

RUSOPHYCUS INEXPECTUS ISP. NOV. FROM THE FURONGIAN (UPPER CAMBRIAN) OF THE HOLY CROSS MOUNTAINS (POLAND)

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Abstract: A new trace fossil *Rusophycus inexpectus* isp. nov. is described from the Furongian (Upper Cambrian) strata of the Holy Cross Mountains. This ichnospecies is probably non-trilobite in origin and is commonly preserved as an undertrace. This preservation style resembles that of *Rusophycus ramellensis* Legg, an index fossil of the Cambrian Series 3. Therefore, previous workers misinterpreted material from the Wiśniówka Sandstone Formation as *Rusophycus ramellensis* Legg (recorded by them as *Cruziana barbata*) and put the Cambrian Series 3 and Furongian boundary within this unit. *Rusophycus inexpectus* isp. nov. differs from *Rusophycus ramellensis* Legg: 1) in having a smooth trapezoidal area behind the lobes; 2) in the presence of a direct contact between the endopodal lobes and cephalic margin imprints and 3) in the restriction of the occurrence of the endopodal lobes and scratches to the cephalic region of the trace fossil. Care must be taken, when dealing with the undertrace preservation style of *Rusophycus ramellensis* Legg in other assemblages, as it may represent *Rusophycus inexpectus* isp. nov.

Key words: *Rusophycus ramellensis*, *Rusophycus inexpectus*, Furongian, Cambrian, ichnostratigraphy, new ichnotaxa.

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INTRODUCTION

Wiśniówka Duża (or Wiśniówka Wielka in older literature) is a well known site with Cambrian trace fossils (Orłowski *et al.*, 1970, 1971; Orłowski, 1992; Orłowski and Żylińska, 1996; Sadlok, 2010, 2011; Sadlok and Machalski, 2010). Orłowski (1992) used the ichnostratigraphical scheme proposed by Seilacher (1970, 1994, 2007) for stratigraphical subdivision of the Wiśniówka Sandstone Formation as exposed at this quarry (see the critical opinion in Kowalczewski, 1995). The Furongian (Upper Cambrian) trace fossils (*Cruziana semiplicata* Salter and *Rusophycus polonicus* Orłowski, Radwański and Roniewicz) were well known from the Wiśniówka Sandstone Formation (Orłowski *et al.*, 1970, 1971; Seilacher, 1970; Radwański and Roniewicz, 1972). Subsequently, a trace fossil resembling *Rusophycus ramellensis* Legg was recorded from this unit under the name *Cruziana barbata* Seilacher, 1970 by Orłowski (1992). *Rusophycus ramellensis* Legg is a typical Cambrian Series 3 ichnospecies (Seilacher, 1970; MacNaughton, 2007; see Cambrian subdivision in Babcock and Peng, 2007). This material came from the lowermost part of the succession accessible in the Wiśniówka Duża Quarry and it was the basis for recognition of the Cambrian Series 3

– Furongian boundary within the Wiśniówka Sandstone Formation (Orłowski, 1992). Later, Żylińska *et al.* (2006) studied acritarchs and trilobites from the Wiśniówka Sandstone Formation and concluded that the strata with *R. ramellensis* (their *C. barbata*) (Fig. 1) belonged to the lower part of the Furongian. This most recent view is followed herein.

This paper provides new data on trace fossil from the Wiśniówka Sandstone Formation that previously was assigned to *Rusophycus ramellensis* Legg (Orłowski, 1992). New data show that the material from the Wiśniówka Sandstone Formation represents a new ichnospecies. The implications of this discovery for local stratigraphic study and palaeogeographical considerations are briefly discussed.

LOCATION AND GEOLOGICAL SETTINGS

The Wiśniówka Sandstone Formation belongs to the Furongian, as indicated by body fossils (Żylińska *et al.*, 2006). From a stratigraphic point of view, the unit is located between the Pepper Mountains Formation (Cambrian Series 3 to Furongian) and the Klonówka Shale Formation (Furongian, see Żylińska *et al.*, 2006). The strata of this formation

