

NEW DATA ON THE TRACE FOSSIL, *CRUZIANA SEMIPLICATA* (FURONGIAN, WIŚNÍÓWKA SANDSTONE FORMATION, POLAND): ORIGIN, ETHOLOGY AND PRODUCER

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Abstract: *Cruziana semiplicata* Salter is a well known ichnospecies, ascribed to trilobites. Despite that, there are still contradicting views on its origin (infaunal vs. epifaunal), the ethology represented (crawling vs. feeding) and the identity of its producer (a few trilobite genera were proposed). In this paper, new data are presented and combined to create a coherent interpretative model for *Cruziana semiplicata*. According to this new model, *Cruziana semiplicata* is a fossilized version of an epifaunal, pascichnial (feeding) trace produced by an organism, positioned above the seabed with only a few frontal appendages touching the depositional surface and processing the sediment below. This model is based on observations of trace fossil morphology and neoichnological observations of the feeding behaviour of *Triops australiensis*. Also, a short geometrical comparison with the co-occurring *Rusophycus polonicus* is made to show that these trace fossils most likely had different trace makers.

Key words: *Cruziana semiplicata*, *Triops*, fossilized behaviour, neoichnology, Furongian, Poland.

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INTRODUCTION

Cruziana semiplicata Salter is a trace fossil occurring in the siliciclastic strata of the Cambrian (Furongian) and Lower Ordovician (see the most recent overview in Jensen *et al.*, 2011). This trace fossil is commonly interpreted as a fossilized trace of trilobites (Crimes, 1970a; Seilacher, 1970, 2007; Radwański and Roniewicz, 1972; Fortey and Seilacher, 1997; Fortey and Owens, 1999; Żylińska, 1999) and has been used as a Furongian index trace fossil in ichnostratigraphical schemes (Crimes, 1970b; Seilacher, 1970, 1994, 2007; MacNaughton, 2007).

Cruziana semiplicata is known from several locations around the world, including Poland, Russia, Argentina and Wales (Jensen *et al.*, 2011 and references therein). It is encountered most commonly in areas mainly representing the former shelves of Furongian Gondwana (Seilacher, 2007), but its palaeogeographic range also could have included the "Lower" Cambrian strata of recent North America, as indicated by some limited material illustrated by Magwood and Pemberton (1990). Despite the long history of study and relatively wide geographical distribution, there still are contradictory views on the origin (infaunal vs. epifaunal) of the trace fossil, its behaviour (crawling vs. feeding) and on its producer. These issues are addressed in this paper

The Wiśniówka Sandstone Formation is well known

from the Wiśniówka Duża (Wielka) Quarry, an important ichnological site, and material from the unit was studied by various workers (Żylińska and Radwański, 2008 and references therein) However, no systematic study of *Cruziana semiplicata* from this site has been undertaken and the primary aim of this paper is to fill this gap.

LOCATION AND GEOLOGICAL SETTINGS

The Wiśniówka Sandstone Formation (see Orłowski, 1975, 1992b) is a Furongian unit, sandwiched between the Pepper Mountains Formation (Cambrian Series 3 to Furongian) and the Furongian Klonówka Shale Formation (Orłowski, 1975; Żylińska *et al.*, 2006, see new Cambrian subdivision in Babcock and Peng, 2007). The Wiśniówka Sandstone Formation is exposed in the Wiśniówka Duża Quarry (in older literature known as the Wiśniówka Wielka Quarry), located in the western part of the Holy Cross Mountains (Fig. 1).

MATERIAL AND METHODS

The methodological basis for this study was the observation of trace fossil morphology. The material studied

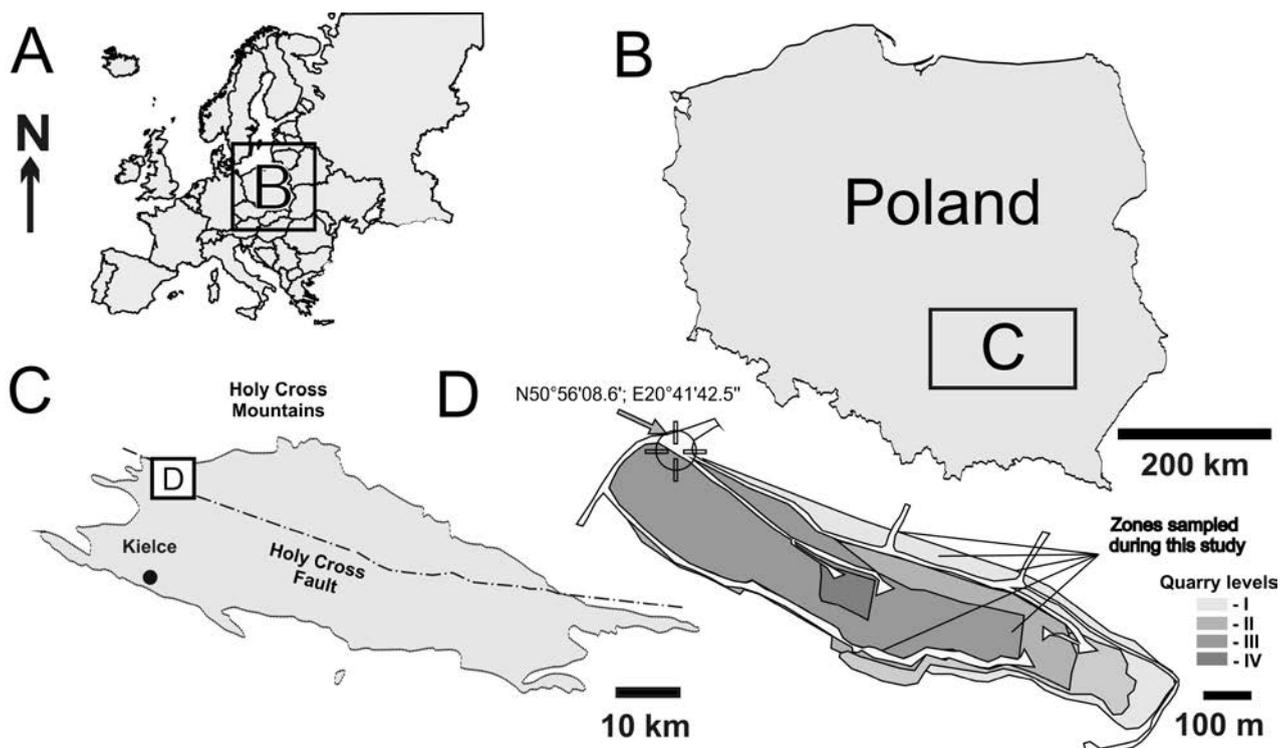


Fig. 1. Location of study area. **A.** Poland in relation to Europe. **B.** Holy Cross Mountains in Poland. **C.** Wiśniówka Duża Quarry in Holy Cross Mountains. **D.** The approximate plan of Wiśniówka Duża Quarry (compilation from various sources).

belongs mainly to *Cruziana semiplicata*. Some specimens of the co-occurring trace fossil *Rusophycus polonicus* Orłowski, Radwański and Roniewicz were also studied, as a comparison was needed for considerations of the differences and similarities between the trace makers of these trace fossils.

The material studied comes from the Furongian Wiśniówka Sandstone Formation (Orłowski, 1992a, b). This material is a part of the trace fossil collection (ZPAL Tf. 4), stored at the Institute of Paleobiology of the Polish Academy of Sciences (Warsaw, Poland). 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.

The following fifty-four specimens of *Cruziana semiplicata* were analyzed: ZPAL Tf. 4/7, 18, 48, 80, 82, 105, 111, 113, 117, 123–125, 127–129, 132, 133, 137, 138, 160, 167, 182, 189, 191, 225, 228, 284, 295, 300, 314, 346, 402, 413, 414, 416, 419, 422, 427, 430, 432, 436, 440–442, 447, 448, 459, 466, 585, 596, 734, 1314, 1460, 1462. Forty-two specimens of *Rusophycus polonicus* also were studied: ZPAL Tf. 4/87, 108, 139, 159, 240, 259, 260, 263, 271, 272, 453, 487, 499, 504, 565, 567, 578, 669, 701, 714, 731, 781, 892, 936, 972, 990–991, 994, 1025, 1026, 1229, 1261, 1315–1317, 1324–1327, 1333, 1342.

The Furongian material from the Wiśniówka Sandstone Fm was compared with specimens of *Cruziana semiplicata* from northern Spain (Furongian, “Molinos Schicht”), North Wales (Furongian, Ffestiniog Beds, *Lingula* Flags, Cwm Graianog) and Oman (Furongian, Andam Fm). All this material is stored at the Museum of Eberhard Karls Universität in Tübingen (Palaeontological Collection of Tübingen University, Sigwartstraße 10, 72076 Tübingen, Germany).

Standard sedimentological and morphological observations of fossil material were supplemented with neoichnological observations of traces, left by living crustaceans (*Triops australiensis* Spencer and Hall). Since the work of Bromley and Asgaard (1979), it has been a widely accepted view that the trace fossils assignable to ancestors of Recent notostracans are morphologically analogous to those produced by Lower Palaeozoic marine arthropods, including trilobites (e.g., Bromley and Asgaard, 1972; Pollard, 1985; Gradziński and Uchman, 1994; Jensen, 1997; Sadlok, 2010).

The crustaceans were kept and observed in a tank, 20 × 20 × 40 cm. The tank contained a layer of sand, ~5 cm thick and fresh water. An attempt at simulating the clay-covered-by-sand conditions was made, but the results were inconclusive – the sand grains tended to sink below the upper surface of clay and the traces produced were very poorly preserved with only gross morphological features visible, because of the lack of a well defined splitting surface. Therefore, in this paper only the reproducible results of observations on surficial structures are used.

