

COMPACTION-RELATED STYLE OF *RUSOPHYCUS* PRESERVATION FROM FURONGIAN (UPPER CAMBRIAN) OF HOLY CROSS MOUNTAINS (POLAND)

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Abstract: In general, the trace fossil *Rusophycus*, preserved as a concave-upward structure on the top of a bed, is considered to be a fossilized marking, made by a trace maker. The structures described from the Cambrian (Furongian) of central Poland are genetically related to *Rusophycus*. However, despite their occurrence on the tops of beds, they are not fossilized traces, but compaction-related features, resulting from differential sandstone and mudstone compaction with possible mediation by organic-rich, heterolithic sediments. The preservation of these structures probably was influenced by biofilms or biomats.

Key words: *Rusophycus*, trace fossil, preservation, compaction, Cambrian, Furongian, Poland.

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INTRODUCTION

Rusophycus is a resting trace fossil (cubichnion; Bromley, 1996; Seilacher, 2007). It is most commonly attributed to the life activity of arthropods. Palaeozoic examples occur mainly in marine strata and have been ascribed to trilobites (Crimes, 1970a, b; Seilacher, 1970). Mesozoic, non-marine forms of *Rusophycus* have been attributed to crustaceans (Bromley and Asgaard, 1972; Pollard, 1985; Schlirf *et al.*, 2001). Small ichnospecies of *Rusophycus*, made by representatives of both of these arthropod groups, are morphologically indistinguishable (Bromley and Asgaard, 1979).

Previously, concave, epichnial *Rusophycus* – a trace fossil on the upper surface of a sedimentary bed (Martinsson, 1970) – was interpreted to be actually a true trace, a depression in bottom sediment, excavated by a trace maker. There are two hypotheses on the mode of formation of the concave *Rusophycus*: (1) concave *Rusophycus* is a fossilized epifaunal trace, produced at the sediment-water interface (Crimes, 1975), and (2) *Rusophycus* is a fossilized infaunal trace, created at the sand-mud interface within the substrate (Seilacher, 1970, 1985).

Both of these scenarios assume that the depressions made by trace makers were subsequently filled with sediment, usually sand. The timing of the addition of the fill is the main difference between these scenarios. The epifaunal trace would be filled just after the biological activity or with a delay, after some period of non-deposition and possible

erosion. In the case of infaunal traces, filling occurred immediately after the burrowing activity and this “instant casting” mechanism is considered as leading to high-resolution preservation of the shallow traces (Seilacher, 1970, 1985). The sand-filled epifaunal or infaunal true traces are preserved as hypichnia that are natural casts of these traces, occurring on the lower surfaces of a sand bed (Martinsson, 1970). Hypichnia constitute the most commonly encountered mode of preservation of *Rusophycus* in the fossil record.

According to this widely accepted interpretation, all *Rusophycus*-shaped structures occurring on bed tops in the Upper Cambrian Wiśniówka Sandstone Formation previously were interpreted as the true traces of arthropods, namely of trilobites (Radwański and Roniewicz, 1963; Żylińska and Radwański, 2008). The results of this study indicate that at least some of these structures, occurring on tops of beds/laminae, appear to be compaction-related phenomena, resulting from differential compaction involving mud and sand (Baldwin, 1971; Nadon and Issler, 1997).

MATERIAL AND METHODS

The material studied comes from the Wiśniówka Sandstone Formation (Fig. 1). The observations and conclusions presented in this paper are based on numerous field observations and studies of trace fossils from the collection ZPAL Tf. 4. The collection comprises material collected by the Author

