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The trace fossil *Rusophycus versans* from the Furongian (Upper Cambrian) of central Poland – an example of behavioural convergence amongst arthropods

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ABSTRACT:

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Traces assigned to *Rusophycus versans* are recorded for the first time from Furongian (Upper Cambrian) strata, as exposed at Wiśniówka Wielka quarry, Holy Cross Mountains, central Poland. These traces are ascribed to the life activity of trilobites in a fully marine environment. In contrast, previous records of *R. versans* have been attributed to notostracans, isopods or arthropleurids and are preserved in non-marine settings. The relatively wide phylogenetic distribution of *R. versans* within various arthropod groups indicates that this ichnotaxon represents behavioural convergence amongst arthropods.

Key words: Trace fossils; *Rusophycus*; Arthropods; Behavioural convergence; Cambrian; Furongian; Poland.

INTRODUCTION

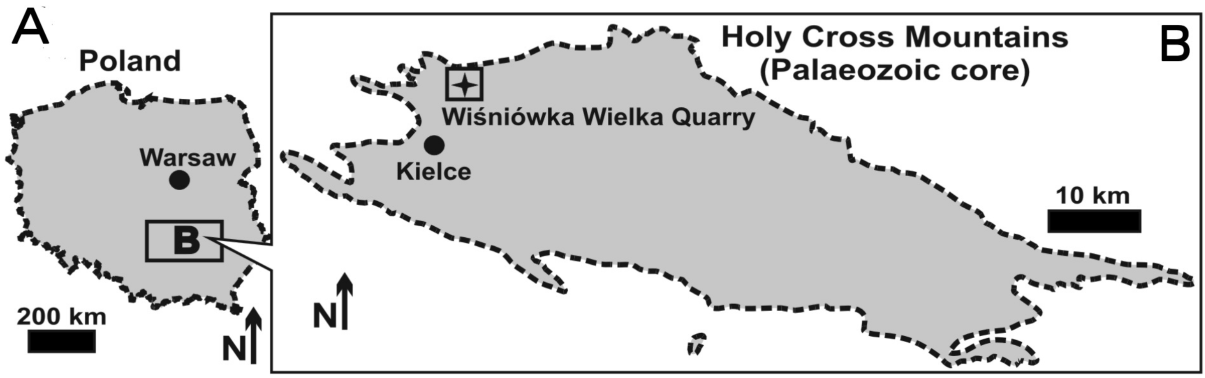
The large quarry at Wiśniówka Wielka hill, Holy Cross Mountains, central Poland, is an important locality for the study of Furongian (Upper Cambrian) trace fossils (Żylińska and Radwański 2008 and references therein; Text-fig. 1, herein). There are several records of arthropod, priapulid and anemone trace fossils from that locality by Dżułyński and Żak (1960), Radwański and Roniewicz (1960, 1963, 1967, 1972), Orłowski *et al.* (1970, 1971) and Orłowski and Żylińska (1996).

The aim of the present note is to record the presence of the trace fossil *Rusophycus versans* Schlirf and Uchman in Schlirf *et al.* (2001) in Furongian deposits at Wiśniówka Wielka quarry, and to discuss its significance in terms of arthropod paleoecology. The presence of *R. versans* at Wiśniówka was earlier announced by the authors during the Ichnia 2008 conference at Cracow (Machalski and Sadlok 2008).

STRATIGRAPHY AND PALAEOENVIRONMENT

The material studied comes from the Wiśniówka Formation, which is of Furongian (Late Cambrian) age as indicated by trilobites and acritarchs (Żylińska 2002; Żylińska *et al.* 2006). Strata of the Wiśniówka Formation are sandwiched between the Middle Cambrian–Furongian Pepper Mountains Formation and the Furongian Klonówka Shale Formation (Żylińska 2002; Żylińska *et al.* 2006).

The Wiśniówka Formation consists of quartzitic sandstones, siltstones and claystones (Żylińska 2002;



Text-fig. 1. Location of the study area, Wiśniówka Wielka quarry. A – Position of the Holy Cross Mountains within Poland; B – Position of the Wiśniówka Wielka quarry within the Holy Cross Mountains (based on Żylińska *et al.* 2006 – modified)

Żylińska *et al.* 2006). These sediments were deposited in a fully marine environment, ranging from inner to outer shelf (Jaworowski and Sikorska 2006; Żylińska *et al.* 2006).