Previous ichnological observations of living notostracans (under laboratory conditions) yielded no traces comparable to *Cruziana* (Trusheim, 1931; Gand *et al.*, 2008; Knecht *et al.*, 2009). Bromley and Asgaard (1972) observed the activity of *Lepidurus* Leach (furrowing of bottom muds) in the natural habitat of these notostracans (ephemeral ponds in Greenland). They made no observations on any trace morphologically analogous to *Cruziana*, but they speculated that the infaunal expression of the surface furrows observed (not similar to *Cruziana*) could be similar to *Cruziana* (not observed). Therefore, the *Cruziana*-like traces, observed in the present study, are the first obtained under laboratory condi-

tions. The behaviour of crustaceans, observed in this study, is used in this work as an interpretative basis for consideration of the fossilized Furongian material.

PREVIOUS WORK

Crimes (1970a, fig. 6) studied the morphology of *Cruziana semiplicata* and other co-occurring trace fossils, i.e. *Diplichnites* Dawson or *Petalichnus* Miller (see Rindsberg, 1994) and *Rusophycus* Hall. He concluded that *Cruziana semiplicata* was a fossilized trace of trilobite locomotion at speeds intermediate between resting ($V = 0$ m/s) and fast locomotion, as recorded for *Diplichnites* or *Petalichnus*, and that the co-occurring trace fossils were produced by the same or closely interrelated trilobites. For Crimes (1970a, 1975), these trace fossils were fossilized epifaunal traces. This view was followed by workers, studying material from the Wiśniówka Sandstone Formation (Radwański and Roniewicz, 1972; Żylińska and Radwański, 2008).

On the other hand, Seilacher (1970, 1985, 2007, 2008) considered all trace fossils, most likely to have been produced by trilobites (including *Cruziana semiplicata*), to be fossilized infaunal traces. Seilacher (1970, 2007) linked the ethology of *Cruziana semiplicata* to feeding. This view was also followed by some other workers (e.g., Fortey and Owens, 1999).

Historically, the challenge of differentiation between the epifaunal and infaunal origins of trace fossils assignable to arthropods was undertaken in detailed sedimentological studies of the internal structures of trace fossils (lamination), as revealed by the cross-sections and longitudinal sections of the trace fossils. This methodology allows an understanding of the internal structure (e.g. massive vs. laminated). Baldwin (1977) and Goldring (1985) studied the internal structures of arthropod trace fossils and came to different conclusions. Baldwin (1977) supported an epifaunal origin on the basis of the presence of primary sedimentary structures within the specimens studied and the current-aligned orientation of some of them. Goldring (1985) favoured an infaunal origin and postulated that the presence of primary sedimentary structures is the result of the burrows being washed out and recast. In the present study, emphasis was placed on how the laminae are developed and how the trace fossil morphology is transmitted from one lamina to another.

RESULTS

Behaviour and traces of *Triops australiensis*

The observations of the behaviour of *Triops australiensis* performed in this study show that this species routinely produces epifaunal bilobed traces in fine sand. The observed morphologies resembled *Diplopodichnus* Brady and *Cruziana* d'Orbigny (Fig. 2) with the largest, *Cruziana*-like traces showing the perpendicular scratch pattern known from the trace fossil *Cruziana* (Fig. 2E). The morphological differences between *Diplopodichnus* and *Cruziana*, as discussed by Keighley and Pickerill (1996), are due to the pro-

portion of the width of the trace fossil that is occupied by a central ridge or groove (depending on preservation). *Cruziana* has lobes that are wider than the ridge between them and *Diplopodichnus* is dominated by a ridge separating two grooves (Keighley and Pickerill, 1996). Some of traces appear to comprise a wide central ridge and two narrow grooves (Fig. 2B, C, G). However, the width of the central ridge is exaggerated, owing to the free movement of loose sand from the elevation into the flanking depressions, after *Triops* Schrank had passed by (grooves, Fig. 3F).

When these traces are formed, *Triops* is positioned above the substrate, touching the bottom with only its frontal appendages (Fig. 3A–E). These appendages manipulate the substrate sorting through it in search of food, whereas the more distal appendages are used for propulsion, as in a normal swimming mode. In this case, the organism's locomotion (progressive movement) is not directly related to the action of the frontal appendages, as used during feeding. Finally, *Triops* was also observed to dig downward, with its head shield dipping into the substrate, but this behaviour was not seen as often as that related to feeding; the resulting traces were oval and not similar to *Cruziana*.

Internal lamination and infaunal vs. epifaunal origin

The main limitation on drawing firm conclusions from the presence or absence of lamination within *Cruziana semiplicata* is that lamination may indicate: 1) the original epifaunal character of the trace or, alternatively, 2) partial erosion of the trace and subsequent filling of it. In the second case, conclusions about the infaunal or epifaunal origin of the trace are not possible. However, new data were obtained from observations on naturally fractured specimens of *Cruziana semiplicata* from the Wiśniówka Sandstone Formation.

Two main types of lamina development can be illustrated with reference to the material studied (Fig. 6). These types differ in the presence or absence of distortion in the primary lamina that covers the original trace. The first type of lamina development is where the lamina, covering the trace transmits imperfectly the trace morphology on the top of the lamina (Fig. 6A, C). In this case, the lower side of the lamina bears the full set of morphological features of *Cruziana semiplicata* (a typical hypichnion, Fig. 6C), i.e. an external set of scratches, an internal set of scratches (a V-shaped pattern) and lateral ridges (cephalon- or pleura-made). The top of the same lamina bears only the detail-depleted morphology of *Cruziana semiplicata*, which includes a wide groove that is the counterpart of the external and internal scratches of the hypichnion below and well defined lateral grooves (counterparts of the ridges in the hypichnion below) bordering the wide groove. This detail-depleted morphology is mediated on the lower side of the succeeding, higher lamina ("imperfect hypichnion"; Fig. 6A, C). Finally, the second type of lamina development is where the top of the primary lamina that covers the trace is not disturbed at all and is flat (no "imperfect hypichnion" on the sole of the higher lamina; Fig. 6B, D).

These two types of lamina development may reflect differences in the timing of deposition of the primary lamina.

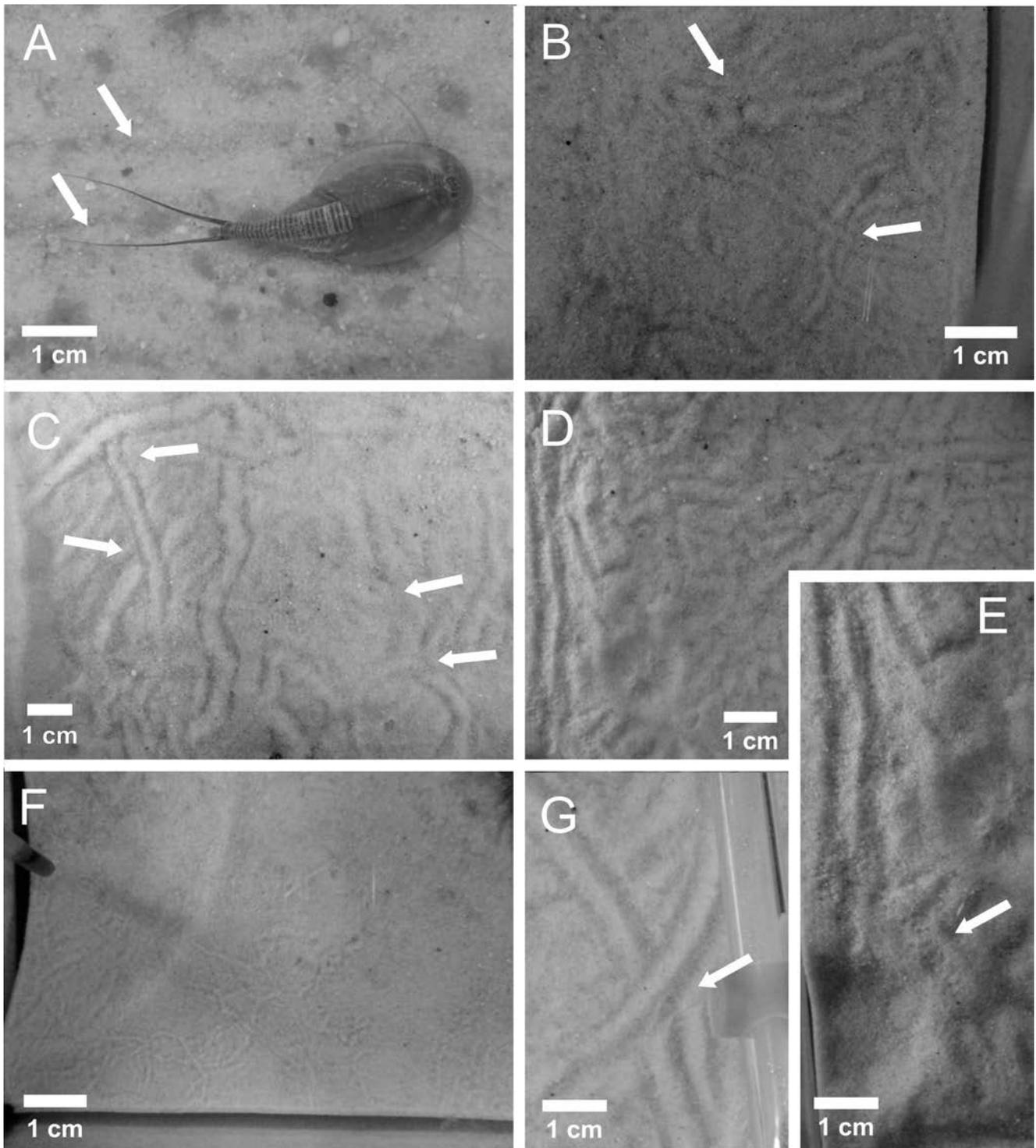


Fig. 2. *Triops australiensis* and traces it produces. **A.** *Triops* in dorsal view during production of traces (paired grooves arrowed). **B.** Paired furrows formed by *Triops*. The width of the internal ridge is exaggerated, owing to gravitational movement of loose sand grains (grains move down from ridge into the grooves) and the trace resembles *Diplopodichnus*. The cross-cutting of paths is arrowed. **C.** Paired furrows formed by *Triops*. The width of the internal ridge is exaggerated, owing to gravitational movement of loose sand grains (grains move down from the ridge into the grooves) and the trace resembles *Diplopodichnus*. Cross-cutting of paths is arrowed. **D.** Paired furrows resembling *Cruziana* formed by *Triops*. The transverse scratches are visible in the trace (see arrowed part in E). **E.** Magnified part of trace, figured in D. Here, transverse scratches are observed (arrowed). **F.** Numerous small traces, displaying cross-cutting relationships. **G.** Two cross-cutting paths.

