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UPPER CAMBRIAN TRILOBITE ICHNOCOENOSIS FROM WIELKA WIŚNIÓWKA (HOLY CROSS MOUNTAINS, POLAND)

Abstract. — Description is given of the Upper Cambrian trilobite ichnocoenosis, i.e. a trace assemblage of the various life activities of trilobites, from the shallow-water marine deposits at Wielka Wiśniówka in the Holy Cross Mountains (Góry Świętokrzyskie). These traces occur either on the upper sides of layers (true traces) or on the lower sides of layers covering grooves made by trilobites on the sea bottom (sole markings = hieroglyphs). Hieroglyphs are the more common forms. Out of them, *Rusophycus* sp., *Cruziana* sp., *Diplichnites* sp. and *Dimorphichnus* sp. have been described in greater detail. *Bergaueria perata* Prantl and *Diplocraterion* sp. hieroglyphs are also encountered in the trilobite ichnocoenosis here reported.

INTRODUCTION

The aim of the present paper is to discuss the various types of traces, presumably made by trilobites, in the Upper Cambrian sediments of the Holy Cross Mountains. Among other places, these deposits crop out in a big quarry at Wielka Wiśniówka near Kielce (western part of the Holy Cross Mountains), and all the material described below was obtained from that site. Other problems discussed here concern the trilobite mode of life, rest and locomotion on the sea floor, also the conditions that favour the preservation of trilobite traces in the sediments.

The sedimentology of the Upper Cambrian series cropping out in the Wielka Wiśniówka quarry has previously been investigated by Dżułyński and Żak (1960), as well as by the present writers (Radwański & Roniewicz, 1960). These investigations permit to reconstruct the outstanding features of the environment under which the sediments were formed. The data obtained have been useful in the present discussion of the life conditions of trilobites.

The material was collected at Wielka Wiśniówka between 1959 and 1962. A short chapter dealing with trilobite traces is contained in a paper published by the writers (Radwański & Roniewicz, 1960). An acknowledgement is here due to Professor Dr. A. Seilacher of the Georg August University in Göttingen, Germany, for his kind readiness to carry on an exchange of correspondence with the writers. His letters contained most valuable information, suggestions and comments for which the writers here convey their most sincere thanks. They also thank Dr. Z. Kotański for the permission to use a photograph published in his "Geological Guide to the Holy Cross Mountains" (1959).

REVIEW OF PREVIOUS INVESTIGATIONS OF TRILOBITE TRACES

The various types of traces in the sediments, commonly referred to trilobites, are reported from the Cambrian to the Devonian — the periods of the greatest flourishing of trilobites. The basic data concerning the trilobite traces were given by Abel (1935) and Lessertisseur (1955). Many valuable suggestions concerning the interpretation of these structures have been also given by Richter (1919, 1920) and Seilacher (1959) who deal with the trilobite mode of life, and by Henningsmoen (1957) with regard to the life conditions of the Olenidae.

Holm (1887) was the first to carry out detailed investigations of the trilobite traces encountered in Cambrian rocks. He concerned himself with structures of the *Cruziana* type from Östergötland in Sweden. These traces occur within a rock series which Holm assigned to the Upper Cambrian, but whose Ordovician age was proved by Westergård (1922). In 1937 Fenton and Fenton when describing the traces from the Lower Cambrian of Alberta, Canada, postulated that their origin was due to trilobites burrowing in search for food or for the laying of eggs (trilobite "nests"). The most important work on trilobite traces which contained very suggestive reconstructions is that by Seilacher (in Schindewolf & Seilacher, 1955). It is based on excellently preserved material from the Lower Cambrian of the Salt Range in Pakistan. In a number of other papers Seilacher (1956, 1959, 1960) published some information on various trilobite traces, their mode of occurrence, geographic range and stratigraphic distribution.

From the Lower Devonian Hunsrück Shales, in the Rhineland, Seilacher (1962) recently described characteristic tracks closely comparable with the claws and appendage setae of the trilobite genus *Phacops*, preserved within the same series with these details.

In the Holy Cross Mountains the traces of the *Cruziana* type were encountered by Czarnocki and Samsonowicz in various Cambrian stages, and were mentioned in several papers (cited by Radwański and Roniewicz, 1960). No trilobite traces have been discovered at Wielka Wiśniówka until quite lately (Dżułyński & Żak, 1960; Radwański & Roniewicz, 1960). Dżułyński and Żak mention the presence of *Crossochorda, Rusophycus* and *Diplichnites*, Radwański and Roniewicz — of *Rhysophycus* and *Cruziana*.

TRILOBITE ICHNOCOENOSIS FROM WIELKA WISNIOWKA

The term ichnocoenosis (Davitašvili, 1945) means an assemblage of various traces imprinted by animals in the sediment or on its surface. They may represent traces of crawling or burrowing, tracks or faecales (coprolites) of animals which lived in the sediment or moved on its surface.