All specimens studied were collected from a set of thin sandstone and mudstone intercalations rich in well-preserved trilobite trace fossils, including *Cruziana semiplicata, Cruziana* isp., *Rusophycus polonicus, Rusophycus* isp. and *Diplichnites* isp., as exposed at the northern wall of the quarry, immediately below and above the main quarry road (see fig. 2a in Żylińska *et al.* 2006). Some horizontal burrows (cf. *Planolites* isp. and cf. *Palaeophycus* isp.) and sea-anemone burrows (*Bergaueria*) are also present.

Aside from the trace fossils, the sole surfaces of the sandstone beds contain numerous inorganic marks, including prod, bounce and chevron marks. In contrast, current ripple-marks are preserved on top surfaces. The thin sandy layers are provisionally interpreted as distal tempestites preserved in an outer shelf environment. No body fossils were found in the discussed unit. The scarcity of body fossils is a typical feature of the whole Furongian sequence exposed at Wiśniówka Wielka quarry (cf. Orłowski *et al.* 1970; Żylińska *et al.* 2006).

MATERIAL AND METHODS

The described material forms part of the Cambrian trace fossil collection housed by the Institute of Paleobiology, Polish Academy of Sciences in Warsaw, Poland (abbreviated: ZPAL Tf. 4/). The specimens were photographed in low-angle light from the upper left corner.

ICHNOTAXONOMY

Ichnogenus *Rusophycus* Hall, 1852

Rusophycus versans Schlirf and Uchman in Schlirf *et al.* (2001)
(Pl. 1)

DIAGNOSIS: The original diagnosis of the ichnospecies is as follows: "Clusters of short, poorly sculptured, bilobate, coffee-bean-shaped, hypichnial mounds, displaying additional, more or less fan-like or irregularly arranged side lobes" (Schlirf *et al.* 2001). This, however, consists mostly of descriptive and non-differential characteristics. The diagnosis given by Pollard *et al.* (2008) is, "Curved, clustered, or laterally repeated hypichnial lobes, commonly displaying transverse striations or ridges." This diagnosis differs from the original in terms of surface morphology of individual bilobate structures (sculptured *versus* smooth).

In practical terms, only the presence of additional fan-like and irregular lobes allows discrimination between *R. versans* and all other known *Rusophycus* ichnospecies, which consist of one bilobate element (see remarks in Schlirf *et al*. 2001, p. 80).

MATERIAL: Seven slabs with *R. versans*: ZPAL Tf. 4/286–287, 289–291, 563, 570.

DESCRIPTION: Traces are preserved as positive hypichnia on the thin-bedded quartzitic layers and comprise recurrent clusters of short bilobate structures, some of them displaying additional, fan-like (Pl. 1, Figs 1–2, 4) or irregular lateral lobes (Pl. 1, Figs 1, 3). One specimen (Pl. 1, Fig. 4) exhibits additional morphological features in marginal areas of bilobate structures indicated by arrows in Pl. 1, Figs 5–6.

REMARKS ON BEHAVIOUR: Fan-like or irregular lateral lobes in *Rusophycus versans* reflect rotational movements of the tracemaker during sediment processing (Schlirf *et al.* 2001). As in the type material of the ichnospecies, two behavioural variants of *R. versans* may be distinguished in the material studied. The first variant is documented by fan-like, lateral multiplications of the short bilobate structures (Pl. 1, Figs 2, 4). In these cases the tracemaker first burrowed vertically, abandoned the excavation and repeated this behaviour several times next to the previous structure. The second variant is recorded by a specimen (Pl. 1, Fig. 3) with a short bilobate structure passing into an additional side-lobe. These two strategies can also be combined in a single trace as is exemplified by the specimen figured in Pl. 1, Fig. 1.

ICHNOTAXONOMY AND BEHAVIOURAL CONVERGENCE

In the past, lack of agreement on the choice of ichnotaxobases led to the creation of ichnotaxa based on diverse and in some cases inappropriate criteria, such as producer, age and environment (Bertling *et al.* 2006). The complicated ichnotaxonomic history of bilobed and diplichnitiform arthropod trace fossils illustrates this problem (Bromley and Asgaard 1972, 1979; Machalski and Machalska 1994; Keighley and Pickerill 1996). The current consensus is that trace fossils are named according to their morphology (Pickerill and Keighley 1997; Bertling *et al.* 2006), which reflects the producer's behaviour and affinity as well as the substrate type (Bertling *et al.* 2006; Minter *et al.* 2007).

