slab was illustrated by Pie kowski and Nied wiedzki (2009, fig. 4: 2) and named as “aligned *Lockeia amygdaloides* burrows”. The paratypes are the slabs MUZ PGI 80.VI.140, PGI 80.VI.141. Seven small slabs in the Institute of Geological Sciences of the Jagiellonian University (INGUJ 211P1-7); the paratype is INGUJ 211P5.

D i a g n o s i s. — Straight to slightly winding chain of hypichnial, mostly conical mounds, which can partly overlap.

D e s c r i p t i o n. — Rows of hypichnial mounds on a sandstone bed. The mounds are conical or pouch-like, isometric or elongate, round to oval or slightly lobate oval in outline, 13–38 mm wide, 18–35 mm long, as much as 30 mm high. The surface of the mounds is smooth, or only having irregular, gently sloping concavities of convexities. Their top is hemispherical or flat.

The rows contain 3 to at most 16 mounds. Edges of the mounds in the row overlap (Figs. 4A, 5A, B, 6A and 7A, B) or less commonly are isolated (Figs. 4C and 5C–E). Apices of the mounds are located 15–25 mm apart and as much as 63 mm between the isolated mounds. The longest rows observed are at least 350 mm long, with 15 or 16 mounds (Fig. 6A). They are truncated by the edge of slabs, and probably are much longer. In some larger slabs the rows run sub-parallel or cross-cut at an acute angle up to 50° following more or less the same direction (Fig. 6A). In some slabs the rows are so crowded that they are difficult to follow (Fig. 6B); the sandstone sole looks like a field of mounds. In the crowded specimens, curved, semicircular ridges, about 5 mm wide, run irregularly between the mounds (Fig. 6B). It is not clear if they belong to *Ptychoplasma* or not.