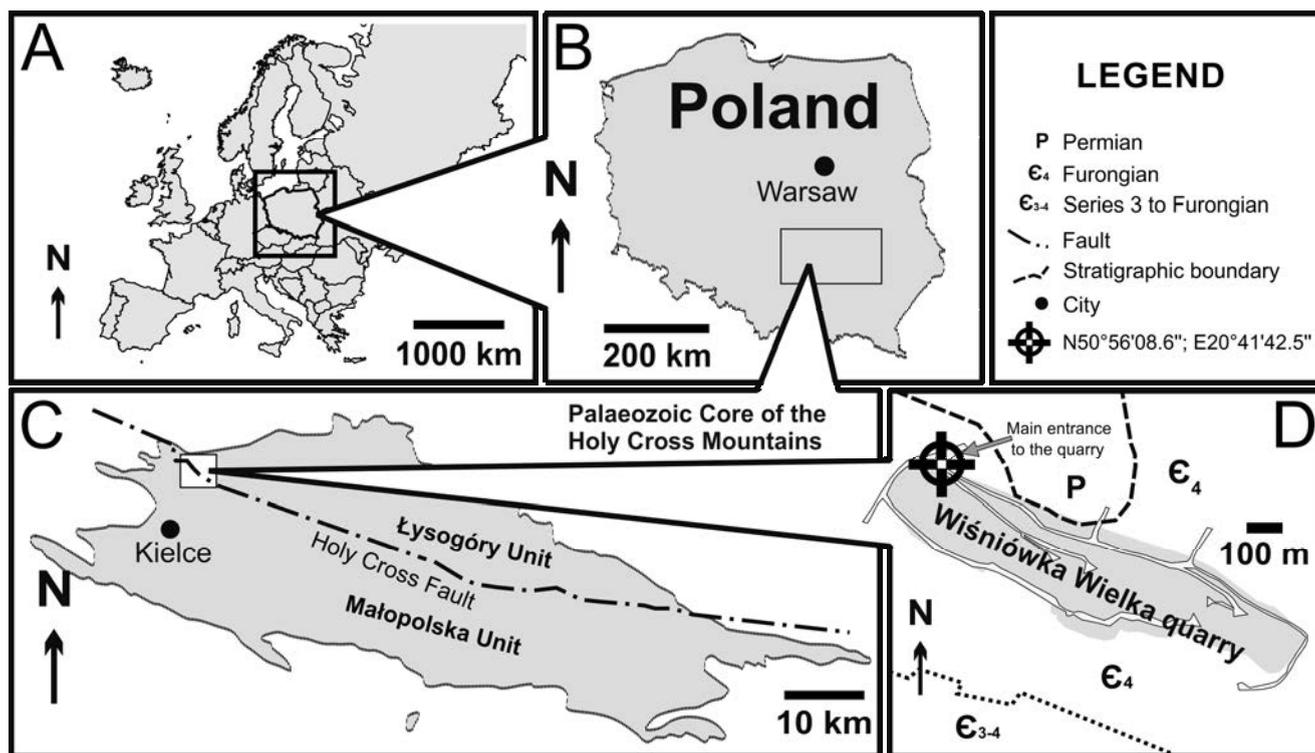


Fig. 1. Location of study area. **A.** Position of Poland in Europe. **B.** Map of Poland, showing location of Holy Cross Mountains. **C.** Holy Cross Mountains (Palaeozoic core). **D.** Plan of Wiśniówka Wielka Quarry (stratigraphy based on Żylińska *et al.*, 2006)

(80%) and by Marcin Machalski (20%) from the Institute of Paleobiology of Polish Academy of Sciences, Warsaw. The following specimens from the collection ZPAL Tf. 4 best document the type of toponymy and preservation described: 192, 513, 518, 600, 791, 1151, 1238, 1468, 1471, 1472, 1473.

The heterolithic intervals of the Wiśniówka Sandstone Formation were split with a scissor knife to search lamina-by-lamina for trace fossils. Both the top and bottom surfaces of each lamina were investigated. This mode of bed examination allowed direct observation of the laminae surrounding the hypichnial *Rusophycus*, including their relationship with the hypichnial trace fossil.

LOCATION AND GEOLOGICAL SETTINGS

The material studied was collected from the Cambrian (Furongian) Wiśniówka Sandstone Formation (Orłowski, 1992a, 1992a; Żylińska *et al.*, 2006). The siliciclastic deposits of this unit comprise quartz-dominated sandstones, mudstones and heterolithic intervals and are exposed best at a few quarries in westernmost part of the Holy Cross Mountains (Wiśniówka Wielka, Wiśniówka Mała and Podwiśniówka), as well as in the Opatów area (Kowalczewski *et al.*, 2006 and references therein). The estimates for the thickness of the Wiśniówka Sandstone Formation range from 80–200 m, up to 400–1400 m, depending on the tectonic model applied (Kowalczewski *et al.* 2006 and references therein). The present study was conducted in the Wiś-

niówka Wielka Quarry, in the westernmost part of the northern Holy Cross Mountains, Poland (Fig. 1).

The Wiśniówka Sandstone Formation is poor in index body fossils (Żylińska *et al.*, 2006). The unit was dated as “Middle to Upper Cambrian” by Orłowski (1992a, b), who (Orłowski, 1992b) based his conclusions on “*Cruziana* stratigraphy”, an ichnostratigraphical scheme applied to Lower Palaeozoic non-fossiliferous marine siliciclastics (Seilacher, 1970, 1994, 2007; MacNaughton, 2007). Żylińska *et al.* (2006), studying acritarchs and rare trilobite body fossils, concluded that the unit is lower Furongian.

Sedimentary environment and diagenetic history

The Wiśniówka Sandstone Formation is composed of thick, amalgamated quartzite sandstone beds (quartz-arenites *sensu* Nagtegaal, 1978), mudstones and heterolithic intervals characterized by flaser, wavy and lenticular bedding (Studencki, 1994; Jaworowski and Sikorska, 2006; Żylińska *et al.*, 2006). Studencki (1994) interpreted the sandstone intervals as deposited on the proximal inner shelf, and the heterolithic sediments as deposited on the distal inner shelf. Jaworowski and Sikorska (2006) interpreted this unit in a similar way, as, storm-affected deposits on a shelf, with the sands as tidal sand ridges or tidal sand waves and the heterolithic intervals as transitional to shelf muds. However, Dżułyński and Żak (1960) noted in their sedimentological study of the Wiśniówka Sandstone Formation that a shift from mud- to sand-dominated sedimentation could have taken place in the same depth zone, as a result of dynamic changes in the bottom topography and variation in the cur-

rent paths, typical for shallow subaqueous environments. Numerous and various ripple types, preserved very well in the heterolithic intervals, also were taken as indicating shallow- to very shallow-water conditions (Dzuleński and Żak, 1960; Radwański and Roniewicz, 1960).

The Wiśniówka Sandstone Formation hosts numerous structures that may have originated as a result of microbial binding of the sediment, the so-called microbially induced sedimentary structures (MISS; Noffke *et al.* 2001). These occur on bedding planes and appear to be genetically diverse (see the classification in Eriksson *et al.*, 2007). These structures were observed in the same intervals that yielded the trace fossils studied. The most characteristic of these are wrinkle marks (Fig. 2A–C), cracks developed within the sandstone lithologies (Fig. 2D), interference ripples (Fig. 2E) and “sand chips” (Fig. 2F), that is, oval and flat clasts of sandstone, occurring within sandstone or mudstone lithologies. This association of structures is a strong indication of the presence of biofilms and/or microbial mats within the sedimentary environment (cf. Hagadorn and Bottjer, 1997; Pflüger, 1999; Bottjer and Hagadorn, 2007; Eriksson *et al.*, 2007; Porada and Bouougri, 2007; Porada *et al.*, 2008). All of these MISS resulted from the presence of a microbially produced extracellular polymeric substance that makes the sandy substrate atypically cohesive and resistant to erosion (Bottjer and Hagadorn, 2007).