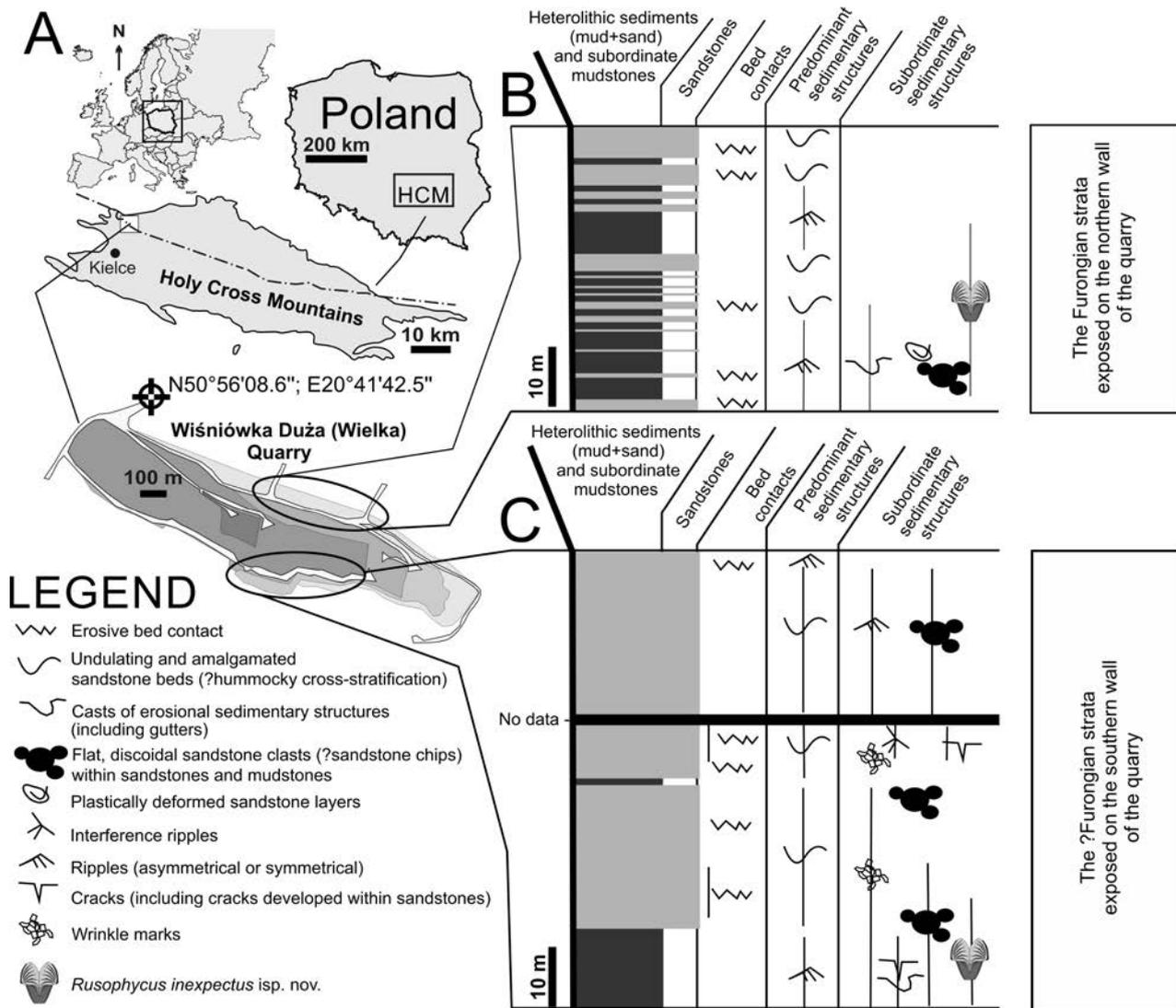


Fig. 1. Location of Wiśniówka Duża (“Wielka” in older literature) Quarry and general profiles of strata, exposed on northern and southern walls. **A.** Location of Wiśniówka Duża Quarry. **B.** The general profile of northern wall. **C.** General profile of southern wall. A question mark for the Furongian age in description of southern wall profile comes from the lack of direct body index fossils for this interval (see text).

are best exposed at the Wiśniówka Duża Quarry and a few smaller quarries in the westernmost part of the Holy Cross Mountains (Wiśniówka Mała and Podwiśniówka), as well as in the Opatów area (Kowalczewski *et al.*, 2006 and references therein; Fig. 1A). The estimated thickness of the Wiśniówka Sandstone Formation ranges from 80–200 m, up to 400–1400 m, depending on the tectonic model applied (Kowalczewski *et al.*, 2006 and references therein).

The Wiśniówka Sandstone Formation comprises mainly sandstones, heterolithic intervals and mudstones (Fig. 1B, C). Sandstones display pervasive silicification that obscures the original textural characteristics (Sikorska, 2000). These deposits appear to be well sorted and both texturally and mineralogically mature (close to quartz arenites *sensu* Nagtegaal, 1978; thin sections were studied, but no point-count modal analysis was done and actual percentage values are not available). The heterolithic beds display numerous and various current- and wave-ripple structures (Radwański and

Roniewicz, 1960; Fig. 1B, C) and flaser to lenticular bedding. The characteristic feature of the sandstone interbeds is their common amalgamation and undulation of bedding planes, with lateral changes in the thickness of beds (possibly due to ?hummocky cross stratification). The strata of the Wiśniówka Sandstone Formation have been interpreted as shallow marine by most authors (Dźułyński and Żak, 1960; Radwański and Roniewicz, 1960; Jaworowski and Sikorska, 2006).

MATERIAL AND METHODS

This study was based on: 1) collection of trace fossils, in order to test the presence of *Rusophycus ramellensis* Legg in the part of the section with Furongian body fossils (see Żylińska *et al.*, 2006), and 2) observations on trace fossil morphology; material from the Wiśniówka Sandstone

Formation was compared with the type material and with other similar ichnospecies of Seilacher (1970), on the basis of material from the Museum of Eberhard Karls University in Tübingen; Palaeontological Collection of Tübingen University, Sigwartstraße 10, 72076 Tübingen, Germany (abbreviation GPIT).

The material studied from the Wiśniówka Sandstone Formation is a part of a trace fossil collection stored at the Institute of Paleobiology of Polish Academy of Sciences (Warsaw, Poland; abbreviation ZPAL Tf. 4). The collection comprises material amassed by the Author (80%) and by Marcin Machalski (20%) from the Institute of Paleobiology of Polish Academy of Sciences, Warsaw.

Terms, such as “cephalon”, “endopod” and “exopod” (and respective adjectives), correspond to terms applied previously to various parts of the trace fossils discussed (see Seilacher, 1970). However, all of these terms are interpretative. The validity of their application to *Rusophycus inexpectus* isp. nov., which is thought to represent a non-trilobite trace fossil, is even more problematic, but for the sake of simplicity these terms are retained herein. The application of other terms would be also interpretative.

SYSTEMATIC DESCRIPTION

Ichnogenus *Rusophycus* Hall, 1852

Diagnosis: Short, bilobate, rarely multilobate traces. Lobes predominantly bilaterally symmetrical. Convex forms (hypichnia) with distinct median furrow; concave forms (epichnia) with median ridge. Outline ovate to coffee-bean-shaped; sculptured with oblique to transverse or longitudinal striae in various arrangements, or almost smooth (Schlirf and Uchman in Schlirf *et al.*, 2001).

Discussion: Seilacher (1970) proposed that all trace fossils of presumed trilobite origin should be treated under one ichnogenus *Cruziana*. However, Seilacher’s approach to ichnotaxonomy is not accepted by most workers (e.g., Keighley and Pickerill, 1996; Schlirf *et al.*, 2001 and references therein) and is not followed here. Most workers differentiate between an elongated, ribbon-like trace fossil (*Cruziana*) and a short, vertically burrowed trace fossil (*Rusophycus*; see discussion in Jensen, 1997). The differentiation is not always straightforward, but simple criteria, such as length-to-width ratio, can be used (Keighley and Pickerill, 1996).

Rusophycus inexpectus new ichnospecies

Figs 2, 3A–C, 3E, F

1992 *Cruziana barbata* Seilacher, 1970 – Orłowski: p. 24, fig. 7.

Material and holotype: holotype – ZPAL Tf. 4/1329; other material – ZPAL Tf. 4/1, 2, 8, 13, 104, 112, 122, 145, 150, 161, 166, 231, 237, 250, 265, 275, 292, 350–351, 366, 395, 368, 389, 445, 450, 478, 831, 895–896, 898, 907, 910, 912, 914, 917–918, 958, 963–964, 673, 975, 998–999, 1023, 1029, 1067, 1081, 1239, 1331, 1328, 1329, 1330, 1335, 1359, 1361.