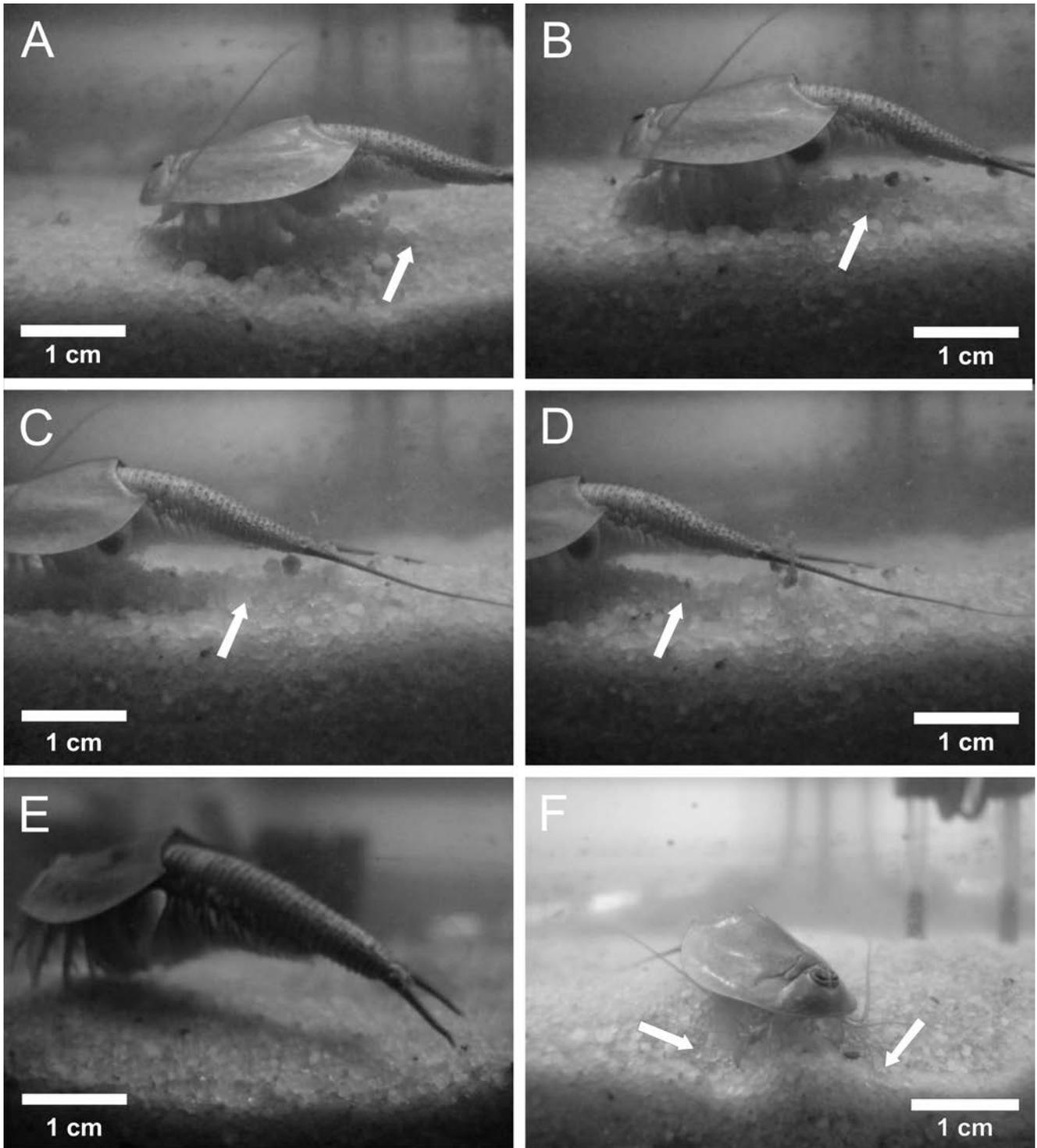


Fig. 3. *Triops* during production of *Cruziana*-like traces. **A–D.** A single sequence of movement showing that *Triops* is positioned above the substrate during trace production (central ridge arrowed). **E.** Other view of *Triops* positioned above the substrate. **F.** Frontal view of *Triops* producing *Cruziana*-like traces: the central ridge and lateral grooves are observed (grooves arrowed).

In the first case, the primary lamina covering the trace could have been present before the organism's activity occurred. This is because the detail-depleted morphology of *Cruziana simplicata*, as expressed at the top of the primary lamina, appears to represent the "collapse" structure, resulting from the movement of loose grains into the void or depression created in the mud below, i.e., into the trace. The compac-

tion-related preservation (cf. Sadlok, 2013) probably may be excluded in this case, because of the decrease in detail preservation on the higher lamina and the lithological similarity of laminae involved (i.e., there is no mud intercalation between the sand laminae observed). The deposition of the higher lamina had to take place after the activity of the trace maker. This view is based on the preservation of the inter-

face between the primary and higher lamina, including transmission of the trace fossil morphology with depletion of morphological detail. If the higher lamina had been present at the time of the activity of the trace maker, the interface between the primary and higher laminae would have been homogenized and therefore would not have been preserved. The first type of lamina development indicates that most likely no successive erosion and reburial occurred and shows by this that *Cruziana semiplicata* from the Wiśniówka Sandstone Formation represents a fossilized epifaunal trace made in mud, covered with millimetre-scale sand lamina.

The second type of lamina development, with the flat top, probably reflects deposition after the end of the activity of the organism. This is because no disturbance is observed (i.e., an unmodified substrate). However, this second type of lamina development is inconclusive, with regard to differentiation between deposition over an epifaunal or infaunal trace (e.g. after initial reburial).

Morphology of *Cruziana semiplicata*

Cruziana semiplicata is a long groove or ridge, depending on preservation (Figs 4, 5). It exhibits two types of scratches: internal, thought to have been produced by endopods, and external, thought to have resulted from exopod action. These scratches form parallel zones that are externally outlined by cephalon traces (Seilacher, 1970; Jensen *et al.*, 2011).

Internal scratches and locomotory model

Internal scratches (endopodal) form a V-pattern (Figs 4A–C, 5A, C). It is widely accepted that the “V” gaps toward the travel direction (head-end) (Crimes, 1970a; Seilacher, 1970; Birkenmajer and Bruton, 1971). The individual scratches produced by appendages occur in sets. Crimes (1970a) pointed out that the number of grooves in the original trace would depend on the morphology of the *pretarsus* (the actual number of claws) and on the contact angle between the appendage and the substrate – a lower angle means that less claws scratch the substrate (Fig. 6F). In the sample studied, the sets appear to be composed by mostly of two ridges or grooves, depending on the preservation. The scratches in sets are not identical and in plan view the frontal one is always wider than the one positioned farther back (Fig. 4C, D). In cross-section, the sets also are clearly asymmetrical, with the steeper slope facing forward (Fig. 5B). This asymmetry indicates that the appendage-substrate contact angle was low and the claws of the appendage were directed forward. Therefore, the widest scratch of the set is also the largest, i.e. the deepest one (Fig. 6E).

The morphological features described are in contradiction with a locomotory interpretation. This is because the cross-sectional view of the scratches indicates that the appendages were directed forward and it might be expected that the appendages propelling the organism would be directed backward. This negative evidence is in agreement with the results of a study of *Olenoides serratus* (Rominger) – one of the trilobites with the best studied appendages – from the Cambrian Series 3, indicating that those arthropods

could not have produced a V-pattern of scratches during a propulsive backstroke (Whittington, 1980).

A noteworthy outcome of this study is the observation that at least two types of morphologically different internal scratches can be observed in *Cruziana semiplicata* from the Wiśniówka Sandstone Formation. Scratches with the morphology described above are typical. However, in two well preserved specimens, finer scratches, comprising sets of two equal traces, were observed in distal part of *Cruziana semiplicata* (Fig. 4B). This may indicate some degree of heteropody, with regard to the number of claws on the pretarsus of the trace maker; this would be atypical for trilobites. Trilobites in general displayed weak differentiation of appendages along their body length (Harrington, 1959; Bergström, 1969, 1972; Whittington, 1980; Ramsköld and Edgecombe, 1996), with only minor differences noted in some cases, e.g. variation in stance (see Stein *et al.*, 2013). However, this feature so far was observed in only two specimens.

Vector-based interpretation of V-pattern and relationship to organism's speed

So far, Crimes (1970a) proposed the only model, explaining the origin of the V-pattern and factors, influencing the value of the acute angle of the “V”. According to Crimes (1970a), the transition from *Rusophycus* to *Cruziana* is associated with a decrease in the value of the acute angle of the “V” and the value of the acute angle of the “V” is thought to be inversely proportional to the speed of the organism: the higher the speed of locomotion, the smaller the angle. In his model, trilobites during speeding dragged their appendages toward the plane of symmetry and in this way their exopodites passively came into contact with the substrate and left scratches there (see Crimes, 1970a). Crimes (1970a) noted that specimens with a lower acute angle in the “V” also had wider zones, covered with exopodal scratches.