Recent microbial mats typically occur within tidal settings, where specific prerequisites as to substrate texture, high moisture, low hydrodynamic energy and low metazoan activity are met (Porada and Bouougri, 2007). MISS in the fossil record are also most commonly encountered in shallow marine conditions (intertidal to supratidal; e.g. Carmona *et al.*, 2012). However, microbial mats are by no means restricted to such settings (Schieber *et al.*, 2007) and in the Precambrian and Lower Palaeozoic microbial mats were much more widespread. Some workers even postulate a Precambrian–Cambrian shift from “matground” (microbial mats) to a “mixground” (microbial covers around individual grains) type of substrate structure and link this significant event to the increasing activity of bioturbators (Seilacher and Pflüger, 1994). Pflüger (1999) showed a wide environmental range for the MISS that he described from the Silurian Tanezzuft Shale and the Acacus Sandstone in Libya. In his examples, the MISS occurred in strata, characterized by ichnofossils typical of the *Skolithos* and *Cruziana* ichnofacies (Pflüger, 1999, fig. 7). Therefore, the occurrence of MISS in strata, characterized by the *Cruziana* ichnofacies (including studied *Rusophycus*) as in the case of the Wiśniówka Sandstone Formation, is not unusual for the Lower Palaeozoic.

The significance of microbial activity for the preservation of trace fossils is well known (e.g. Carmona *et al.*, 2012). However, in the present paper, a potentially new aspect of the taphonomical significance of microbial mats is briefly discussed.

The postdepositional history of the Wiśniówka Sandstone Formation is not known exactly, especially for post-Silurian time (Sikorska, 2000). However, it has been postulated that the Wiśniówka Sandstone Formation experienced deep burial within the Cambrian to Silurian time interval, reaching

a burial depth of about 1,700 m in the Silurian (Sikorska, 2000). Late diagenetic silification occurred at that time under conditions of high temperature and pressure, resulting in the obliteration of the original grain boundaries by the extensive formation of quartz overgrowths (see Sikorska, 2000).

RESULTS

Observations

The individual sandstone and mudstone laminae can be as thin as 1 mm in these intervals and are usually 1–2 mm thick. *Rusophycus* is an abundant trace fossil in the heterolithic intervals studied. Hypichnial *Rusophycus* is embedded in the surrounding mudstone laminae; mudstone laminae run below and above the *Rusophycus*, which in cross-section take the form of sandstone lenses (Fig. 3A–E). The tops of these lenses are more or less flat (Fig. 3E). Locally, arthropod trackways occur on the upper surfaces of the lenses. The sandstone bodies in the form of lens-like hypichnial *Rusophycus* deform the muddy laminae below and above. The laminae above are slightly convex-upward (Fig. 3E) and those below mimic the morphology of the lower surface of the hypichnial *Rusophycus* (Fig. 3F): the laminae are concave-upward below the endopodal lobes and convex-upward between the lobes (Fig. 3C, D).

Typically, no interruption of the lower muddy laminae was observed. Therefore the cross-sections of these laminae mostly are not observed on the lateral margins of the bed-top *Rusophycus*-shaped structure, except for rare, thin cut laminae, associated with hypichnial *Rusophycus* (Fig. 5D). The laminae within the *Rusophycus*-shaped filling are typically continuous (Fig. 4A, C–F). Some discontinuities or “windows” in the lower muddy laminae were observed, but these result mainly from weathering and/or damage during sampling (Fig. 4B). Finally, bed-top *Rusophycus* displays fewer morphological details (e.g. sculpturing of the lobes), than does the counterpart, hypichnial *Rusophycus* (Figs 4E, F, 5A, B). In the sample studied, the reverse situation was not observed, i.e. more details were seen on the bed-top *Rusophycus*-shaped structure.

Interpretation

Preservation of hypichnial Rusophycus

The sandy lens-like occurrences of *Rusophycus* are typical hypichnia (see Martinsson, 1965, 1970), with a laterally restricted extent of the casting medium (a lens-like appearance). This mode of preservation may be explained as an example of concealed bed-junction preservation, a special type of trace-fossil preservation, in which the filling material differs in texture significantly from the host sediment and has no connection with similar layers above, e.g. a sandy filling of burrows within a mudstone (Simpson, 1957; Jensen, 1997; Jensen *et al.*, 2005). Hypichnial *Rusophycus* in the form of sandstone lenses are the results of preferential preservation of trace-infilling sandy material, deposited in a sheltered depression (the actual trace made by the organism).