Etymology: “*inexpectus*” form Latin means unexpected and refers to the unexpected morphology of the well preserved, full versions of the ichnospecies.

Diagnosis: *Rusophycus* with two heart-shaped lobes and with a smooth trapezoidal area behind those lobes. The lobes are connected with elongated imprints laterally and meet medially, forming a groove which becomes a deeper depression toward one end of the trace fossil. The depression forms a V-shaped gap in the

frontal part of the lobes. The extent of the lobes corresponds with the extent of elongated lateral imprints. The lobe-covering ridges (scratches) have divergent patterns and in deep undertraces a “moustache-like” pattern is apparent.

Description: *Rusophycus* occurring most commonly as a hypichnion with two large lobes, covered with ridges (scratches). This trace fossil appears to be strongly biased toward undertrace preservation and therefore its dimensions are controlled by taphonomy. Well preserved specimens have lengths of between ~30 and ~50 mm and widths of between ~20 and ~40 mm. There is a V-shaped gap occurring within the lobes. The lobes at one end of the trace fossil are at a higher angle to the centre-line in deeper specimens; the angle ranges from ~25° to ~50° (Fig. 2B, C). Unexpectedly, the well preserved version of *Rusophycus inexpectus* isp. nov. also has a smooth rear area, which is trapezoidal and occurs just behind the main lobes. This smooth area tapers backwards. Well preserved *Rusophycus inexpectus* isp. nov. also displays the presence of elongated lateral imprints, in contact with and bordering the lobes; the lobes and lobe-covering scratches extend across the entire width of the trace fossil (Figs 2C, 3A–C). In lateral view, the extent of the lobes corresponds with the extent of the elongated lateral imprints (Fig. 3B, C). The lobe-covering ridges (scratches) have a typical “moustache-like” pattern (Fig. 2B), in which the frontal ridges (scratches) change their direction from transverse to diagonal with respect to the long axis of the trace fossil (with a typical divergent angle of ~50°, Fig. 2A–C) and the rear ones form a narrow incision (acute angle), cutting into the smooth trapezoidal area behind the lobes (Figs 2, 3A, B, E, F). The trace fossil studied displays sets of lobe-covering ridges, composed of two ridges (scratches) each. The distance between the ridges within a set is typically 1–3 mm (Fig. 2D). The appearance of lobe-covering ridge sets (scratches) depends on preservation and locally they may appear to be composed of a single ridge (Fig. 2E). A ridge is typically ~1 mm wide (Fig. 3A–C). The ichnospecies is U-shaped in longitudinal cross-section with the frontal and rear parts fused with the overlaying bed. This ichnospecies displays significant variation in preservation style and the observed range has been illustrated in Figures 2 and 3.

Remarks: In earlier papers, specimens from Wiśniówka Wielka site assigned herein to *Rusophycus ramellensis* Legg, were referred to as *Cruziana barbata* Seilacher, 1970 by Orłowski (1992: p. 24, fig. 7.) The latter ichnospecies was created by Seilacher (1970) on the basis of material from the Cambrian Series 3 of Spain. Later, Legg (1985) relocated the short *Rusophycus*-like variants of this ichnospecies to *Rusophycus ramellensis* Legg. The characteristic feature of *Rusophycus ramellensis* Legg is its divergent pattern of endopodal scratches, which has been referred to as a “moustache-like” pattern by Seilacher (1970). However, in *Rusophycus ramellensis* Legg the cephalic imprints do not contact directly the endopodal lobes and in this ichnospecies, the extent of the endopodal lobes is not restricted to the cephalic area in the lateral view, and the smooth trapezoidal tapering backwards area is missing (Seilacher, 1970; Legg, 1985; Fig. 3D). The divergent pattern of endopodal scratches occurs also in *Rusophycus dispar* Linnaeus. However, in *Rusophycus dispar* the endopodal scratches are not restricted to cephalic area.

STRATIGRAPHICAL DISTRIBUTION

Rusophycus inexpectus isp. nov. was recovered from the lower part of the profile of the Wiśniówka Duża (Wielka) Quarry (southern wall, Figs 1C, 2A, B, 3E, F). Orłowski (1992) found in this interval an undertrace version of the trace fossil, assigned by him to *Cruziana barbata*