However, neoichnological observations indicate that in notostracans the progression of the organism and movement of the frontal appendages used during feeding are not tightly interconnected, when the organism is positioned above the substrate with the frontal appendages sorting through it for food. These observations may be used as a basis for the interpretations of *Cruziana semiplicata*, on the assumption that its producer had a similar mode of life and the organism was positioned above the substrate, in order to feed.

At the most basic level, the shape of the scratch, the V-pattern and the value of the acute angle in the “V” are records of movements of the distal part of the appendages of the trace maker. Assuming independence of the progressive movement of the whole organism and the movement of the appendage, the actual course for each given terminal part of an appendage will be the result of the superposition of the forward movement of the entire organism and the backward (backward and medial) movement of the appendage (Fig. 7A). Both of these movement vectors would be directed oppositely and would have different signs (+ and -). The resultant vector would have an intermediate value: the speed and shape of the course of the terminal part of the appendage would be resultants of the speed and course of the organism and of the appendage.

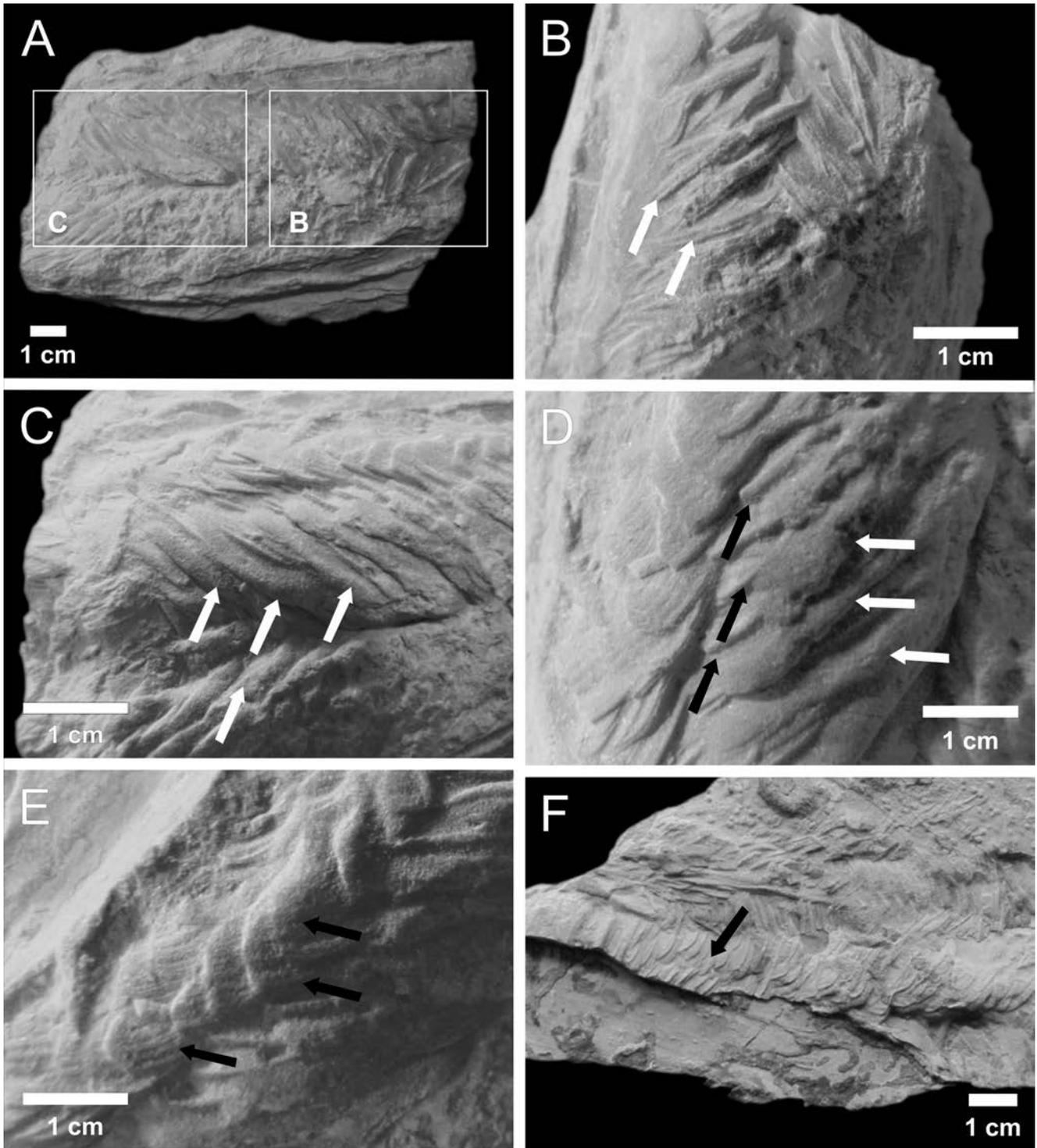


Fig. 4. *Cruziana simplicata* from Furongian Wiśniówka Sandstone Formation. All figures: ZPAL Tf. 4/1460. **A.** General view of trace fossil. **B.** Magnification of distal part of trace fossil with visible paired, similar scratches (arrowed). **C.** Magnification of the frontal part of trace fossil with typical paired scratches. Arrowed are larger frontal scratches in sets. **D.** Magnification of endopodal scratches (arrowed), showing larger frontal scratches (white arrows) and smaller distal scratches (black arrows). **E.** Magnification of side of trace fossil with very well preserved exopodal scratches (arrowed). **F.** Deep *Cruziana simplicata* with detail-depleted morphology preserved; only endopodal scratches are observed (arrowed).

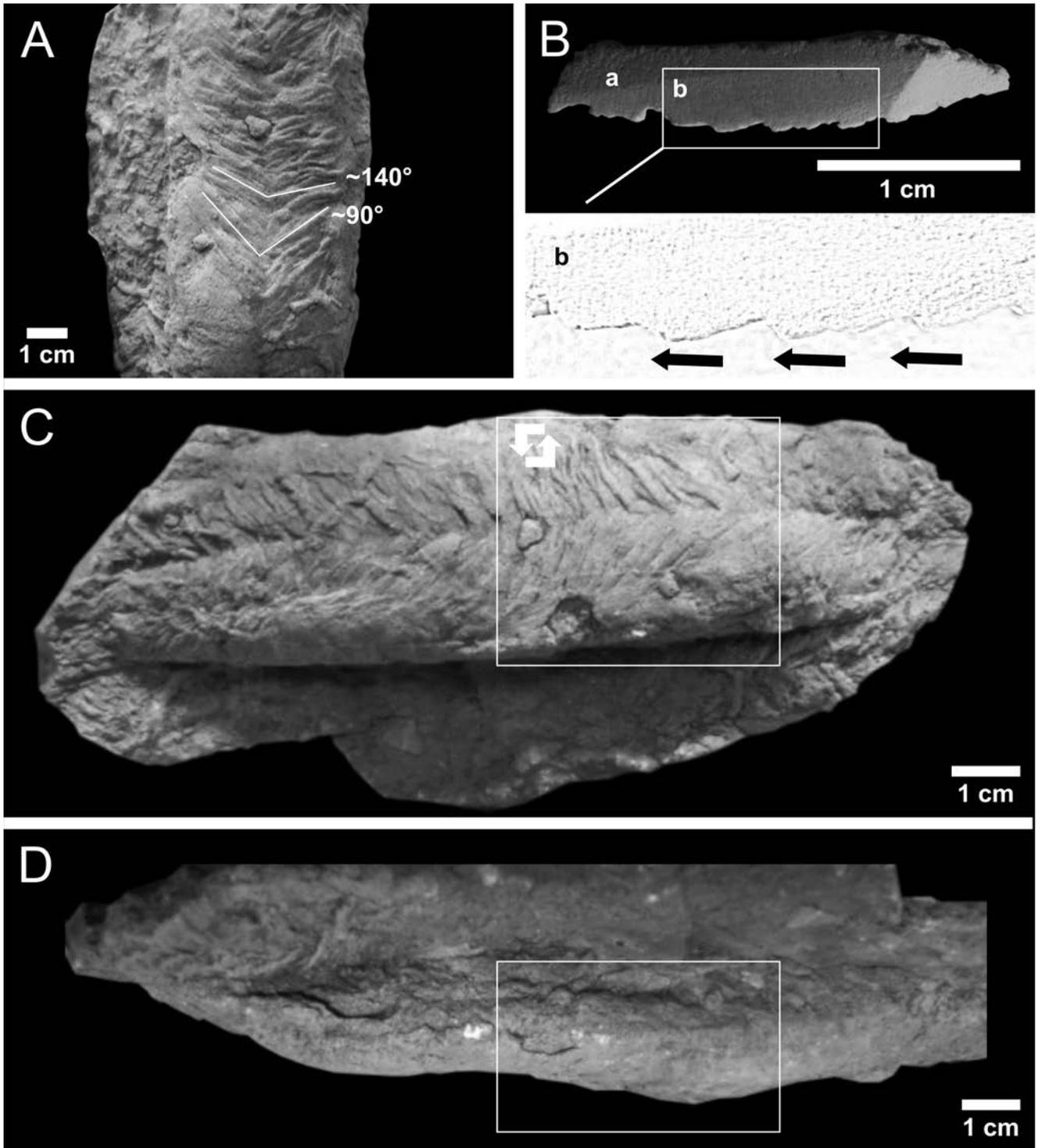


Fig. 5. *Cruziana semiplicata*: morphology of scratches and V-pattern. **A.** General view of trace fossil with marked changes in size of acute angle of "V" (GPIT/IC/00148). Larger value of angle corresponds to shallower parts of trace fossil (compare A, C and D). **B.** Longitudinal section of *Cruziana semiplicata* (a) with visible asymmetry of scratches (ZPAL Tf. 4/314). Drawing made from same specimen (b, Gimp 2: FilterEdge Detection used with settings: radius 1 = 0.0 and radius 2 = 20.0); black arrows show direction of movement as indicated by gaping direction of "V". **C–D.** The same specimen as in A (GPIT/IC/00148).