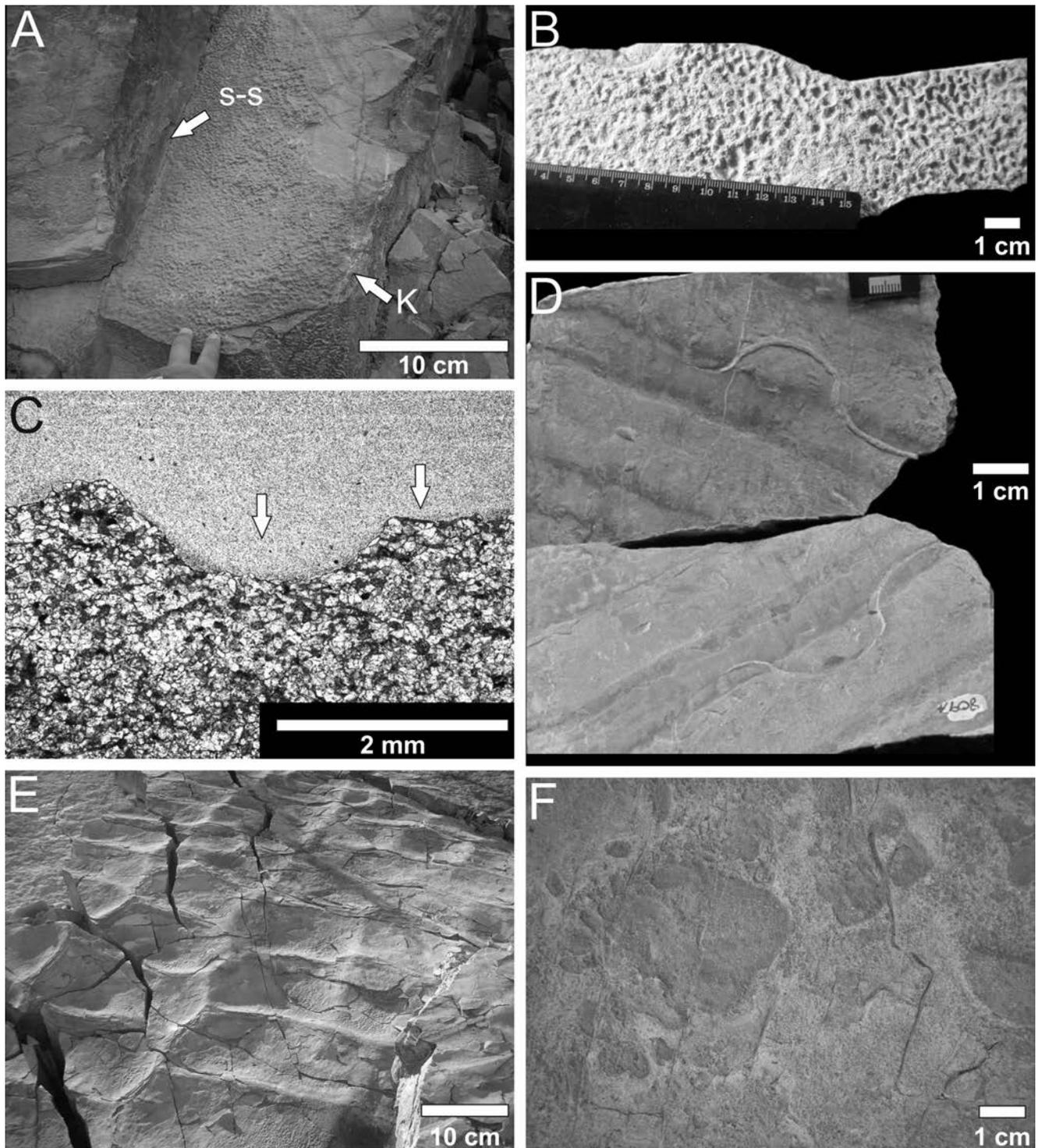


Fig. 2. Microbially induced sedimentary structures from Wiśniówka Sandstone Formation. **A.** Top surface of sandstone bed with wrinkle marks (marked with arrow and letter K), note that structure occurs at sandstone-sandstone contact (arrowed as s-s) with no clay or silt intercalation between sandstone strata (field photograph; compare Bottjer and Hagadorn, 2007). **B.** Wrinkle marks with clearly visible relief (bed top). **C.** Thin section of wrinkle marks with visible flat crest and trough (arrowed) typical features, known from similar structures (compare Calner and Eriksson, 2011; picture taken in plane-polarized light close to bed top). **D.** Sinusoidal crack within sandstone with no clay or silt intercalation at parting surface. **E.** Interference ripples (field photograph). **F.** “Sand chips”, rounded and flat sandstone intraclasts, preserved on top of another sandstone bed (compare Bottjer and Hagadorn, 2007). These display locally characteristic properties, as they seem to be glued together (central part of the picture; field photograph)