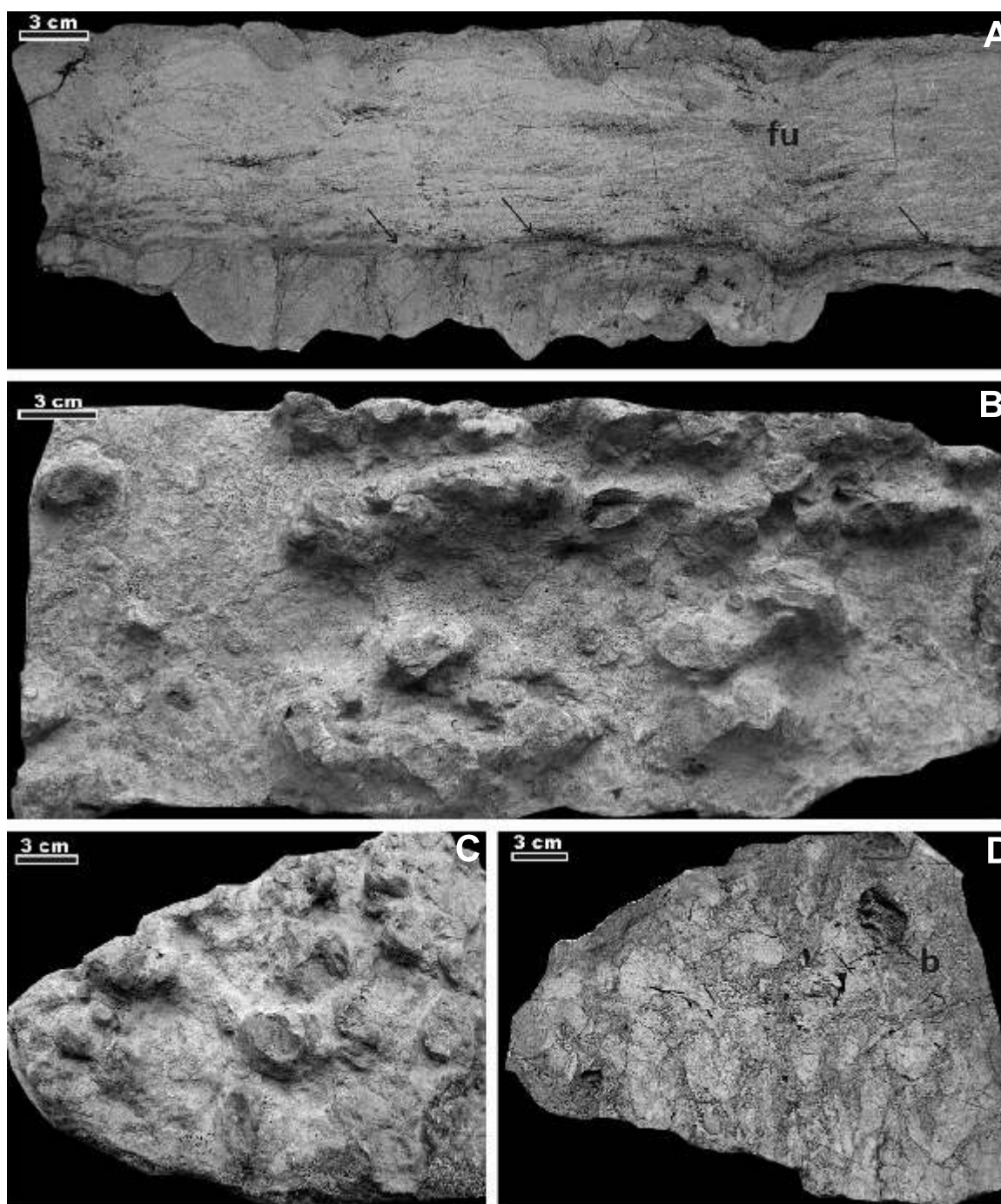


Fig. 4. *Ptychoplasma conica* isp. nov. in sandstone slabs

A — vertical cross-section. Note the basal layer with cross section along a row of *Ptychoplasma conica* isp. n., which is separated by an amalgamation surface (arrows) from the upper layer. The upper layer is cross cut by an escape structure (fugichnion) of the tracemaking bivalve (fu), MUZ PIG 80.VI.139 (holotype); **B** — lower surface of the cut slab shown in A; **C** — lower surface of a sandstone bed with mounds of *Ptychoplasma conica* isp. n., MUZ PIG 80.VI.140; **D** — horizontal section of the slab shown in B. Note elongated bioturbational structures and a depression of a bivalve external mould (b)

Some of the mounds display single cavities, which show steep, smooth walls, an oval outline with semi-rounded margin at one side, and pointed margin at the opposite side of longer axis of the oval (Fig. 6B). The depressions are 30 mm long, 15 mm wide, and as much as 10 mm deep, 23–27 mm long and 11–15 mm wide. In some broken mounds, an outline of a bivalve shell can be visible (Fig. 7A).

The trace-fossil bearing sandstone beds locally display meniscate vertical structures, with menisci convex down, about 25 mm wide, without distinct margins (Fig. 4A). These are considered as escape (fugichia) structures of the tracemaker. Commonly, the trace fossil bearing layer is separated from the higher layer by an amalgamation surface, which truncates the burrows (Fig. 4A). In horizontal sections, the trace-fossil bear-