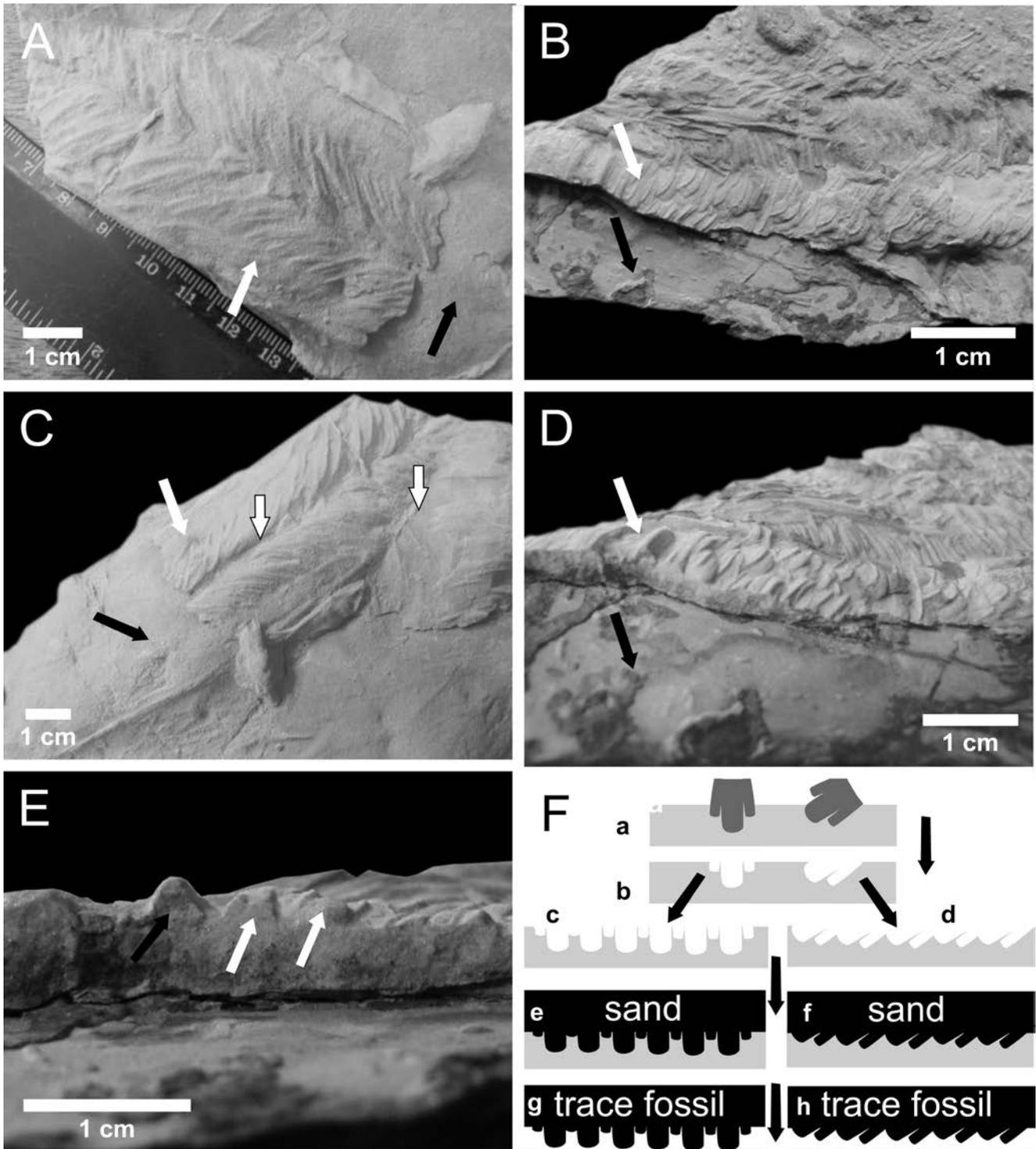


Fig. 6. Development of internal lamination in *Cruziana semiplicata*. **A.** *Cruziana semiplicata* preserved with primary lamina, bearing "perfect hypichnion" (white arrow) and transmitting "imperfect hypichnion" on sole of higher lamina (black arrow, ZPAL Tf. 4/228). **B.** *Cruziana semiplicata* preserved with the primary lamina bearing hypichnion, but with no trace fossil morphology transmitted to the higher lamina (ZPAL Tf. 4/734). **C.** Same specimen as in A (different view). **D.** Same specimen as in B (different view). **E.** Close-up of natural fracture through *Cruziana semiplicata* scratches, showing symmetrical scratch (conical shape indicated by black arrow) and asymmetrical scratches (white arrows). **F.** Drawing, showing interrelationships between angle of appendage-substrate contact, morphology of trace (a-d) and resulting trace fossils (e-h).

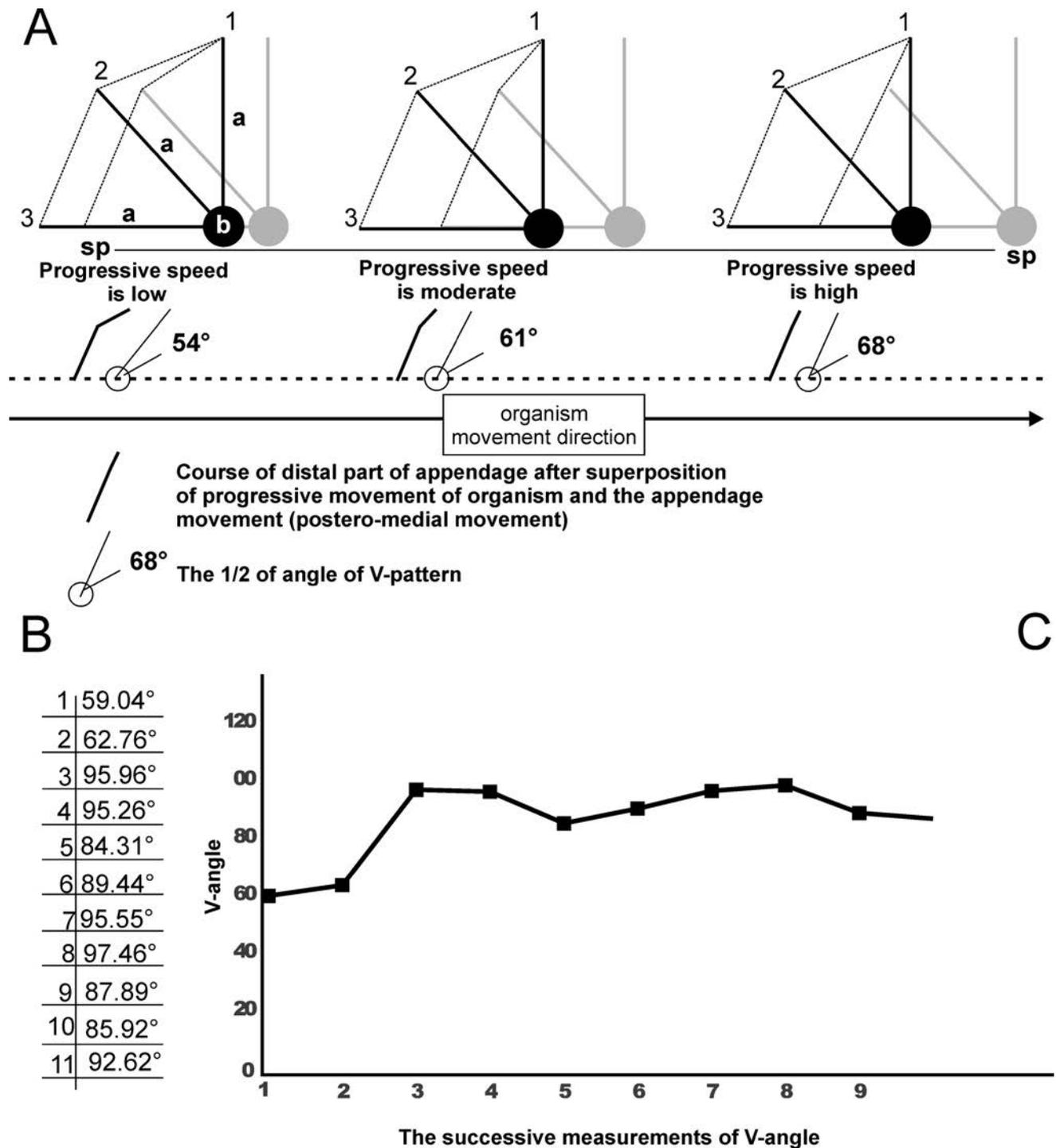


Fig. 7. Origin of V-pattern in *Cruziana semiplicata*: the presumably backward and medially directed movement of the appendage, superimposed with the progressive movement of the trace maker. **A.** Three instances characterized by different speeds of progression of the trace maker positioned above substrate. The drawings represent the appendage (a), appendage attachment point and axis of rotation (b) and trace-maker symmetry plan (sp) – all viewed from above (plan view). Numbers: 1, 2 and 3 show three selected successive positions of the terminal part of the appendage. For simplicity, the appendage is treated in this model as a rigid frame with constant length, but in reality it would be a moveable chain of podomeres. The inward-bending action of the appendage would result in a decrease in the apparent length of the appendage (as seen from above – in the plane view). Therefore, the inward movement of the appendage, superimposed on the general backward movement (see Whittington, 1980), would create a resultant backward and medially directed course of the distal part of the appendage, in which the “V” would have even higher values, in accordance with a given speed of progression than has been presented in this model. **A.** Shows that with increasing value of the speed of the organism’s progression, the values of the acute angle of the “V” increases. Therefore, a directly proportional relationship is inferred between these values (see text). **B., C.** Measurements made digitally from the composite specimen of *Cruziana semiplicata* and *Rusophycus* isp. illustrated by Crimes (1970a). The measurement numeration starts from *Rusophycus* toward *Cruziana*. The measurements given in Table (B) correspond with those on the chart (C).