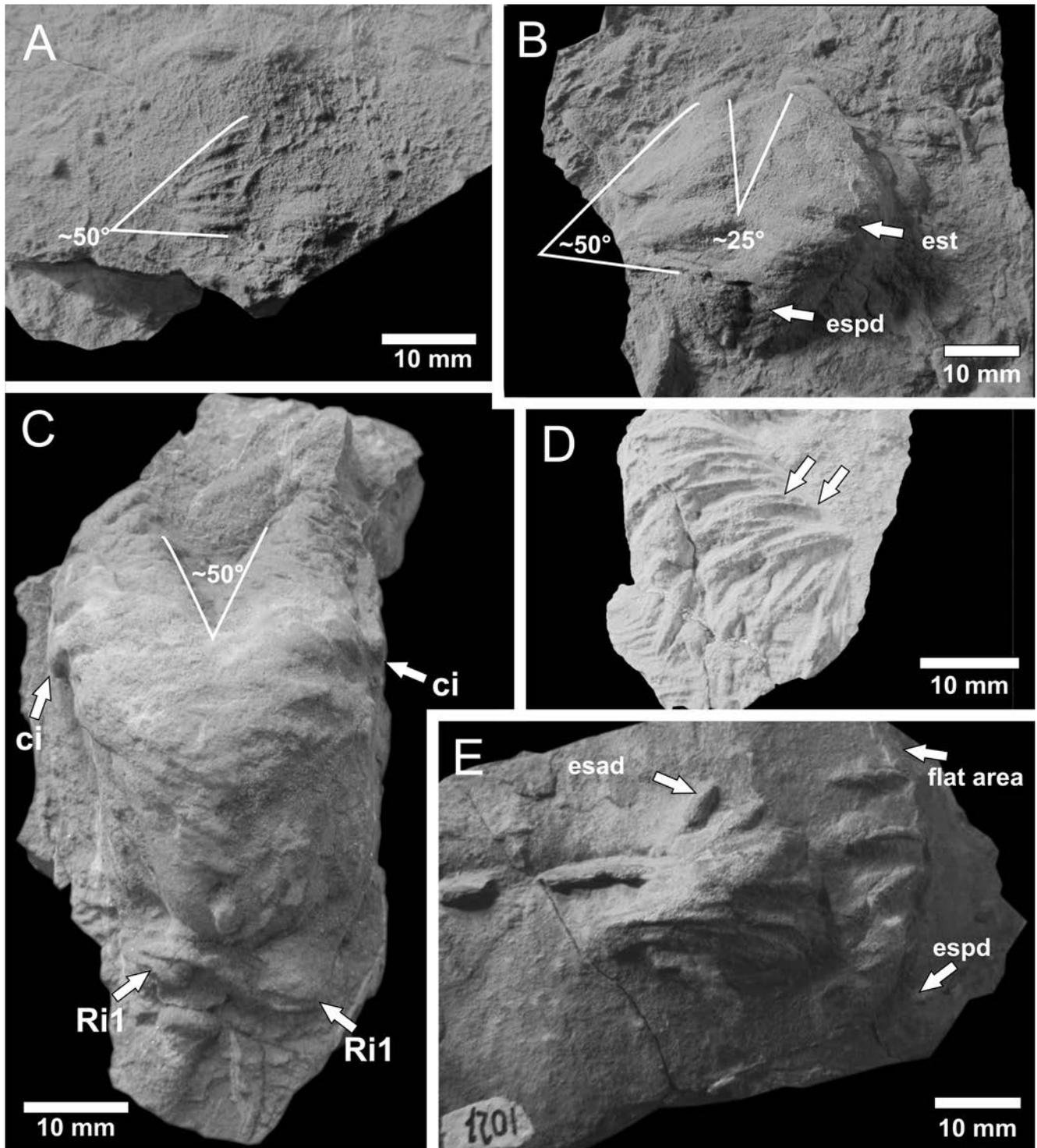


Fig. 2. *Rusophycus inexpectus* isp. nov. from the Wiśniówka Sandstone Formation. Symbols used on figures: esad – endopodal scratches anteriorly directed, espd – endopodal scratches posteriorly directed, esapd – endopodal scratches anteriorly to posteriorly directed, esatd – endopodal scratches anteriorly directed to transverse, est endopodal scratches transverse, ci – cephalon imprint, Ri1 – first *Rusophycus inexpectus*, ?c/?p – ?cephalic/?pleural imprints, el – endopodal lobe, sa – smooth area, exa – exopodal area, pi – pleurae imprints, cmi1, 2, 3 – cephalic margin imprint number 1, 2, 3. **A.** Shallow expression of the trace fossil (ZPAL Tf. 4/1335). **B.** Deeper expression of the trace fossil (typical “moustache-like” pattern of scratches; ZPAL Tf. 4/912). **C.** Full version of the trace fossil (ZPAL Tf. 4/1329), note the shallow version of the trace fossil, located close to the posterior margin of this specimen (Ri1). **D, E.** Two shallow expressions of the trace fossil (D: ZPAL Tf. 4/1331; E: ZPAL Tf. 4/1023).

Seilacher. However, in this study, a fully preserved *Rusophycus inexpectus* isp. nov. also was recovered, in addition to the commonest undertrace variant of *Rusophycus inexpectus* isp. nov., which is comparable to a typical undertrace of *Rusophycus ramellensis* Legg. Figures 2C and 3A–C show this full style of preservation (see also Fig. 3G). *Rusophycus inexpectus* isp. nov. was recovered also from the uppermost part of the profile (northern wall, Figs 1B, 2C, D, 3A–C). This may confirm previous undocumented information on the presence in the uppermost Furongian part of the profile (*Cruziana barbata* Seilacher in Żylińska *et al.*, 2006 and references therein) of a trace fossil resembling *Rusophycus ramellensis* Legg.

COMPARISON WITH *RUSOPHYCUS RAMELLENSIS* LEGG

Rusophycus ramellensis, considered as the index trace fossil for the Cambrian Series 3, is known from locations, representing the ancient shelves of Gondwana (Seilacher, 1970, 2007). The most common mode of occurrence is as a deep undertrace, where only the endopodal scratches with their characteristic “moustache”-like pattern are preserved (Seilacher, 1970). This type of occurrence, due to preservation biases, is also most typical of *Rusophycus inexpectus* isp. nov. (Figs 2A, B, D, E, 3G). The more complete morphologies of *Rusophycus ramellensis* (Seilacher, 1985; Seilacher, 2007; Figure 3D) display wide, exopodal, brushed zones at the sides of the trace fossil (Fig. 3D), in contrast to material of *Rusophycus inexpectus* isp. nov. from the Wiśniówka Sandstone Formation. The difference between these trace fossils indicates that their trace makers probably differed in:

1) the presence/absence or the size of exopodites; there is no evidence for their presence in trace fossils from the Wiśniówka Sandstone Formation. The exopodal traces are usually recognized on the basis of a regular, parallel pattern of scratches (Bergström, 1972, 1976; see Fig. 4C). No such parallel scratches are observed in the material from the Wiśniówka Sandstone Formation. This might be a taphonomy-related feature, but the fact that the material studied appeared to be generally well preserved may imply that there was an actual exopod size difference that could be related to taxonomic differences between the trace makers;

2) the degree of trace maker tagmosis, reflecting the degree of body differentiation into morphologically and functionally unique units, as recorded in *Rusophycus ramellensis* Legg, is low as the change in appendage size (exopods vs. endopods) was only in their proportions, as was proposed by Seilacher (1985). The material from the Wiśniówka Sandstone Formation shows that *Rusophycus inexpectus* isp. nov. has endopodal scratches, which are restricted to the zone adjacent to the cephalic imprints (see the lateral view in Fig. 3B, C). This may indicate that the “cephalic” part was the “tagma” with the endopods. The smooth posterior of *Rusophycus inexpectus* isp. nov. (Fig. 3) implies an absence of appendages, or a different structure of them. Trilobites do not show such tagmosis (Harrington, 1959; Bergström, 1972; Whittington, 1980; Hughes, 2003a, b). The

contrast with trilobite-made trace fossils is visible, when it is compared with *Rusophycus arizonensis* Seilacher, 1970 (Cambrian Series 3; *Cruziana arizonensis* in Seilacher, 1970), which bears distinct imprints of the cephalic margin (Fig. 4). In contrast with the Furongian material from the Holy Cross Mountains, *Rusophycus arizonensis* has endopodal scratches that extend beyond the rear margin of the cephalic imprint (Fig. 4B, D). This is a tagmosis pattern expected from a trilobite trace maker, as a dorsally expressed subdivision does not correspond with appendage differentiation (cf. Hughes, 2003a, b). Therefore, *Rusophycus inexpectus* isp. nov. appears to be a good candidate for being a non-trilobite trace fossil, the trace maker of which could display some behavioural convergence to *Rusophycus ramellensis* trace maker, as the patterns of appendage movement appear to be similar in both trace fossils.