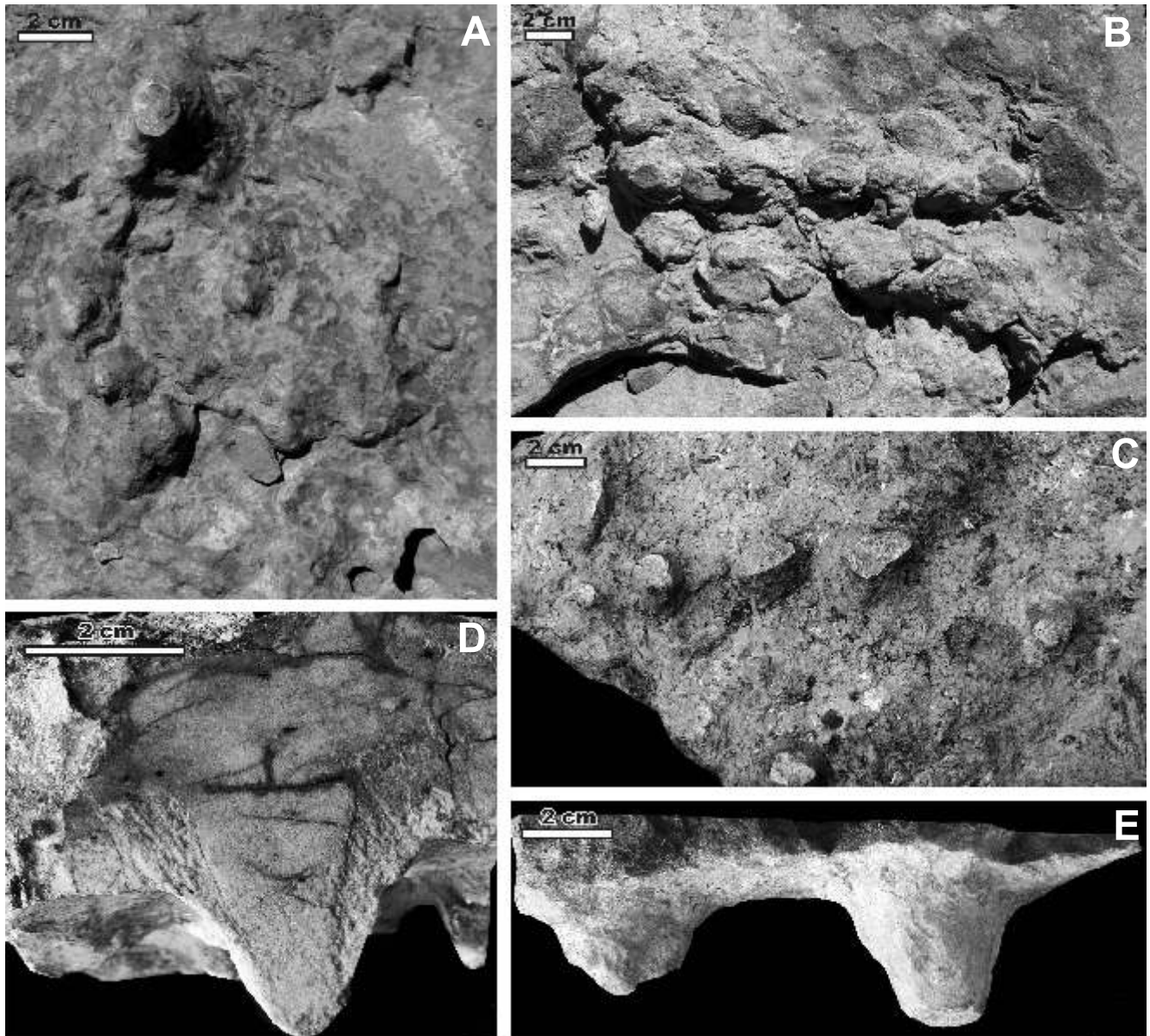


Fig. 5. Different appearance of *Ptychoplasma conica* isp. nov. in sandstone slabs

A, B — *Ptychoplasma conica* isp. nov. in rows with overlapping mounds, field photographs; C — row with isolate mounds, field photograph; D — vertical section of a mound, ING UJ 211 P1; E — side view of two separated mounds, ING UJ 211P3a

ing layer displays mostly elongated bioturbational structures, with poorly expressed concentric structures (Fig. 4D). In vertical section, the mounds display a conical core surrounded by an envelope of slightly different lithology (Fig. 5D). The internal structures are related to the sequential movements of the tracemaker.

R e m a r k s. — *Ptychoplasma excelsa* Fenton and Fenton, 1937 displays less distinct, slightly elongated mounds. *Tuberculichnus vagans* Ksi kiewicz, 1977 and its junior synonym *Hostynichnium duplex* Pli ka et Sirá ova, 1989, which are included in *Ptychoplasma* (Mikuláš, Rindberg and Uchman, submitted) displays elongate mounds pointed at both ends, arranged in a commonly strongly wind-

ing or looping row. As yet, no more ichnospecies of *Ptychoplasma* are known.