For a given time (T_1), the distance covered by the terminal part of the appendage (S_a) and by the organism (S_{or}) in that time may be considered. The way considered will be measured in a plane parallel to the body symmetry plane. As it is known that $V = S/T$, therefore for the appendage, $V_a(T_1) = S_a/T_1$ and for the organism, $V_{or}(T_1) = S_{or}/T_1$. Because $T = S/V$, then for the appendage $T_1 = S_a/V_a$ and for the organism, $T_1 = S_{or}/V_{or}$. As a result, $S_a/V_a = S_{or}/V_{or}$ and from this, $S_a \sim 1/V_{or}$. This theoretical consideration indicates that the way (S) travelled by the distal part of the appendage, is shorter, when the organism moves forward faster (Fig. 7A). The resultant “V” is therefore wider and the acute angle of “V” has higher values. Therefore, the value of the acute angle of the “V” is thought to be proportional to the speed of the organism, contrary to the inverse proportionality, proposed in the previous model (Crimes, 1970a).

The model predicts that the *Rusophycus*, associated with *Cruziana semiplicata*, as a cubichnion (“resting trace”) should have low angle of “V”. However, the specimen illustrated by Crimes (1970a, pl. 12b) is inconclusive with regard to this matter, because the *Rusophycus*, grading into *Cruziana semiplicata* as illustrated by that author, appears to have no visible appendage traces. Within the material studied by the present author, there was no a single composite trace of *Cruziana semiplicata* and *Rusophycus*. However, the deeper parts of the *Cruziana semiplicata* observed, where the trace maker presumably dug more vertically, thus decreasing its progression speed, do have low “V” angles (Fig. 5A, C, D).

The theoretical considerations of the variation of the “V” angle in *Cruziana semiplicata* are confirmed by the fossil record and the most important element here is the widely cited composite specimen of *Cruziana semiplicata* and *Rusophycus* isp., as figured by Crimes (1970a, pl. 12b). Figure 7B, C shows the measurements made digitally from Crimes (1970a) figure and these results appear to verify positively the theoretical predictions of the proposed model, as the “V” has a lower acute angle, closer to that of *Rusophycus* (see also Fig. 7B, C). Finally, the correlation noted by Crimes (1970a) as to the decrease in the value of the acute angle of the “V” and the increase in the wideness of the zones covered with exopodal scratches may be explained by a decrease of progressive speed. In this case, the exopods could have turned toward the substrate for a more supportive and/or digging function (compare with Bergström, 1972).

***Cruziana semiplicata*: potential producer**

In most cases, it is impossible to point a trace-making organism with a precision reaching genus or species (Aceñolaza, 2003; Gibb *et al.*, 2010). However, a few such attempts have been made with respect to the *Cruziana semiplicata*. Fortey and Seilacher (1997) proposed a trilobite from the genus *Maladoidella* Endo. These authors based their conclusions on criteria, such as, e.g., overlap in size range (between the trace and body fossils) and geographical and stratigraphical distribution. As yet, representatives of *Maladoidella* have not been found in the Wiśniówka Sandstone Formation and therefore researchers working on this

unit try to link the local *Cruziana semiplicata* with other trilobites (Radwański and Roniewicz, 1972; Żylińska, 1999; Żylińska and Radwański, 2008). Bergström (1972) proposed the trinucleid trilobite, *Cryptolithus* Green, as a potential producer of *Cruziana semiplicata*. This view was based on the interpretation of appendage functional morphology. Jensen *et al.* (2011) favoured a more likely scenario, in which this trace fossil had been produced by various organisms.

Here, no attempt is made to connect *Cruziana semiplicata* with a particular trilobite, but rather some conclusions based on geometric analysis are made, solely with reference to trace fossil morphology. *Cruziana semiplicata* has internal scratches meeting in the plane of symmetry of the trace fossil (trace-maker body symmetry, see Figs 4, 5). There is no flat area between the endopodal lobes, comparable to the one that is observed in *Rusophycus polonicus*, a trace fossil from the same strata (Fig. 8C).

A simply two-dimensional model (Fig. 8A) of trilobite appendage may be considered, assuming the biomechanical characteristics of the appendages, as proposed by Whittington (1980). The active part of the appendage, the part below the pivot knee-like joint (see Whittington, 1980) has a given length (A). For the simplicity of the model, only appendage movement in a plane perpendicular to the symmetry plane of the organism is considered. In this configuration, it is possible to see that the length of the active appendage (A) always will be longer than the way travelled by its terminal part (a scratch; see S in Fig. 8A, B) during appendage movement in a plane perpendicular to the body symmetry plane. If the length of the way travelled (S) would be equal to the length of the active appendage (A), then a triangle with equal arms ($A = S$) would be obtained and in this case, the hypotenuse would be equal to square root of a sum of A^2 and S^2 and therefore the hypotenuse $> A$ (Fig. 8A).

If the length of a scratch (measured perpendicular to the symmetry plane) is always shorter than the length of the active appendage (Fig. 8A), then it may be used as a minimal approximation of the “height” of the trace maker: the minimal height to the pivot joint should be at least equal to the width of endopodal lobe (Fig. 8A). Therefore, by reconstructing the schematic cross-section for the trace maker of *Cruziana semiplicata*, a relatively “high” organism is obtained (Fig. 8B). This reconstruction would be similar to some previously proposed trace makers (e.g. trinucleids; see Bergström, 1972).

***Cruziana semiplicata* and *Rusophycus polonicus*: a geometrical comparison**

Cruziana semiplicata co-occurs in the strata studied with *Rusophycus polonicus* (Orłowski *et al.*, 1970, 1971; Radwański and Roniewicz, 1972) and both these trace fossils were used by Seilacher as index trace fossils in his ichnostratigraphical scheme (Seilacher, 1970, 1994, 2007). Some ichnologists tended to treat these two trace fossils as the products of different kinds of behaviour, performed by the same organisms (Crimes, 1970a; Radwański and Roniewicz, 1972). Others did not agree with this view (Seilacher, 1970). However, if similar geometrical consideration

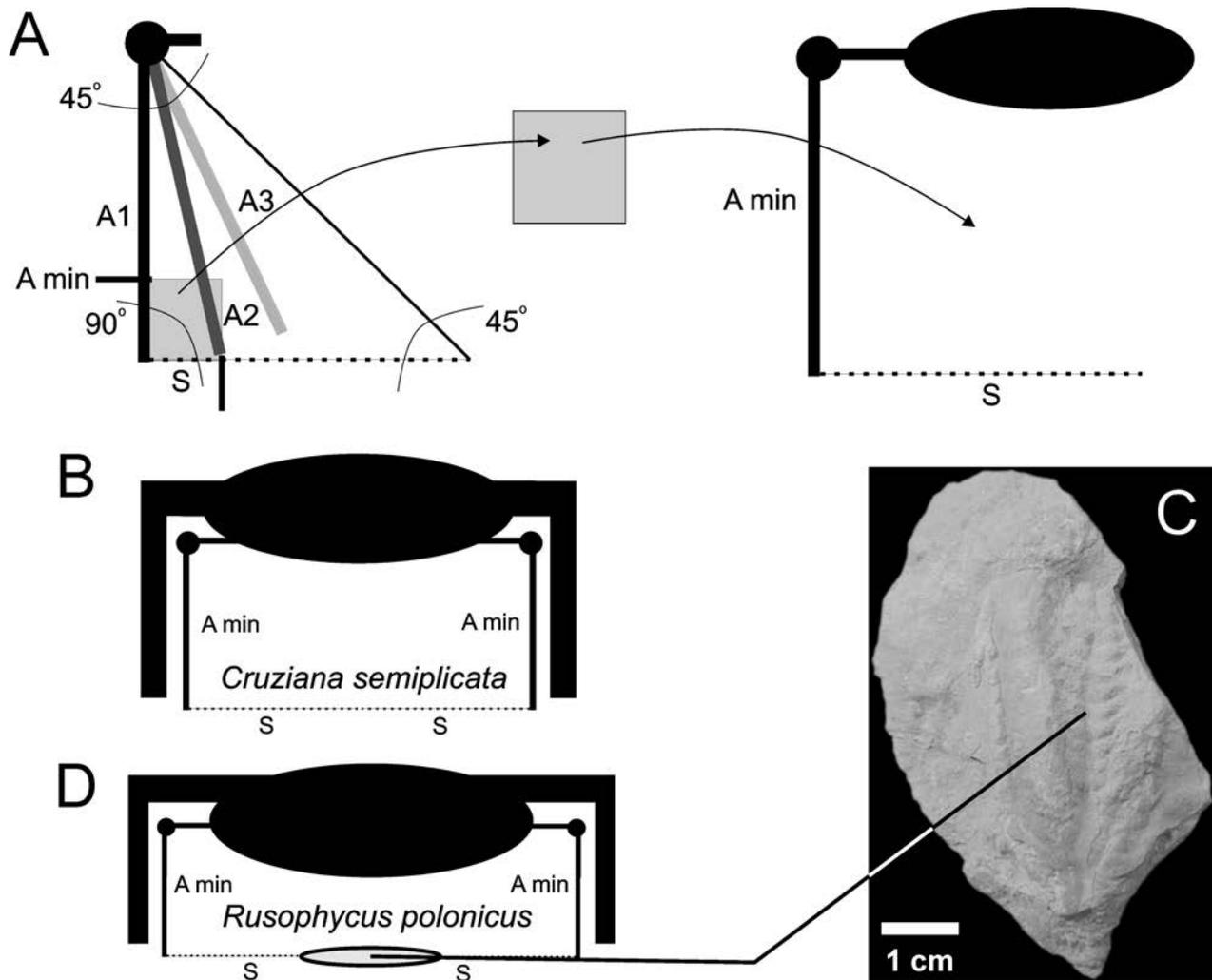


Fig. 8. Geometrical considerations of trace-maker features, based on trace-fossil morphology. **A.** Simple geometrical consideration, showing that minimal length of active part of appendages (A_{\min}) at least must be equal to width of endopodal lobe, measured perpendicular to trace-fossil symmetry (S). **B.** Schematic reconstruction (cross-section) of *Cruziana semiplicata* trace maker: the “high” type of trace maker (on the basis of considerations, shown in A). **C.** *Rusophycus polonicus* from Wiśniówka Sandstone Formation (ZPAL Tf. 4/1324). Wide flat area between endopodal lobes is marked. **D.** Schematic reconstruction of *Rusophycus polonicus* trace maker (on the basis of considerations, shown in A): relatively “flat” trace maker and trace with undisturbed area in middle part – corresponding to flat area between endopodal lobes (see C).