DISCUSSION

Rusophycus inexpectus isp. nov. from the Wiśniówka Sandstone Formation differs from the Cambrian Series 3 *Rusophycus ramellensis* Legg and represents a new ichnospecies (Fig. 5). The limited biostratigraphic data, collected from the upper part of the profile, indicates that the trace fossil described in the present account come from the Furongian series (Żylińska *et al.*, 2006). Therefore, currently there is no evidence that the lower part of the profile exposed at Wiśniówka represents the Cambrian Series 3 series (see Orłowski, 1992; Kowalczewski, 1995).

Rusophycus ramellensis Legg is still considered to be a Cambrian Series 3 index fossil, but the presence of behavioural convergence with *Rusophycus inexpectus* must be kept in mind, when dealing with undertrace material. The similarity between these two ichnospecies is a result of an undertrace deficiency in morphological details (cf. Seilacher, 1970, 2007).

Taking into consideration the endemism of the Furongian Wiśniówka Sandstone Formation trilobite fauna (Żylińska, 2002), it may well appear that similar endemism is characteristic of the arthropods, responsible for *Rusophycus* in the region, and that the potential for applying the *Cruziana* ichnostratigraphy, an ichnostratigraphical scheme applied to Gondwana, is locally limited.

Trace fossils from the Wiśniówka Duża Quarry (mainly the presence of *Cruziana semiplicata* and *Cruziana barbata*), were used as a one of the supportive arguments for linking the Łysogóry Block, the structural unit forming the northern part of the Holy Cross Mountains (see Bełka *et al.*, 2000; Jaworowski and Sikorska, 2006), with Gondwana (Seilacher, 2007). However, *Cruziana semiplicata* has been reported from other non-Gondwanan areas (see the most recent overview in Jensen *et al.*, 2011). Therefore, the significance of this trace for palaeogeographic reconstructions is limited. The difference between the Holy Cross Mountains material and the typical Cambrian Series 3 *Rusophycus ramellensis* Legg, as noted in the present paper, appears to preclude the possibility of applying the material from the Wiśniówka Duża Quarry in palaeogeographical reconstruction.

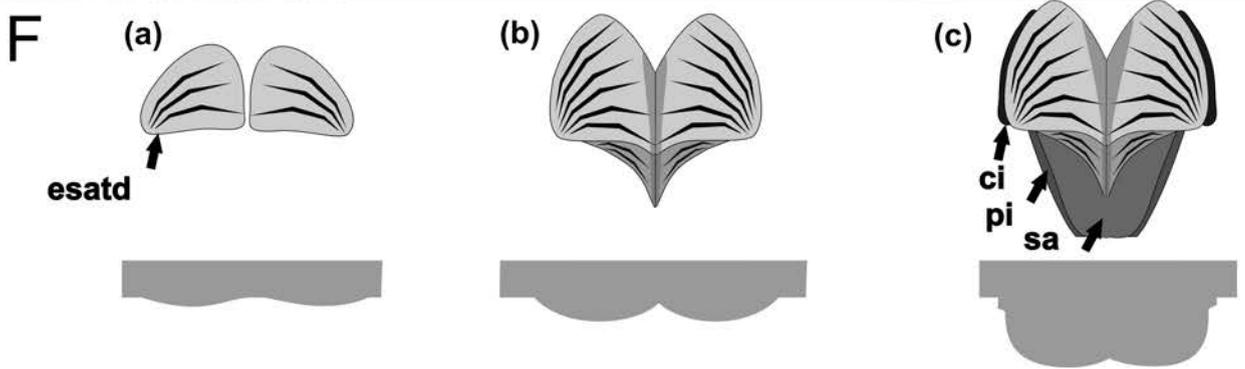
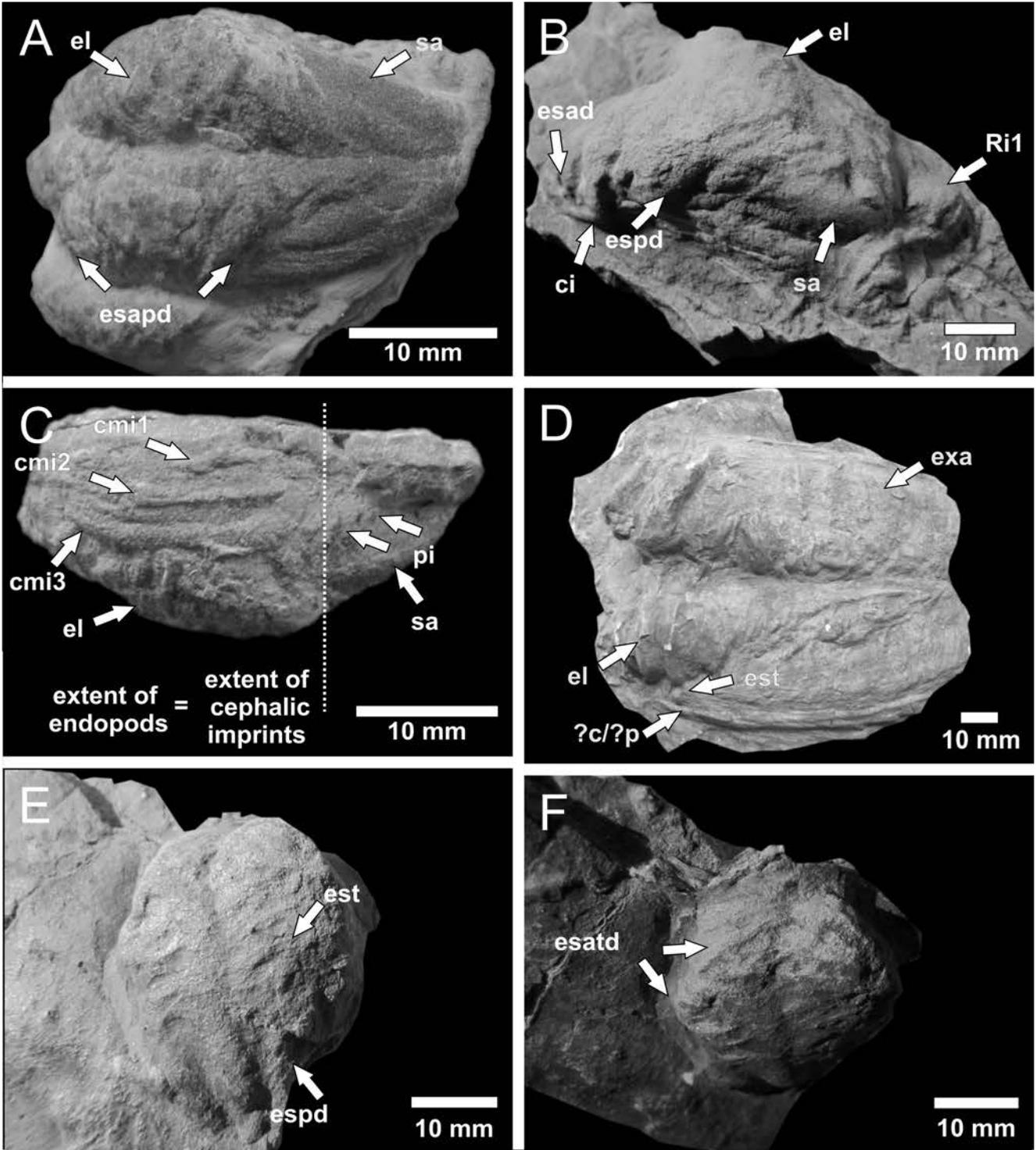