Seilacher and Seilacher (1994) proposed a new ichnospecies *Lockeia serialis*, which was referred to the material termed “Muschelspur” i.e. “bivalve trace” and illustrated by Linck (1949) from the Upper Triassic Stuttgart Formation (“Schilfsandstein”) of the Keuper Group (megafacies) in Germany. It was diagnosed by Seilacher and Seilacher (1994) as a “...repichnial version of *Lockeia*, expressed by serial alignment of amygdaloid undertraces...”. Linck (1949) did not use the term “Muschelspur” but described and illustrated it (p. 666–669, pl. 8, figs. 1–2) as an “einzeilige Reihenhöcker-Spur”, i.e. “... a single row of humps...”, which accords with the

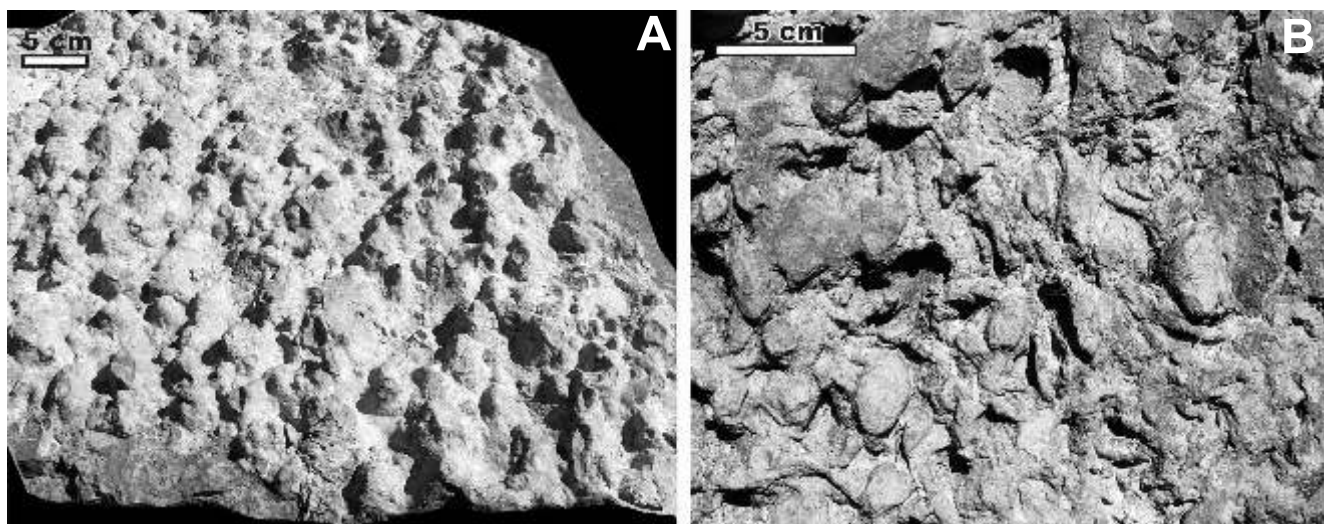


Fig. 6. Other appearances of *Ptychoplasma conica* isp. nov. on the lower surface of sandstone slabs, field photographs

A — two generations of subparallel rows showing partial crossing; B — crowded *Ptychoplasma conica* isp. nov. associated with curved ridges

diagnosis by Seilacher and Seilacher (1994). Because no holotype was designated, *Lockeia serialis* Seilacher et Seilacher, 1994 is a *nomen nudum* (Schlirf *et al.*, 2000). Rietschel (1965), Vossmerbäumer (1970) and Pie kowski (1991) illustrated locomotion trails of bivalves from nearshore-coastal plain lower Hettangian deposits from Helsingborg, Scania, Southern Sweden. Also, escape structures made by bivalves, similar to those described herein (although smaller), were described by these three authors. The first two authors named these rows of amygdaloid trails as *Pelecypodichnus amygdaloides*, the third author assigned those trails to *Imbrichnus* isp. In all cases they differ from *Ptychoplasma conica* isp. nov. by having smaller, more regular, non-conical, almond- to lens-shaped mounds in the chain. The trails from Scania represent *Ptychoplasma* isp., but they should be defined as a separate ichnogenus. Pie kowski and Nied wiedzki (2009) described aligned *Lockeia amygdaloides* from Sołtyków locality, which is identical to those described herein (one slab illustrated by Pie kowski and Nied wiedzki is actually the holotype of *Ptychoplasma conica* isp. nov.). They also illustrated similar but smaller forms (their fig. 6).