as the one applied to *Cruziana semiplicata*, are applied to *Rusophycus polonicus*, then this will lead to a different reconstruction of a trace maker. This is because in *Rusophycus polonicus* the endopodal scratches do not meet medially and a wide, flat area occurs in this trace fossil (often covered with *coxae* imprints; see Fig. 8C). This area tapers toward the rear end of the *Rusophycus polonicus*, but in the front is typically wider than each of the endopodal lobes. Moreover, the composite specimen figured by Crimes (1970a) does not belong to *Rusophycus polonicus* (Orłowski *et al.*, 1971). In conclusion, *Cruziana semiplicata* and *Rusophycus polonicus* represent different behavioural patterns, but a geometrical comparison of these two trace fossils leads to the view that the morphological features, which appear to depend on trace-maker morphology, do not display continuity and therefore these trace fossils were most likely produced by different organisms: *Cruziana semiplicata* by a

“high” type of producer and *Rusophycus polonicus* by a “flat and low” type of producer (Fig. 8B, D).

DISCUSSION

The ethology of the trace maker of *Cruziana semiplicata* previously was interpreted in two ways. Some workers saw *Cruziana semiplicata* as a feeding structure, formed by furrowing or infaunal behaviour (Seilacher, 1970, 2007). Other workers favoured epifaunal locomotion as an interpretation (crawling) for the behaviour of the trace maker (Crimes, 1970a).

In the present account, neoichnological, sedimentological and morphological observations were used to test these interpretations.

The feeding model of the origin of *Cruziana semi-*

plicata is interconnected with the assumption of an infaunal origin of the trace (Seilacher, 1970, 1985). However, in the case of *Cruziana semiplicata* from the Wiśniówka Sandstone Formation, two types of lamination can be distinguished in the trace fossil. One type is where a lamina covering the trace transmits imperfectly the trace morphology to the top of the lamina and the other is where a lamina covering the trace has a flat top. The first type is interpreted as having been most likely deposited before the activity of the trace maker and without later erosion/reburial. Therefore, this type of lamination appears to demonstrate the epifaunal character of *Cruziana semiplicata* from the Furongian Wiśniówka Sandstone Formation. The second, flat-topped type of lamination is considered here to be inconclusive. The neoichnological observation of traces, created by *Triops*, shows that *Cruziana*-like traces might have been formed epifaunally.

Other ichnologists postulated that other benefits (most likely feeding) than locomotion had to drive the behaviour, resulting in the *Cruziana*-type traces, as the presumed furrowing would be very demanding in terms of energy (Bergström, 1976). The lack of path-by-path disturbance was taken to indicate infaunal origin and feeding ethology, as well (see discussion of *Cruziana tenella* in Jensen, 1997). However, neoichnological data show that no furrowing may occur during this process and the disturbance of previous paths by new ones does not need to occur at all. The lack of this disturbance, in *Triops* traces was the result of being positioned over the substrate and the actual lack of furrowing means that no body contact with the substrate occurred. Therefore, the “energetic expense” argument, used in favour of the feeding hypothesis (Bergström, 1976), cannot be sustained in the light of the data presented, since undisturbed paths were observed in clearly epifaunal traces in the present study (Fig. 2).

In the locomotory model, the velocity of locomotion was interpreted as being intermediate between resting (*Rusophycus*) and the high-speed locomotion of *Diplichnites* or *Petalichnus*. In the locomotory model, the value of the acute angle of the “V” formed by the internal scratches is directly correlated with the velocity of the organism and the value of this angle of the “V” is thought to be inversely proportional to the speed of the organism (Crimes, 1970a; Żylińska and Radwański, 2008). The locomotory scenario for the origin of the V-pattern in *Cruziana* was criticized on the grounds of functional morphology, as interpreted for *Olenoides serratus* (Whittington, 1980): the trilobite legs are thought to have a design, precluding the possibility of production of the V-shaped pattern of scratches and delivering sufficient propulsive power at the same time. Whittington (1980) also indicated that an elongated trace – a scratch – is not a “typical” imprint, left by arthropod appendage during locomotion. The most effective means of locomotion is when the foot or appendage stays at a spot on the surface and the whole energy of movement is transmitted into the body as kinetic energy, resulting in progression: the body moves and the foot stays (Whittington, 1980; Braddy, 2003).

The morphology of *Cruziana semiplicata* was analyzed at two levels: the internal scratches and the V-pattern formed by these scratches. The internal (endopodal) scratches were observed to be asymmetric in side view (Fig. 5B). This

was interpreted as indicating a low angle of contact between the appendage and the substrate, as well as forward facing of the terminal parts of appendages. Forwardly directed terminal parts of appendages preclude the possibility of a propulsive function of these appendages and add to the previous morphological arguments against any link between propulsion and scratch formation (Whittington, 1980). This observation also fits with the neoichnological data, as the scratch asymmetry shows independence of scratch formation and locomotion by the trace maker of *Cruziana semiplicata* from the Furongian Wiśniówka Sandstone Formation. However, the most important consideration is that the asymmetry observed appears to indicate that the analogy between notostracan traces and the Cambrian material studied may be not only morphological, but also behavioural.

The V-pattern is widely interpreted as gaping toward the travel direction (Crimes, 1970a; Seilacher, 1970; Birkenmajer and Bruton, 1971). Assuming independence of action of the frontal appendages and progressive movement by the organism, as was observed for *Triops* and as is indicated by scratch asymmetry in the trace fossil studied, it was possible to reconstruct the origin of the V-pattern on the basis of relationships between movement vectors. The main conclusion, arising from this consideration, is that the “V” is wider (larger acute angle of the “V”), when the organism moved forward faster. Why then is no reversed “V” observed in *Cruziana semiplicata*, – neither in the sample studied, nor described in literature?, The “V” gaping in a direction, opposite to the direction of forward movement, according to the model proposed in this paper, would have originated, when the organism moved faster over the substrate than its appendages were able to process the substrate below. Such a case makes no biological sense and could not be justified as feeding behaviour.

The epifaunal model of *Cruziana semiplicata* origin, as proposed in this paper, also should be discussed in the light of the preservation potential of such traces. Seilacher (1970, 1985, 2007) interpreted all trilobite-made trace fossils as fossilized infaunal traces. His main argument was presumably the very low preservation potential of shallow-tier traces, produced at the sediment-water interface, where a soupy consistency of the substrate would be expected (cf. Seilacher, 1970 and Crimes, 1975). Seilacher (1970, 1985, 2007) postulated that instant filling of such undertraces would facilitate their preservation potential. However, more recent studies of sediment properties at or close to the sediment-water interface show that the application of properties displayed by modern sediments to Lower Palaeozoic strata may be misleading. The “Lower” Cambrian substrates at the sediment-water interface displayed a higher resistance to erosion, owing to low infaunal activity (sediment mixing; Droser *et al.*, 2002; Jensen *et al.*, 2005; Stachacz, 2012). No similar study has been done for the Furongian strata under consideration. However, Sadlok (2013) illustrated cancelled bed-junction preservation of shallow-tier *Rusophycus* – a feature typical of the better studied “Lower” Cambrian associations. Mángano and Buatois (2011) indicated that the process of development of an infauna could occur diachronously with some delay in the higher latitudes. Additionally, Tarhan *et al.* (2012) showed that the shallow firm-

ground condition of sediments, close to the sediment-water interface, could survive until into the Silurian.

If substrate conditions at the sediment-water interface allowed the preservation of epifaunal *Cruziana semiplicata* in the strata studied, than the proposed model should also explain the observed variation in preservation e.g. the preservation of the lateral longitudinal traces that were thought to be products of the cephalic margin or pleurae (e.g., Crimes, 1970a, Seilacher, 1970; Radwański and Roniewicz, 1972; Jensen *et al.*, 2011). The model explains the variation in “V” angle as mirroring the variation in the speed of progression of the trace maker. Therefore, the lack or presence of the morphological features mentioned also may be at least in part dependent on the speed of progression of the trace maker. It is postulated that during relatively high-speed searching for food, the trace maker touched the substrate with other body parts rarely and more randomly. During slower progression, the rigid parts of cephalon could act as additional support, keeping the organism in the right position over the substrate with minimal energetic effort. A similar mode of feeding, but with no forward progression, has been proposed for the Ordovician *Cryptolithus tessellatus* (Green) with *Rusophycus* created at the sediment-water interface as a result (Fortey and Owens, 1999). Also Crimes (1970a) made the observation that a lower “V” angle in *Cruziana semiplicata* is associated with the lower part of the width of the trace fossil being covered by endopodal traces and a greater participation of exopodites could be explained by the proposed new model. It is possible that with a lower speed of progression the exopodites were directed more downward and could take on a function that was partially supportive as well as digging (Fig. 4E).

Finally, the simply geometrical reconstruction of the *Cruziana semiplicata* trace maker shows that it was a relatively “high” organism as the of height to the pivot knee joint should be at least equal to the width of the endopodal lobe. Comparison with the co-occurring *Rusophycus polonicus* shows these two ichnospecies, linked by some workers (Crimes, 1970b; Radwański and Roniewicz, 1972; Żylińska and Radwański, 2008) in having the same trace maker, more likely were produced by different organism.