Fig. 3. More complete morphological version of *Rusophycus inexpectus* isp. nov. from the Wiśniówka Sandstone Formation and comparison with typical Middle Cambrian *Rusophycus ramellensis* Legg (*Cruziana barbata* Seilacher) **A.** Well preserved specimen of the new ichnospecies (ZPAL Tf. 4/1328). **B.** Well preserved version of the new ichnospecies, the same specimen as in Fig. 2C, here a view from different angle shows additional details (ZPAL Tf. 4/1329). **C.** The same specimen as in A, here in a side view. Note an apparent tagmosis: endopodal lobes have extent comparable to cephalon margin. **D.** Full version of typical Middle Cambrian *Rusophycus ramellensis* Legg (*Cruziana barbata* Seilacher; see Seilacher, 1985, 2007; GPIT/IC/00147). **E, F.** Full version of *Rusophycus inexpectus* isp. nov. (ZPAL Tf. 4/674). **G.** Schematic illustration showing correspondence between depth of preservation and undertrace deficiency: (a) the shallowest version, (b) deeper version and (c) the full, well preserved version. Symbols used: see caption of Figure 2.

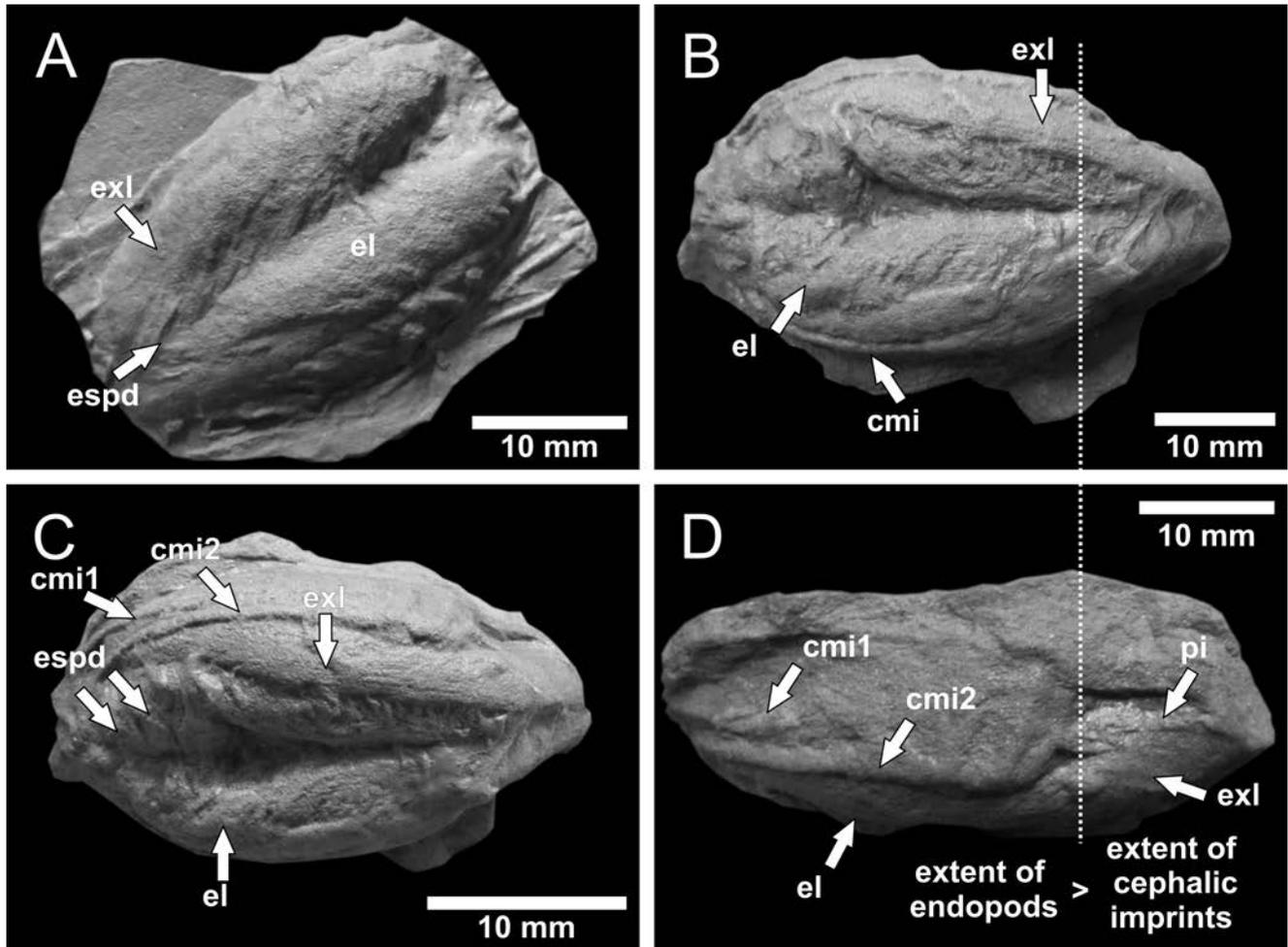


Fig. 4. *Rusophycus arizonensis* (Seilacher) (*Cruziana arizonensis* Seilacher, 1970) displaying trilobite-like pattern of tagmosis. **A.** Trace fossils with all endopodal scratches directed posteriorly; GPIT/IC/00149. **B–D.** Well preserved trace fossils with cephalic imprints (various views of the same specimen; GPIT/IC/00150). Note that endopodal scratches extend beyond rear margin of cephalic imprint (B and D: shown by dashed line). Symbols used: see caption of Figure 2.