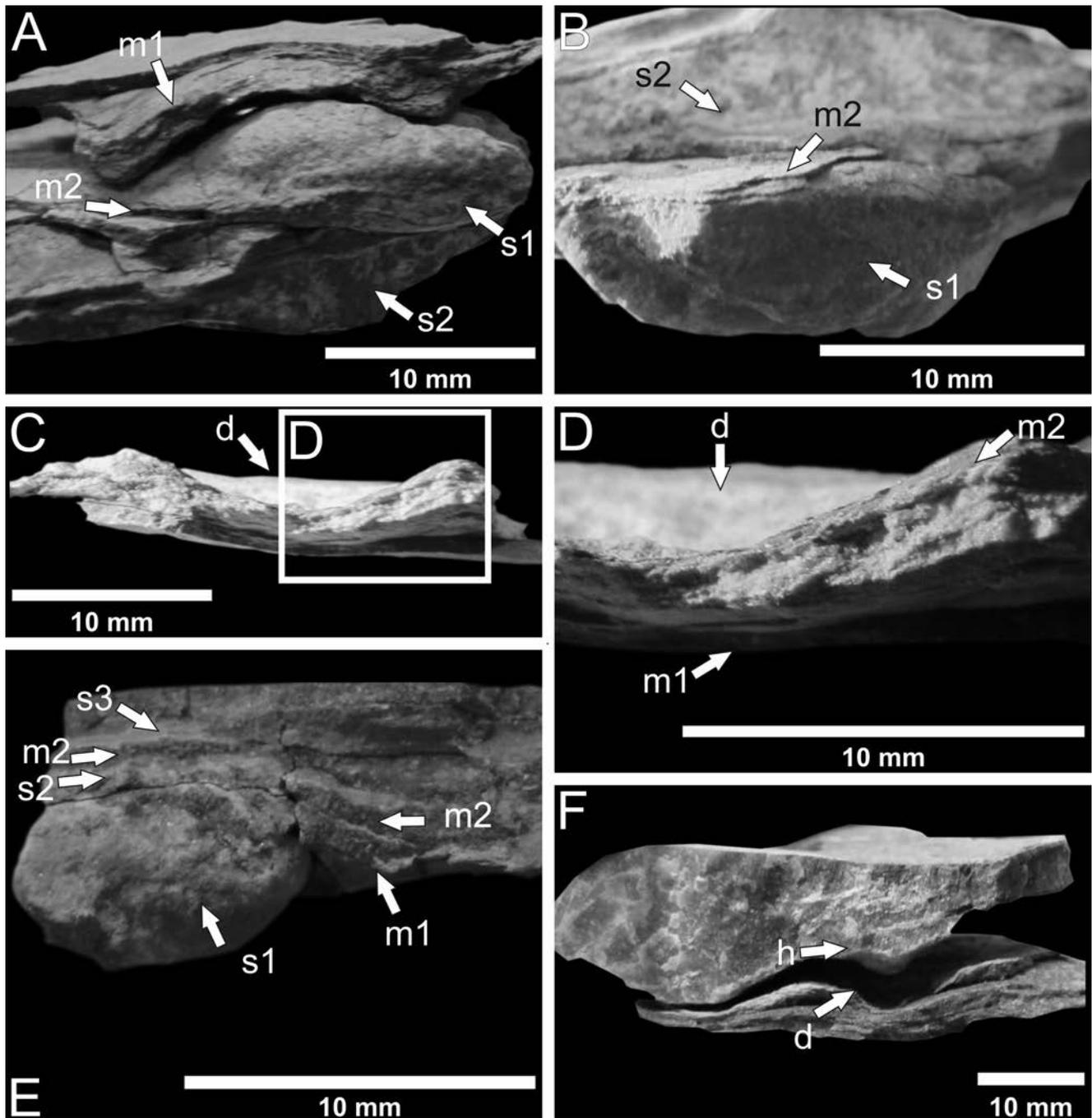


Fig. 3. Hypichnial *Rusophycus* in sandstone, embedded in mudstone laminae, and bed-top *Rusophycus*-shaped depression. **A.** Hypichnial *Rusophycus* with underlying mudstone laminae mimicking *Rusophycus*' morphology (specimen inverted, laminae top points toward bottom of picture), s1 and s2 – sandstone laminae, m1 and m2 – mudstone laminae (ZPAL Tf. 4/1468). **B.** Same specimen as in **A.**, in this case without underlying laminae (laminae top point toward top of picture), s1 and s2 – sandstone laminae, m2 – mudstone lamina (ZPAL Tf. 4/1468). Note: hypichnial *Rusophycus* is embedded in mudstone laminae (compare **A** and **B**), this mode of preservation may be called concealed bed-junction preservation (see Simpson, 1957; Jensen, 1997; Jensen *et al.*, 2005). **C.** Underlying mudstone laminae of specimen, figured in **A.** (ZPAL Tf. 4/1468). Note: bed-top *Rusophycus*-shaped cavity (d) and continuous, deformed mudstone laminae (box; lamina top points toward top of picture). **D.** Focus on detail shown in **C.**, laminae top points toward top of picture (ZPAL Tf. 4/1468). Note: bed-top *Rusophycus*-shaped cavity (d) and continuous, deformed mudstone laminae (m). **E.** Sandstone hypichnial *Rusophycus* (marked with "s") and its relationship to overlying laminae, m1 and m2 – mudstone laminae (laminae top point toward top of picture; concealed bed-junction preservation; ZPAL Tf. 4/1151). **F.** Side view of small hypichnial *Rusophycus* (marked as h) deforming underlying mudstone laminae (marked as d), the laminae continue below *Rusophycus* (laminae top points toward top of picture). Note: this is not concealed bed-junction preservation. *Rusophycus* is "fused" with the overlying sandstone bed (ZPAL Tf. 4/1473)