DISCUSSION

The ichnogenus *Lockeia* James, 1879 is a resting trace (cubichnion), but *Ptychoplasma conica* isp. nov., even if its basic morphological elements are composed of *Lockeia*-like structures, is a locomotion trace fossil that belongs to a different ethological category, i.e. repichnion. This distinction requires a separate ichnogenetic assignment, and the ichnogenus *Ptychoplasma* Fenton and Fenton, 1937 is the best choice for this repichnion.

The characteristic mound-like shape and body fossils in *Ptychoplasma conica* isp. nov. indicate bivalves as the tracemakers of this trace fossil. Preservation of the body fossils

as moulds of shells does not allow for closer determinations but according to Nied wiedzki (pers. comm., 2008) and Fürsich (pers. comm., 2008), they belong to the Unionidae. Members of this family are typical freshwater taxa, which are common in fluvial environments.

Ptychoplasma conica isp. nov. occurs in amalgamated sandstone beds deposited in a river crevasse. Tracemaking bivalves moved more or less toward the direction of flow. Modern river-dwelling unionoids show preferred orientation with the sagittal plane of the shell parallel to current flow, with the long axis of the shell dipping downstream (Thoms and Berg, 1985; Johnston and Hendy, 2005). Pie kowski and Nied wiedzki (2009) claimed that alignment of this trace fossil was preferred and parallel to the palaeocurrent direction. The authors also noted the adaptation of bivalve's behaviour to sedimentation. Bivalves penetrated throughout a sand layer a few centimetre thick, and commonly the lowest part of their foot entered the underlying mud. The sand was introduced in the resulting depression in the mud. The flat top of some mounds can be the result of filling of the lowest part of the depression by mud. After weathering, the muddy part was eroded from the sandy part. The nearly isometric shape of the hypichnial mounds indicates that lateral movement of the bivalve was made in the shallower layer of sand. The mounds are a record of resting with a downward and upward movement, lacking any significant lateral component.

The morphology of *Ptychoplasma conica* isp. nov. reflects repetitive, rhythmic undulatory movement of the tracemaking bivalve. Such a movement can be explained in different ways. It can reflect diurnal rhythm, where the bivalve moves up and feeds, moving laterally during the day when waters are warmer and digging down during night for resting, or moving laterally to feed during the night and digging down during days when predatory danger is high. Alternatively, the rhythm can be related to rhythmic changes of flow in the crevasse channel related to precipitation.