CONCLUSIONS

1) The presence of *Rusophycus ramellensis* Legg in the Wiśniówka Sandstone Formation (reported as *Cruziana barbata* Seilacher by earlier authors) has not been confirmed. The material represents a new ichnospecies *Rusophycus inexpectus* isp. nov.

2) *Rusophycus inexpectus* isp. nov. differs from the Cambrian Series 3 *Rusophycus ramellensis* Legg: a) in having a smooth trapezoidal area behind the lobes; b) in the presence

of a direct contact between the endopodal lobes and the cephalic margin imprints; and c) in the restriction in the occurrence of endopodal lobes and scratches to the cephalic region of the trace fossil. These morphological differences between the trace fossils are rooted in different body plans of the trace makers, as evidenced by well preserved specimens.

3) *Rusophycus inexpectus* isp. nov. appears to represent a trace fossil probably produced by a non-trilobite trace maker, as indicated by the non-trilobite-like appendage tagmosis pattern.

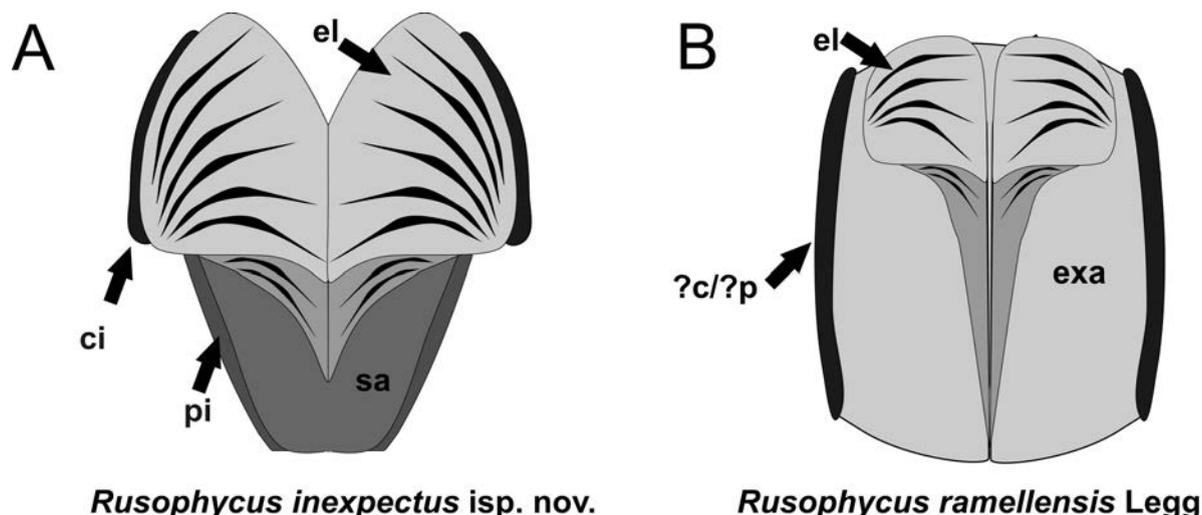


Fig. 5. Comparison of *Rusophycus inexpectus* isp. nov. and *Rusophycus ramellensis* Legg: schematic drawing. Drawing in B is based on specimen, illustrated in Fig. 3D. Symbols used: see caption of Figure 2.

4) On the basis of available biostratigraphical data, the *Rusophycus inexpectus* isp. nov. appears to come from the Furongian strata (see Żylińska *et al.*, 2006 and references therein). There is no evidence at present that the lower part of the profile accessible at the Wiśniówka Duża (Wielka) Quarry represents the Cambrian Series 3.

5) In general, the applicability of *Rusophycus ramellensis* Legg to ichnostratigraphical subdivision and palaeogeographic reconstruction is in need of careful reappraisal, since the presence of morphologically convergent non-trilobite trace fossils representing *Rusophycus inexpectus* isp. nov. also cannot be excluded in other assemblages.

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REFERENCES

- Babcock, L. E. & Peng, S. C., 2007. Cambrian chronostratigraphy: Current state and future plans. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 254: 62–66.
- Bełka, Z., Ahrendt, H., Franke, W. & Wemmer, K., 2000. The Baltica–Gondwana suture in central Europe: evidence from K–Ar ages of detrital muscovites and biogeographical data. *Geological Society Special Publication*, 179: 87–102.
- Bergström, J., 1972. Appendage morphology of the trilobite *Crypotolithus* and its implications. *Lethaia*, 5: 85–94.
- Bergström, J., 1976. Lower Palaeozoic trace fossils from eastern Newfoundland. *Canadian Journal of Earth Sciences*, 13: 1613–1633.
- Dźułyński, S. & Żak, C., 1960. Sedimentary environment of the Cambrian quartzites in the Holy Cross Mountains, Central Poland, and their relationship to the flysch facies. *Rocznik Polskiego Towarzystwa Geologicznego*, 30: 213–241.
- Harrington, H. J., 1959. General description of Trilobita. In: Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology, Part O: Arthropods*. Geological Society of America and University of Kansas Press, Lawrence, Meriden, pp. 38–117.
- Hughes, N. C., 2003a. Trilobite body patterning and the evolution of arthropod tagmosis. *BioEssays*, 25: 386–395.
- Hughes, N. C., 2003b. Trilobite tagmosis and body patterning from morphological and developmental perspectives. *Integrative and Comparative Biology*, 43: 185–206.
- Jaworowski, K. & Sikorska, M., 2006. Łysogóry Unit (Central Poland) versus East European Craton – application of sedimentological data from Cambrian siliciclastic association. *Geological Quarterly*, 50: 77–88.
- Jensen, S., 1997. Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden. *Fossils and Strata*, 42: 1–111.
- Jensen, S., Bogolepova, O. K. & Gubanov, A. P., 2011. *Cruziana semiplicata* from the Furongian (Late Cambrian) of Severnaya Zemlya Archipelago, Arctic Russia, with a review of the spatial and temporal distribution of this ichnospecies. *Geological Journal*, 46: 26–33.
- Keighley, D. G., & Pickerill, R. K., 1996. Small *Cruziana*, *Rusophycus*, and related ichnotaxa from eastern Canada: The nomenclatural debate and systematic ichnology. *Ichnos*, 4: 261–285.
- Kowalczewski, Z., 1995. Fundamental stratigraphic problem of the Cambrian in the Holy Cross Mts. *Geological Quarterly*, 39: 449–470.
- Kowalczewski, Z., Żylińska, A. & Szczepanik, Z., 2006. Kambr w