CONCLUSIONS

Cruziana semiplicata from the Wiśniówka Sandstone Formation appears to be a fossilized version of an epifaunal, pascichnial (feeding) trace, produced by an organism positioned above the seabed with only a few frontal appendages touching and processing the sediment below.

Morphological observations on *Cruziana semiplicata* indicate that the endopodal scratches were most likely produced by appendages that were directed forward. These appendages are thought to have been incapable of delivering propulsion in this position. However, it is postulated that the action of the scratch-forming appendages and the progressive movement of the trace maker were independent. This assumption is based on observations of the behaviour of *Triops australiensis*, in which the action of the substrate-searching appendages was independent of the progressive

movements of the organism, while it was positioned above the substrate and creating *Cruziana-like* traces.

Theoretical considerations of the interrelationship between the value of the acute angle in the “V” formed by endopodal scratches and the progressive speed of the trace maker indicate that both these values were proportional. The V-pattern changes, predicted by the proposed new model, find confirmation in the fossil material. The model is in opposition to the previously proposed interrelationship (see Crimes, 1970a). Finally, the preservation potential of epifaunal traces is briefly discussed.

Also, geometrical comparison with the co-occurring *Rusophycus polonicus* ichnospecies shows that these trace fossils had different trace makers.

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REFERENCES

- Aceñolaza, G. F., 2003. Olenidae (Trilobita) – *Rusophycus* isp.: Producer organism-resulting ichnofossil. Cases for the analysis in the Cambro-Ordovician of the Argentine Eastern Cordillera. *Ameghiniana*, 40: 573–583.
- Babcock, L. E. & Peng, S. C., 2007. Cambrian chronostratigraphy: Current state and future plans. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 254: 62–66.
- Baldwin, C. T., 1977. Internal structures of trilobite trace fossils indicative of an open surface furrow origin. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 21: 273–284.
- Bergström, J., 1969. Remarks on the appendages of trilobites. *Lethaia*, 2: 395–414.
- Bergström, J., 1972. Appendage morphology of the trilobite *Cryptolithus* 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.
- Birkenmajer, K. & Bruton, D. L., 1971. Some trilobite resting and crawling traces. *Lethaia*, 4: 303–319.
- Braddy, S. J., 2003. Trackways-arthropod locomotion. In: Briggs, D. E. G. & Crowther, P. R. (eds), *Palaeobiology II*. Blackwell Science, Malden, Oxford, pp. 389–393.
- Bromley, R. G. & Asgaard, U., 1972. Notes on Greenland trace fossils. I. Freshwater *Cruziana* from the Upper Triassic of Jameson Land, East Greenland. *Grønlands Geologiske Undersøgelse*, 49: 7–13.
- Bromley, R. G. & Asgaard, U., 1979. Triassic freshwater ichno-

- coenoses from Carlsberg Fjord, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 28: 39–80.
- Crimes, T. P., 1970a. Trilobite tracks and other trace fossils from the Upper Cambrian of North Wales. *Geological Journal*, 7: 47–68.
- Crimes, T. P., 1970b. The significance of trace fossils in sedimentology, stratigraphy and palaeoecology with examples from Lower Palaeozoic strata. In: Crimes, T. P. & Harper, J. C. (eds), *Trace Fossils. Geological Journal Special Issue*, 3: 101–126.
- Crimes, T. P., 1975. The production and preservation of trilobite resting and furrowing traces. *Lethaia*, 8: 35–48.
- Droser, M. L., Jensen, S. & Gehling, J. G., 2002. Trace fossils and substrates of the terminal Proterozoic–Cambrian transition: implications for the record of early bilaterians and sediment mixing. *Proceedings of the National Academy of Sciences*, 99: 12572–12576.
- Fortey, R. A. & Owens, R. M., 1999. Feeding habits in trilobites. *Palaeontology*, 42: 429–465.
- Fortey, R. A. & Seilacher, A., 1997. The trace fossil *Cruziana simplicata* and the trilobite that made it. *Lethaia*, 30, 105–112.
- Gand, G., Garric, J., Schneider, J., Walter, H., Lapeyrie, J., Martin, C. & Thiery, A., 2008. Notostraca trackways in Permian playa environments of the Lodève basin (France). *Journal of Iberian Geology*, 34: 73–108.
- Gibb, S., Chatterton, B. D. E. & Gingras, M. K., 2010. *Rusophycus carleyi* (James, 1885), trace fossils from the Lower Ordovician of Southern Morocco, and the trilobites that made them. *Ichnos*, 17: 271–283.
- Goldring, R., 1985. The formation of the trace fossil *Cruziana*. *Geological Magazine*, 122: 65–72.
- Gradziński, R. & Uchman, A., 1994. Trace fossils from interdune deposits – an example from the Lower Triassic aeolian Tumlín Sandstone, central Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 108: 121–138.
- 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.
- 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 simplicata* 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.
- Jensen, S., Droser, M. L. & Gehling, J. G., 2005. Trace fossil preservation and the early evolution of animals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 220: 19–29.
- 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.
- Knecht, R. J., Benner, J. S., Rogers, D. C. & Ridge, J. C., 2009. *Surculichnus bifurcauda* n. igen., n. isp., a trace fossil from Late Pleistocene glaciolacustrine varves of the Connecticut River Valley, USA, attributed to notostracan crustaceans based on neoichnological experimentation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 272: 232–239.
- 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.
- Mángano, M. G. & Buatois, L. A., 2011. Timing of infaunalization in shallow-marine early Paleozoic communities in Gondwanan settings: discriminating evolutionary and paleogeographic controls. *Palaeontologia Electronica*, 14: 1–21.
- Orłowski, S., 1975. Cambrian and Upper Precambrian lithostratigraphic units in the Holy Cross Mts. *Acta Geologica Polonica*, 25: 431–448. [In Polish, English summary.]
- Orłowski, S., 1992a. Trilobite trace fossils and their stratigraphical significance in the Cambrian sequence of the Holy Cross Mountains, Poland. *Geological Journal*, 27: 15–34.
- Orłowski, S., 1992b. Cambrian stratigraphy and stage subdivision in the Holy Cross Mountains, Poland. *Geological Magazine*, 129: 471–474.
- 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.
- Pollard, J. E., 1985. *Isopodichnus*, related arthropod trace fossils and notostracans from Triassic fluvial sediments. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 76: 273–285.
- Radwański, A. & Roniewicz, P., 1972. A long trilobite trackway, *Cruziana simplicata* Salter, from the Upper Cambrian of the Holy Cross Mts. *Acta Geologica Polonica*, 22: 439–447.
- Ramsköld, L. & Edgecombe, G., 1996. Trilobite appendage structure – *Eoredlichia* reconsidered. *Alcheringa*, 20: 269–276.
- Rindsberg, A. K., 1994. Ichnology of the Upper Mississippian Hartselle Sandstone of Alabama, with notes on other Carboniferous formations. *Geological Survey of Alabama Bulletin*, 158: 1–107.
- Sadlok, G., 2010. Trace fossil *Cruziana tenella* from the Furongian (Upper Cambrian) deposits of Poland. *Acta Geologica Polonica*, 60: 349–355.
- Sadlok, G., 2013. Compaction-related style of *Rusophycus* preservation from Furongian (Upper Cambrian) of Holy Cross Mountains (Poland). *Annales Societatis Geologorum Poloniae*, 83: 317–327.
- 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: 447–476.
- 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, Heidelberg, New York, 226 pp.
- Seilacher, A., 2008. *Fossil Art: an Exhibition of the Geologisches Institut, Tübingen University, Germany*. Silkeborg Bogtryk, Laasby (Denmark), 102 pp.
- Stachacz, M., 2012. Ichnology of Czarna Shale Formation (Cambrian, Holy Cross Mountains, Poland). *Annales Societatis Geologorum Poloniae*, 82: 105–120.
- Stein, M., Budd, G. E., Peel, J. S. & Harper, D. A., 2013. *Arthroaspis* n. gen., a common element of the Sirius Passet Lagerstätte (Cambrian, North Greenland), sheds light on trilobite ancestry. *BMC Evolutionary Biology*, 13: 1–34.
- Tarhan, L. G., Jensen, S. & Droser, M. L., 2012. Furrows and firmgrounds: evidence for predation and implications for Palaeozoic substrate evolution in *Rusophycus* burrows from the

- Silurian of New York. *Lethaia*, 45: 329–341.
- Trusheim, F., 1931. Aktuo-paläontologische Beobachtungen an *Triops cancriformis* Schaeffer (Crust. Phyll.). *Senckenbergiana*, 13: 234–243.
- Whittington, H. B., 1980. Exoskeleton, moult stage, appendage morphology, and habits of the Middle Cambrian trilobite *Olenoides serratus*. *Palaeontology*, 23: 171–204.
- Żylińska, A., 1999. Trace maker of *Cruziana semiplicata* in the Upper Cambrian of the Holy Cross Mts. (Poland), In: Palmer, A. R. (ed.), *Laurentia 99. V Field Conference of the Cambrian Stage Subdivision on Cambrian Stratigraphy, Utah, Nevada, California, USA., September 12–22, 1999*. Institute for Cambrian Studies, Boulder, Colorado, pp. 62–63.
- Żylińska, A. & Radwański, A., 2008. Stop 2 – Wiśniówka Duża, Upper Cambrian. In: Pieńkowski, G. & Uchman, A. (eds), *Ichnological Sites of Poland. The Holy Cross Mountains and The Carpathian Flysch. The Second International Congress on Ichnology, Cracow, Poland, August 29 –September 8, 2008. The Pre-Congress and Post-Congress Field Trip Guidebook* Polish Geological Institute, Warszawa, pp. 37–46.
- 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.