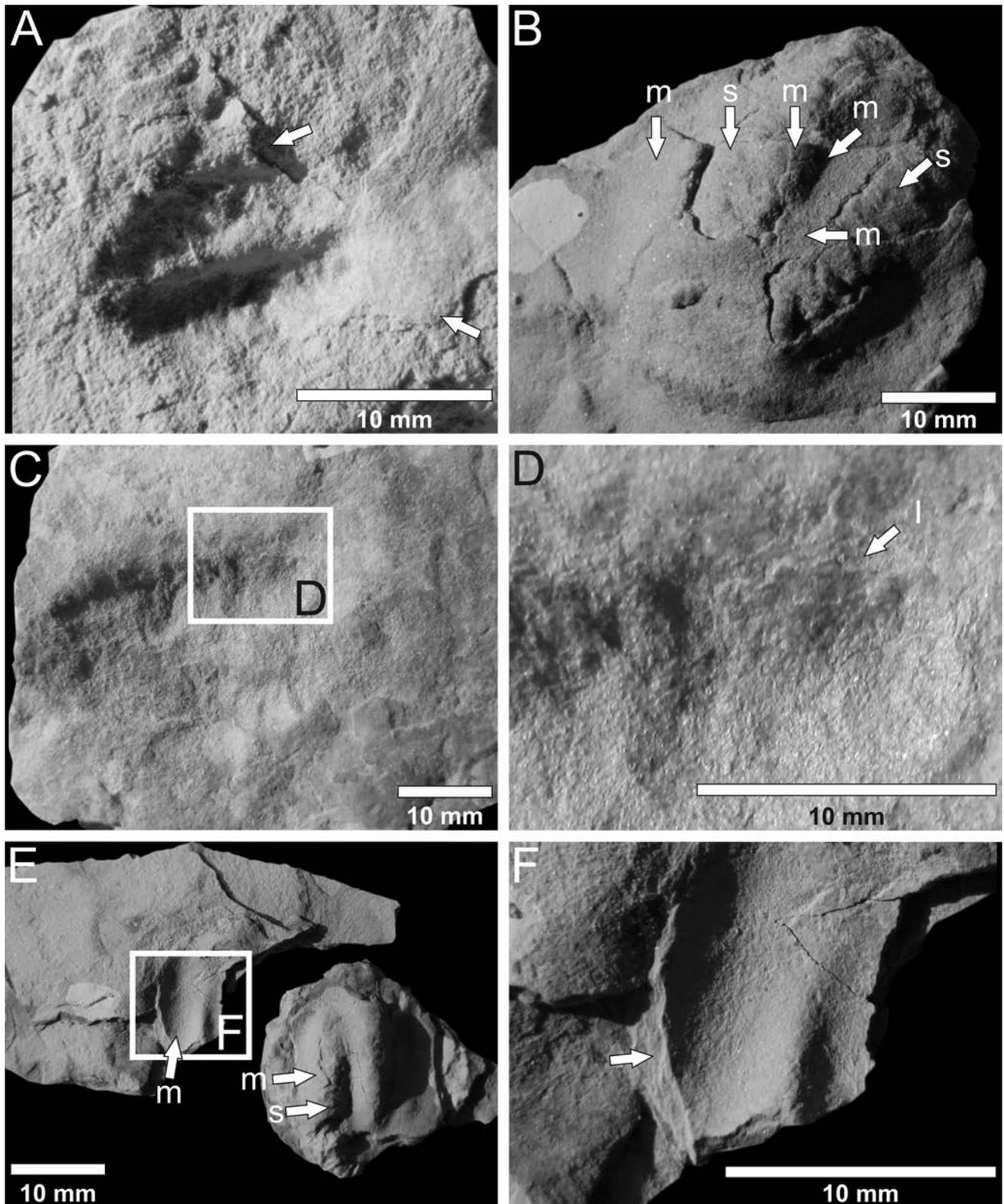


Fig. 4. Bed-top *Rusophycus*-shaped structures and laminae continuity inside structure. **A.** Bed-top *Rusophycus*-shaped structures in continuous lamina (edges of lamina shown by arrows; ZPAL Tf. 4/192). **B.** Hypichnial sandstone *Rusophycus* (marked with “s”) deforming underlying mudstone lamina (marked with m; ZPAL Tf. 4/1470). **C.** Bed-top *Rusophycus*-shaped structure deforming continuous lamina (the edge of lamina is marked with box; ZPAL Tf. 4/600). **D.** Close-up of detail shown in C, edge (marked with l) of continuous lamina deformed by bed-top *Rusophycus*-shaped structure (ZPAL Tf. 4/600). **E.** Hypichnial *Rusophycus* (on right) and bed-top *Rusophycus*-shaped structure (on left), m – mudstone lamina, s – sandstone lamina (ZPAL Tf. 4/1471). Note: total lack of sculpture on epichnial structure. **F.** Close-up of detail shown in E, bed-top *Rusophycus*-shaped structure with no sculpture and with cross-section of mudstone laminae visible outside structure (arrowed; ZPAL Tf. 4/1471)

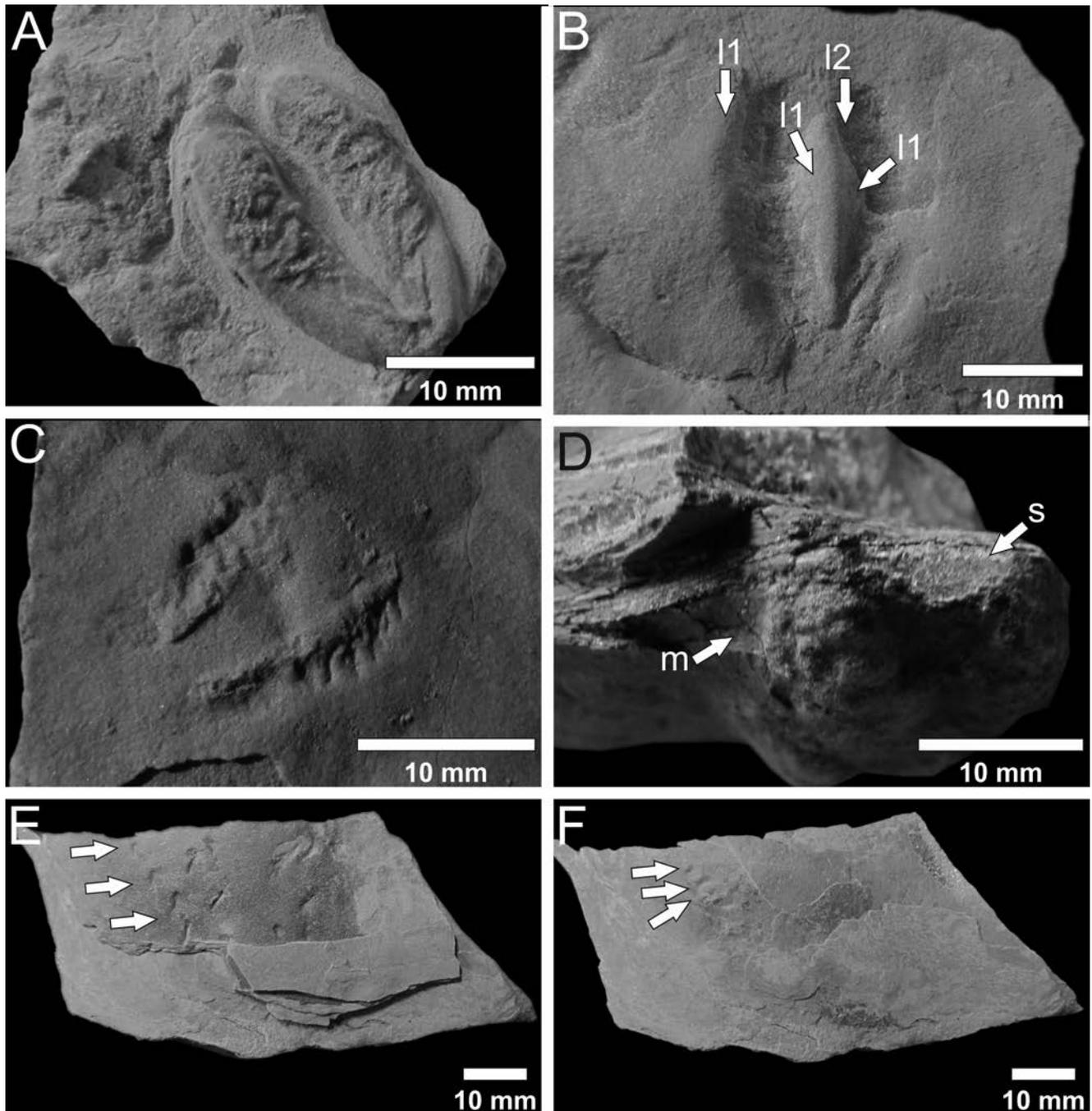


Fig. 5. Bed-top *Rusophycus*-shaped structure, epichnial *Rusophycus* and mud laminae compaction. **A.** Hypichnial *Rusophycus* with well defined sculpture on its lobes (ZPAL Tf. 4/1238). **B.** Bed-top *Rusophycus*-shaped structure with continuous laminae inside cavity, l1-l2 – laminae (ZPAL Tf. 4/1238). **C.** Epichnial *Rusophycus* (true trace or undertrace) with clearly visible displacement of material (ZPAL Tf. 4/513). **D.** Hypichnial sandstone *Rusophycus* (marked with “s”) and single muddy lamina it cuts through (marked with “m”); (ZPAL Tf. 4/1468). **E, F.** Top of rippled sandstone bed bearing arthropod track or undertrack with 1 mm thick set of mudstone laminae on its top (E), and same bed without overlying set of muddy laminae (F) (ZPAL Tf. 4/1472). Note: in E there are arthropod tracks (arrowed) and in F there are corresponding undertracks (arrowed)