- Górach Świętokrzyskich. In: Skompski, S. & Żylińska, A. (eds), *Procesy i zdarzenia w historii geologicznej Gór Świętokrzyskich, LXXVII Zjazd Naukowy Polskiego Towarzystwa Geologicznego, Ameliówka k. Kielc, 28–30 czerwca 2006 r., Materiały Konferencyjne*. Polskie Towarzystwo Geologiczne, Państwowy Instytut Geologiczny, Wydział Geologii Uniwersytetu Warszawskiego, Warszawa, pp. 14–27. [In Polish.]
- Legg, I. C., 1985. Trace fossils from a Middle Cambrian deltaic sequence, north Spain. In: Curran, A. H. (ed.), *Biogenic Structures: Their Use in Interpreting Depositional Environments*. Society of Economic Paleontologists and Mineralogists Special Papers, 35: 151–165.
- MacNaughton, R. B., 2007. The application of trace fossils to biostratigraphy. In: Miller, W., III, (ed.), *Trace Fossils: Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 135–148.
- Magwood, J. P. A. & Pemberton, S. G., 1990. Stratigraphic significance of *Cruziana*: New data concerning the Cambrian–Ordovician ichnostratigraphic paradigm. *Geology*, 18: 729–732.
- Nagtegaal, P. J. C., 1978. Sandstone-framework instability as a function of burial diagenesis. *Journal of the Geological Society*, 135: 101–105.
- Orłowski, S., 1992. Trilobite trace fossils and their stratigraphical significance in the Cambrian sequence of the Holy Cross Mountains, Poland. *Geological Journal*, 27: 15–34.
- Orłowski, S., Radwański, A. & Roniewicz, P., 1970. The trilobite ichnocoenoses in the Cambrian sequence of the Holy Cross Mountains. In: Crimes, T. P. & Harper, J. C. (eds), *Trace Fossils*. *Geological Journal, Special Issue*, 3: 345–360.
- Orłowski, S., Radwański, A. & Roniewicz, P., 1971. Ichnospecific variability of the Upper Cambrian *Rusophycus* from the Holy Cross Mts. *Acta Geologica Polonica*, 21: 341–348.
- Orłowski, S. & Żylińska, A., 1996. Non-arthropod burrows from the Middle and Late Cambrian of the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica*, 41: 385–409.
- Radwański, A. & Roniewicz, P., 1960. Ripple marks and other sedimentary structures of the Upper Cambrian at Wielka Wiśniówka (Holy Cross Mts.). *Acta Geologica Polonica*, 10: 371–400.
- Radwański, A. & Roniewicz, P., 1972. A long trilobite trackway, *Cruziana semplicata* Salter, from the Upper Cambrian of the Holy Cross Mts. *Acta Geologica Polonica*, 22: 439–447.
- Sadlok, G., 2010. Trace fossil *Cruziana tenella* from the Furongian (Upper Cambrian) deposits of Poland. *Acta Geologica Polonica*, 60: 349–355.
- Sadlok, G., 2011. Arthropod tracks from the Furongian (Upper Cambrian) of the Wiśniówka Wielka (Holy Cross Mountains) and their taphonomy: a preliminary report. *Przegląd Geologiczny*, 59: 82–90. [In Polish, with English abstract].
- Sadlok, G. & Machalski, M., 2010. The trace fossil *Rusophycus* from the Furongian (Upper Cambrian) of central Poland – an example of behavioural convergence amongst arthropods. *Acta Geologica Polonica*, 60: 119–123.
- Schlirf, M., Uchman, A. & Kümmel, M., 2001. Upper Triassic (Keuper) non-marine trace fossils from the Haßberge area (Franconia, south-eastern Germany). *Paläontologische Zeitschrift*, 75: 71–96.
- Seilacher, A., 1970. *Cruziana* stratigraphy of “non-fossiliferous” Palaeozoic sandstones. In: Crimes, T. P. & Harper, J. C. (eds), *Trace Fossils*. *Geological Journal, Special Issue*, 3: 447–475.
- Seilacher, A., 1985. Trilobite palaeobiology and substrate relationships. *Transactions of the Royal Society of Edinburgh. Earth Sciences*, 76: 231–237.
- Seilacher, A., 1994. How valid is *Cruziana* stratigraphy? *Geologische Rundschau*, 83: 752–758.
- Seilacher, A., 2007. *Trace Fossil Analysis*. Springer, Berlin. 226 pp.
- Sikorska, M., 2000. Silification history of Cambrian sandstones in the Wiśniówka area, Holy Cross Mts (Central Poland). *Przegląd Geologiczny*, 48: 251–258. [In Polish, with English abstract].
- Whittington, H. B., 1980. Exoskeleton, moult stage, appendage morphology, and habits of the Middle Cambrian trilobite *Olenoides serratus*. *Palaeontology*, 23: 171–204.
- Żylińska, A., 2002. Stratigraphic and biogeographic significance of Late Cambrian trilobites from Łysogóry (Holy Cross Mountains, central Poland). *Acta Geologica Polonica*, 52: 217–238.
- Żylińska, A., Szczepanik, Z. & Salwa, S., 2006. Cambrian of the Holy Cross Mountains, Poland; biostratigraphy of the Wiśniówka Hill succession. *Acta Geologica Polonica*, 56: 443–461.