Some bilobate components of the trace fossils studied are morphologically close to *Rusophycus moyensis* and *R. polonicus* of the *carleyi* group (Seilacher 1970). This is especially true for a structure in the centre of the specimen in Pl. 1, Fig. 1, which is virtually indistinguishable from some specimens of *R. moyensis* from the Cambrian-Tremadocian of Argentina (Mángano *et al*. 2002), and for the bilobates in Pl. 1; Figs 4–6, which reveal features typical of *R. polonicus* (compare Orłowski *et al.* 1971). Accordingly, the present material could be referred to as "clusters of *R. moyensis* and *R. polonicus*", as suggested by Gabriela Mángano (written communication, 2009). However, the material under consideration is regarded here as representing a morphologically distinctive, complex trace fossil (*sensu* Miller 2003), reflecting the specialized behaviour of its producers and deserving its own ichnological name, which is *R. versans*. The ichnotaxonomic attitude of Schlirf *et al.* (2001) is followed here as several bilobate components of clusters assigned by these authors to *R. versans* are virtually indistinguishable from co-occurring solitary individuals referred to as *R. carbonarius* (compare figs 7, 8 *vs* 9, 10 in Schlirf *et al*. 2001).

Rusophycus versans is an example of style D of behaviour complexity *sensu* Miller (2003). In this example of behaviour complexity, invariant behaviour, resulting in formation of individual bilobate structures (*Rusophycus*) is expressed in a repeatable way, resulting in the origin of a trace fossil with a hierarchical structure (*R. versans*). Traces belonging to *Rusophycus versans* represent more complex behaviour than other ichnospecies of *Rusophycus.*

In view of the ubiquity of trilobite trace fossils at Wiśniówka (see Żylińska and Radwański 2008 for review), specimens of *R. versans* from that locality as recorded herein may safely be ascribed to the life activity of these arthropods. This is supported by morphological similarity of individual bilobate structures to well known trilobite-made trace fossils (compare Seilacher 1970) as recorded by traces of pleurae and genal spines visible in specimen illustrated as Fig. 4 in Pl. 1 (see Pl. 1, Figs 5, 6 for details). In contrast, the type material of *R. versans* comes from non-marine Upper Triassic (Keuper) deposits in Germany and was attributed to notostracan crustaceans (Schlirf *et al.* 2001). Specimens of *R. versans* from the Permian of France were also ascribed to the life activity of notostracans (Gand *et al.* 2008). The ichnotaxon was also reported from the Carboniferous (lower Westphalian) coal-bearing strata of Lancashire, UK (Pollard *et al.* 2008). In the last case, the trace fossil was thought to have been produced by *Camptophyllia,* an arthropod of uncertain affinity (isopod crustacean or arthropleurid; Pollard *et al.* 2008 and references therein).

Behaviour, understood as everything an organism does, evolves (Jeanne 1998) and can undergo divergent or convergent evolution. Since trace fossils are fossilised effects of behaviour (Bromley 1990; Magwood 1992), they supply unique insight into the evolutionary history of behaviour (Ekdale and Lamond 2003). The relatively wide phylogenetic distribution of *R. versans* within various arthropod groups (trilobites, notostracans, isopods or arthropleurids) indicates that these structures exemplify behavioural convergence caught in the trace fossil record. The purpose of behaviour reflected in the morphology of *R. versans* is poorly understood but is generally thought to have increased the efficiency of sediment processing during deposit-feeding (Schlirf *et al.* 2001). The increase of efficiency in feeding would have had a considerable adaptive value (compare Jeanne 1998), justifying a wide phylogenetic distribution of such behaviour.

SUMMARY

The present paper records, for the first time, trace fossil assigned to the ichnospecies *Rusophycus versans* from Furongian (Upper Cambrian) strata as exposed at Wiśniówka Wielka quarry, Holy Cross Mountains, central Poland. The specimens studied are thought to have been produced by trilobites in a fully marine environment. In contrast, previous records of *R. versans* were attributed to the life activity of non-marine arthropods (notostracans, isopods or arthropleurids). These facts indicate that *R. versans* represents behavioural convergence amongst various groups of arthropods.