Formation and preservation of bed-top *Rusophycus*-shaped structures

The burrowing activity by the *Rusophycus* trace maker should have removed the deposit from below and displaced it (Fig. 5C), and this action should have produced a cavity in the underlying bed (compare Seilacher, 1970, 1985). Therefore, the laminae inside the cavity should be discontinuous

and the cross-sectional views of these laminae should be exposed at the cavity side margins. On the contrary, the sandstone laminae underneath the sandstone *Rusophycus* typically have not been interrupted by the trace maker and instead are continuous. This type of laminae modification, without any cutting of laminae, indicates that the *Rusophycus*-shaped bed-top cavities are the result of deformation

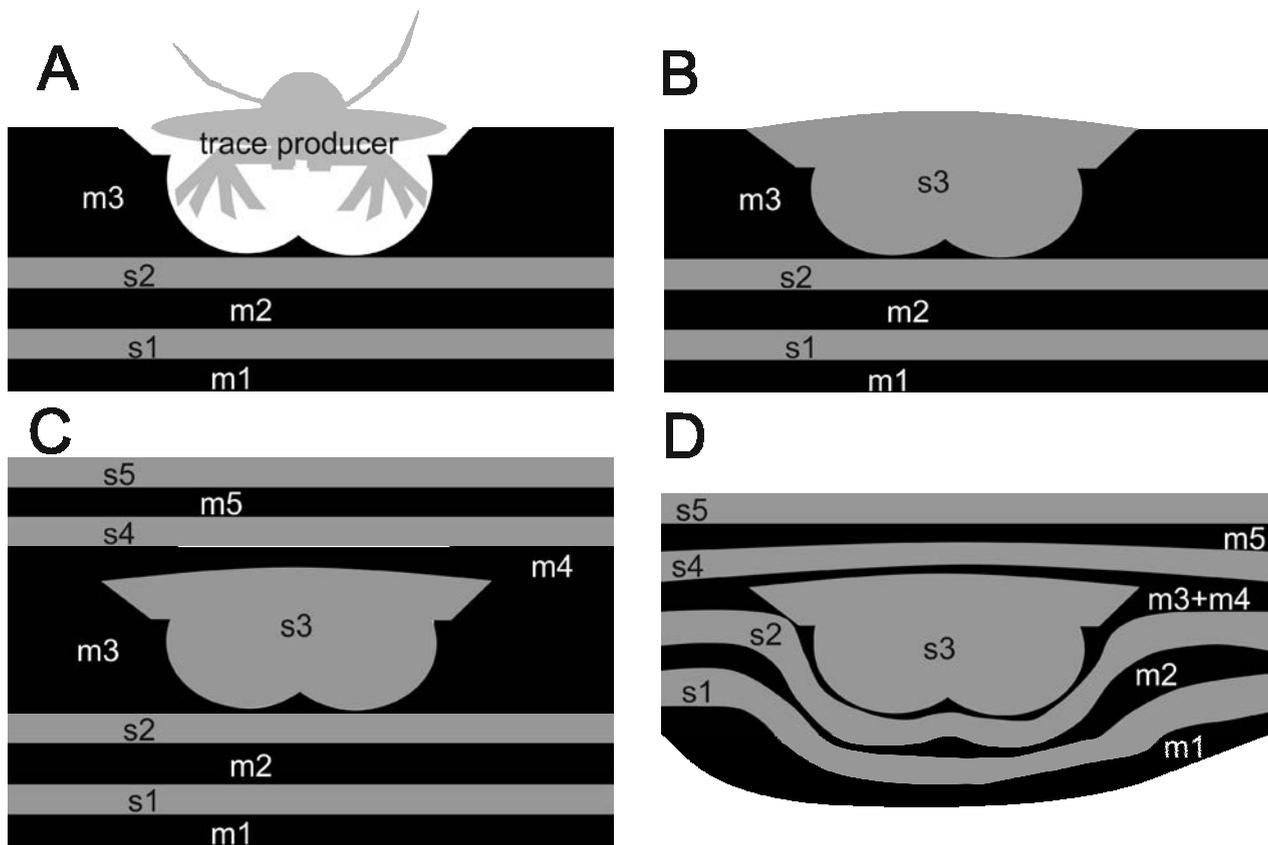


Fig. 6. Schematic drawing to explain origins of bed-top compaction-mediated *Rusophycus*-shaped structures. **A.** The trilobite digs in a muddy substrate. **B.** The trace is filled with sand. **C.** The trace and filling sandy material are buried. Note that the sand-filled *Rusophycus* appears to be embedded in muddy sediment; this is concealed bed-junction preservation (see text for references). **D.** Beginning of compaction. The deformation of the underlying laminae occurs after the activity of the trace-maker and this differentiates these structures from cleavage-relief preservation (“undertrack”; see Frey and Pemberton, 1985). Letters “m” and “s” refer to muddy and sandy lithologies, respectively, whereas the numbers indicate relative ages of laminae (starting from 1 as the oldest). Owing to compaction, the morphology of hypichnial *Rusophycus* is imprinted on the top of the lower lamina and the upper laminae also are affected. The degree of deformation decreases away from the hypichnial *Rusophycus*

that affected the laminae. The mode of deformation indicates that the laminae were not deformed by the trace producer itself, but rather by pressure related to the process of compaction (Fig. 6), caused by an increase in the load during later burial.