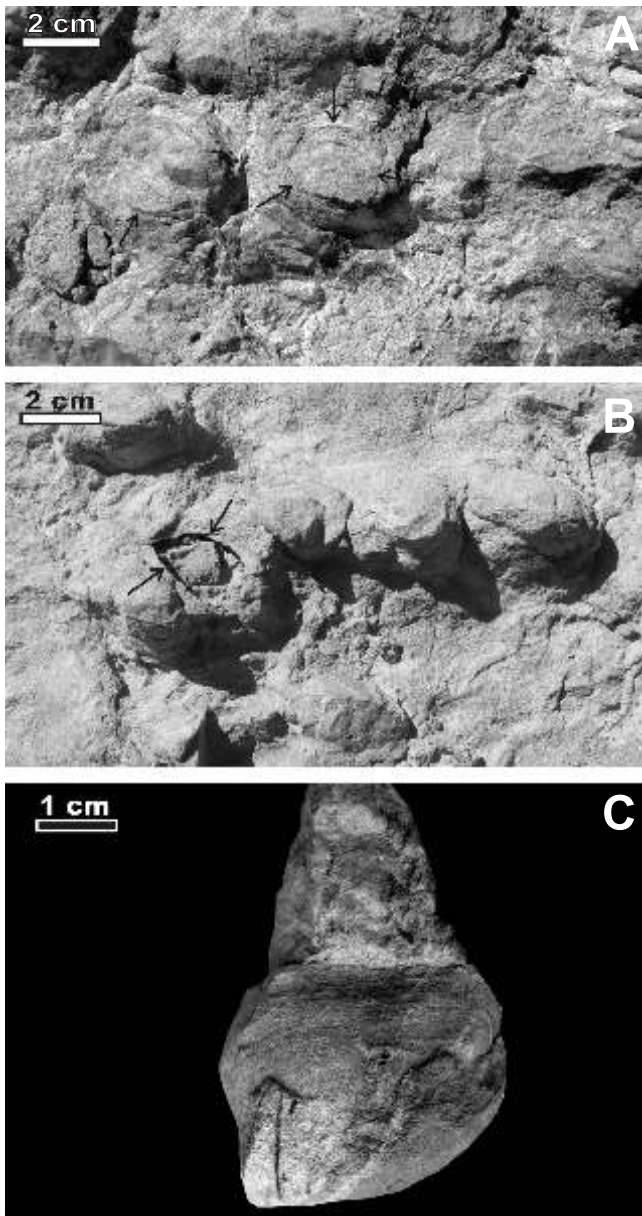


Fig. 7. Evidence of the tracemaking bivalves of *Ptychoplasma conica* isp. nov.

A — broken mounds with outlines of dissolved shells (arrows); **B** — external mould of shell (arrows) at the end of a row; **C** — external mould of a shell preserved at the end of a protrusive burrow, extracted from the trace fossil bearing bed; the shell probably belongs to the Unionidae, MUZ PIG 80.VI.142

We have not excluded the possibility that the mass occurrence of *Ptychoplasma conica* isp. nov. in the base of the crevasse sandstone reflects invasion by the bivalve in the fluvial plain during the humid season. In such a situation, the river channel can play the role of refugium during the dry season. Bivalves can migrate on the fluvial plain when it is flooded during the rainy season.

Channelised crevasse splays show a multistage infilling with reactivation surfaces (Fig. 3) reflecting multiple floods. Certainly, the feeding bivalves were exposed to heavy stress caused by erosion and/or anastrophic depositional events. Such

stress forced the tracemakers to move vertically, either downwards (some deep protrusive structures — Pie kowski and Nied wiedzki, 2009; Fig. 7C), or opposite, upwards, which was caused by rapid deposition associated with waning flood event (retrusive *Scalichnus* isp. described by Pie kowski and Nied wiedzki, 2009 and meniscate escape structures visible in Fig. 4A). These vertical, meniscate fugichnia are “communication channels” joining the previous (deeper) with newer (shallower) tiers (Fig. 4A). Observations of living unionoids show that inundation by sediment prompts an upward escape response produced by downward thrust of the foot (Thoms and Berg, 1985).

Interestingly, external moulds of body fossils of bivalves are locally found at the “blind” ends of protrusive vertical shafts (Fig. 7C) or inside the bed (Fig. 4D). Likely, the “unlucky” bivalves escaping primary erosion faced even worse odds, when their habitat was covered by a thick layer of sandy sediment, rapidly deposited during the flood-waning stage. They could simply stay forever in their refuge (“taphonomic burial”), being unable to overcome the overlying sediment burden. Likely, these bivalves would not even attempt to escape (there are no signs of upward movement).

Works of Rietschel (1965), Vossmerbäumer (1970) and Pie kowski (1991) show that the behaviour of continental bivalves — tracemakers of *Ptychoplasma conica* isp. nov. — did not differ significantly from the brackish-marine tracemakers of the trails from Scania. In the latter case, the nearshore currents and post-storm sedimentation were responsible for alignment of the trails and escape structures, respectively (for post-storm escape structures made by bivalves see also Pie kowski, 1985).

As yet, *Ptychoplasma conica* isp. nov. is limited to the Late Triassic–Hettangian in terms of stratigraphy, and geographically to Central Europe. However, further data are needed to modify or verify this view.

CONCLUSIONS

1. *Ptychoplasma conica* isp. nov. is a new locomotive (repichnion) trace fossil related to freshwater bivalves belonging probably to Unionidae.

2. *Ptychoplasma conica* isp. nov. occurs in crevasse sediments; the tracemaking bivalves moved more or less according to the flow direction.

3. Morphology of this trace fossil reflects rhythmic movement of the tracemaker, where lateral movement took place in the shallow part of the sandstone layer and was interrupted by resting episodes in the deeper sediment layer along the mud-sand interface.

4. The “normal” (background) life conditions were often interrupted by “catastrophic” flood events, exerting stress on the bivalves and forcing them to move vertically — sometimes downwards (escape from erosion), or more often upward (escape from an anastrophic burrow). Resulting vertical meniscate structures commonly link with the horizontal tiers.

5. *Ptychoplasma conica* isp. nov. ranges from Later Triassic to Hettangian.

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