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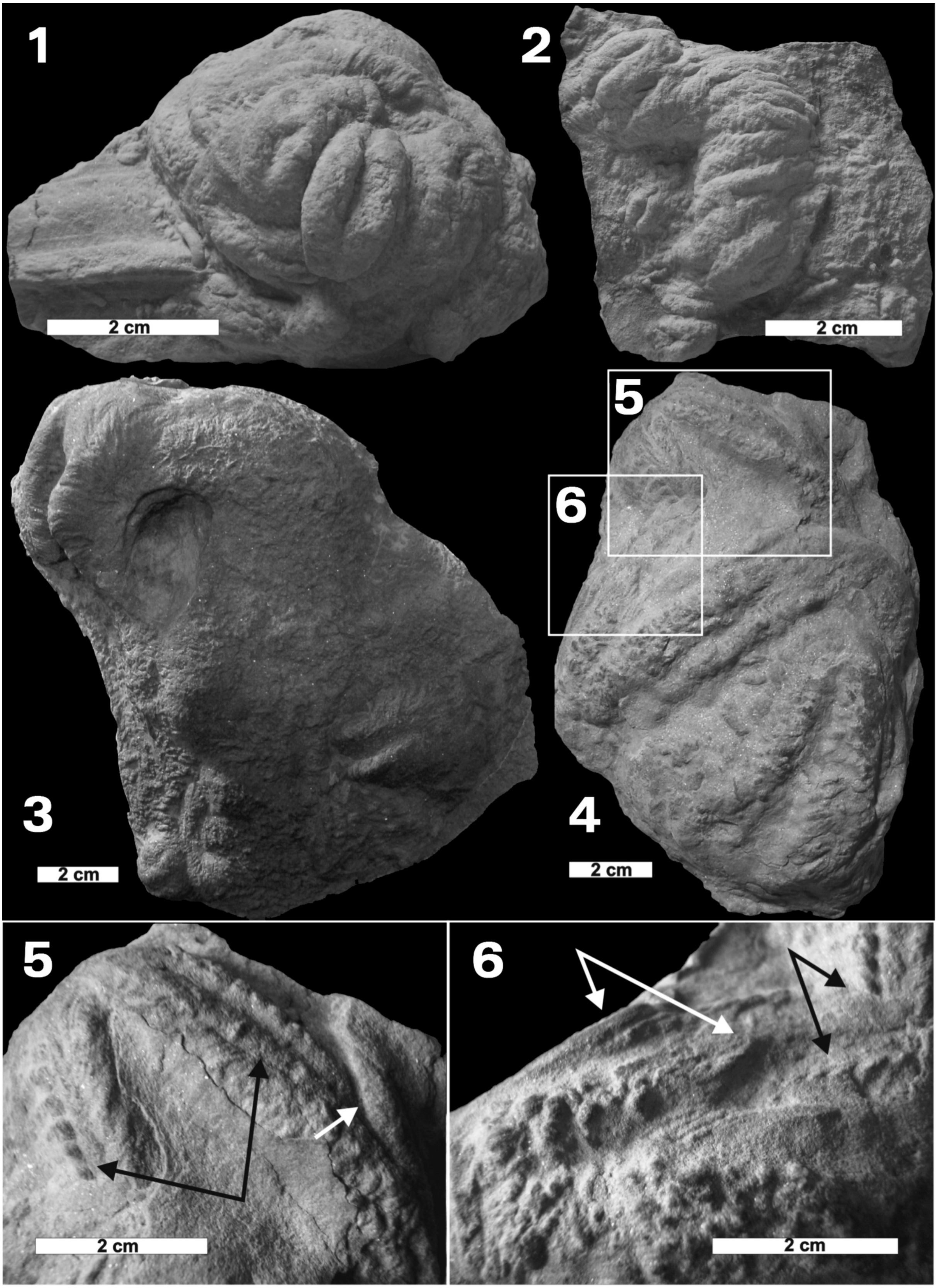
PLATE 1

Rusophycus versans Schlirf and Uchman in Schlirf *et al.* (2001) from Furongian (Upper Cambrian) strata at Wiśniówka Wielka quarry, Holy Cross Mountains, central Poland

1 – specimen ZPAL Tf. 4/287; **2** – specimen ZPAL Tf. 4/286; **3** – specimen ZPAL Tf. 4/563; **4** – specimen ZPAL Tf. 4/570; **5** and **6** – magnified areas of specimen ZPAL Tf. 4/570, arrows indicate traces of pleurae (black) and genal spines (white)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