The hypichnial *Rusophycus* studied displays more morphological details, such as sculpture of the lobes, than the counterparts on the bed tops do (Fig. 5A, B). This phenomenon is difficult to explain in a typical epifaunal or infaunal scenario, in which concave structures are the actual epichnial traces. In such a case, the bed-top structures (epichnia) should display more details of morphology. The model of a compaction-related origin for the bed-top *Rusophycus*-shaped structures, described in this paper, would explain the differences in preservation resolution. The loss of morphological details could be explained by the “copy effect”, where each copy loses the definition of some quality. In the compaction-related model, the concave bed-top structures are detail-depleted copies of the hypichnial *Rusophycus* (sandstone lens-like *Rusophycus*), whereas the hypichnia themselves are copies of epifaunal/infaunal traces.

These observations lead to the final conclusion that the bed-top *Rusophycus*-shaped structures described are not

epifaunal or infaunal traces. The two substrates were originally separated. During diagenesis, the hypichnial *Rusophycus* fill in the upper layer acted as an indenter that shaped the surface of the sandy laminae beneath. The exact match between the hypichnial *Rusophycus* and its impression on the bed top below indicates that vertically acting pressure was involved, rather than lateral bed slides and stress, where more elongated grooves would be expected. This is how the hypichnial *Rusophycus* made the bed-top “imprint mark” on the top of the bed below. In this scenario, the originally burrowed substrate, in which a trace originally was produced, is not preserved in the fossil state and therefore it is postulated that its original composition was very sensitive to diagenetic alteration. Therefore, the organic content of this substrate was likely to be high. The presence of microbially induced sedimentary structures indicates that microbial biofilms and mats played a role in the sedimentary environment of the strata. Thus it is possible that the organic-enriched material, occurring between the laminae and targeted by the trace producer, was a microbial mat or biofilm.

If the origin of the bed-top *Rusophycus*-shaped structures significantly postdates (possibly by millions of years?) the formation of the hypichnial *Rusophycus*, then the pro-

posed mode of the formation of these structures is different from that of cleavage-relief or undertrack preservation (Fig. 5E, F), in which subsurface laminae are deformed during trace-maker activity at the surface (cf. Lessertisseur, 1955; Heyler and Lessertisseur, 1963; Goldring and Seilacher, 1971; Frey and Pemberton, 1985). The trace fossil is a fossilized trace, which is a result of substrate-organism interaction (Bertling *et al.*, 2006). However, the transition from the original trace into the fossil record (trace fossil) is commonly associated with abiotic processes, such as the formation of hypichnial casts, in which no biological activity occurs. The bed-top structures described are not fossilized epichnial traces, but a new type of preservation of them, in which a diagenetic process (compaction) played a major role. The new term “compactional epichnia” is proposed here to cover this type of trace fossil toponomy and preservation. The following model is proposed for the origin of the structures described: 1) an organism burrows the substrate, which probably was covered by a microbial mat or microbial film; 2) the trace is filled with sand; 3) the burrowed substrate and the sandy filling are buried; 4) compaction starts and creates a compactional epichnion (Fig. 6).

DISCUSSION

Because sands and muds (a mixture of silt and clay) differ in original porosity, the deposits represented by these lithologies will tend to compact differentially. Sand has a lower porosity than freshly deposited mud and hence, sand tends to compact less than mud (Baldwin, 1971; Perrier and Quiblier, 1974; Nadon and Issler, 1997). Moreover, in mudstones, the growing pressure increases silica dissolution, but at the same time the precipitation of silica in the same beds is inhibited (Mullis, 1992). This means that the volume of mud decreases, owing to a depletion in silica. On the other hand, in sands silica is precipitated freely as inter-granular cement (Mullis, 1992). Thus, the precipitated silica, transported by pore fluids from the neighbouring muds, can increase the resistance of the sandstone to compaction (Stephenson *et al.*, 1992). Similar processes probably occurred in the strata studied, as sand-dominated beds display pervasive silicification, in addition to pressure solution (see Sikorska, 2000). This is why compaction-related deformations are so well preserved in the mudstone laminae, surrounding *Rusophycus* (compare Nadon and Issler, 1997, fig. 4 therein). As indicated, the difference in preservation of detail, observed in the bed-top and hypichnion structure couplets, can be explained by the “copy effect”, with two originally separate substrates coming into direct contact during diagenesis.

The burrowed substrate appears to be virtually missing in the cases studied as cut laminae are mostly not observed (specimens show no macroscopically visible intercalations between the sandy laminae (Fig. 5A, B)). During differential compaction, beds may exhibit significant reduction of thickness, but typically their continuity is not disrupted and at least a thin remnant of the original lamina is preserved (Wetzel and Reisdorf, 2007). Therefore, it is postulated here that the burrowed substrate had a high content of organic

matter and a significant reduction of its thickness was caused by decomposition processes that could have taken place before differential compaction began and during the compaction the thickness of the laminae was further reduced (see Wetzel and Reisdorf, 2007). The substrate could represent a living or decaying biofilm or microbial mat. The presence of microbial biofilms or mats in the sedimentary environment of the Wiśniówka Sandstone Formation is indicated by microbially induced sedimentary structures, as documented in this paper. The microbial component of these interbeds could have been the real target of the digging arthropods, namely trilobites feeding on the biomat.

CONCLUSIONS

The *Rusophycus*-shaped structures, occurring on the tops of beds in the Cambrian (Furongian) Wiśniówka Sandstone Formation of the Holy Cross Mountains (Poland) resemble true epifaunal or infaunal trace fossils. However, a detailed study of the muddy laminae associated with the sandstones shows that the laminae underlying *Rusophycus* (hypichnion) were not interrupted by the activities of the trace maker, but are continuous. This mode of modification of laminae indicates a compaction-related origin with possible mediation by microbial biofilms or biomats, occurring between them.

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