Davitašvili uses the term ichnocoenosis only with reference to recent assemblages. Any organic assemblage, i.e. a coenosis, buried in the sediment, is referred to by that author as taphocoenosis (W. Quenstedt's definition; 1927, *fide* Davitašvili, 1945). In past condition the taphocoenosis is preserved incompletely as an assemblage called the orictocoenosis (Jefremov, 1945, in Davitašvili, 1945).

Since the term orictocoenosis implies merely a very general meaning applicable to any fossil organic material, the writers use the term ichnocoenosis when discussing the Upper Cambrian traces from Wielka Wiśniówka. Moreover, an attempt is made to discuss the assemblage here described not as the fossil remains of another assemblage but as it actually existed in the Upper Cambrian sea.

Owing to their characteristic shapes, relatively large dimensions and satisfactory state of preservation, the trilobite traces are of greatest importance within the Wielka Wiśniówka ichnocoenosis. Hence, the assemblage here studied is called the trilobite ichnocoenosis.

SEDIMENTARY ENVIRONMENT

General features of the sediments

The Upper Cambrian sedimentary series at Wielka Wiśniówka, containing the trilobite ichnocoenosis, consists of interbedded quartzitic sandstones, siltstones, claystones and clays (fragment of outcrop, pl. I).

The thickness of the individual sandstone layers ranges from a few to several tens of centimetres. Layers from 3 to 5 cm in thickness predominate, those up to and over 1 m in thickness are less frequent. The sandstones are fine-grained and equigranular; they contain admixtures of silt and clay fractions, also muscovite flakes which are concentrated mostly on the upperside of layers. According to Czermiński (1959), the clastic material of this series had experienced a long transport or even many-times repeated redeposition.

The deposits are white or bluish-grey, becoming darker and darker, with the decrease of the fraction. The clays are variously coloured. Some are bluish-grey, others completely black — owing to organic admixtures, whitish-variegated, even cherry-red — owing to ferric oxides. The results of thermic analyses obtained by B. Larsen of Copenhagen (unpublished data) show that illite is the chief constituent of the clays, while chlorite and kaolinite occur in minor quantities (Czermiński, 1959).

The silification of the sandstone layers was paenecontemporaneous, while the silica was most likely of terrigenic origin.

Bathymetric conditions

The bathymetric conditions of the sea basin which accompanied the formation of the discussed series, may be determined on the character of the extremely numerous and diverse ripple marks detectable on most of the sandy layers. The shallow-sea sedimentation of this series, within a zone under the continuous influence of the sea waves and of bottom currents, is indicated by the assemblage of many-times repeated and even coexisting ripple marks. These are symmetrical and asymmetrical oscillation ripples, metaripples, compound-, linguoid- and current ripple marks, associated with numerous bifurcated crests of oscillation ripple marks and various current structures. The depth of the basin may be estimated at from a score or so to several tens of metres. This agrees with the depth values given by Dżułyński and Żak (1960).

Bottom morphology

The character of sediments suggests that the floor of the basin was generally flat, and that its ups and downs, mainly connected with the thick, often rapidly thinning layers, were of a local character. The absence of offshore and beach structures, and the palaeogeographic position of the Upper Cambrian strata in the Holy Cross Mountains indicate that this region was situated at some distance from the sea shores which generally stretched south of the present Holy Cross Mountains area.

Layers up to 30 cm in thickness, displaying current bedding connected with ripple marks, consist of material that was deposited by currents during the rhythmic transportation phase (Dżułyński & Żak, 1960). Thicker, structureless layers, with their upper surface washed out, often contain shale lumps and fragments of shale sets torn out from the bottom. These layers were formed in result of rapid storm currents whose velocity characterizes the regressive sand wave phase (Dżułyński & Żak, 1960).

The sediments laid down by currents of various speed were rather stable and they were not subjected to any major disturbance except those connected with compaction and local loading. The slip and slump structures are associated with thicker layers. Their formation resulted from a local disturbance in the equilibrium of thicker sediments.

TRILOBITE LIFE CONDITIONS

The conditions of the trilobites' life in the Upper Cambrian sea here considered can be discussed only on very general outlines, as the conditions of the whole sedimentary environment. The light colour of most sediments and the presence of sedimentary structures formed by the action of waves indicate clear and well ventilated waters, and rapid decay of organic remains. The comparatively small depth of the basin favoured sufficient light penetration. The sea floor, covered with sand, silt or clay, was more stable than quaggy. Periods of deposition of the particular layers alternated with intervening periods without sedimentation, associated only with the action of waves.

CAUSES OF LACK OF TRILOBITE REMAINS

No trilobite exoskeleton remains, their counterparts or imprints have so far been obtained from Wielka Wiśniówka sediments, except for a single imprint (in the collection of Dr. S. Orłowski). This lack may be reasonably explained by the fact that trilobites could not be buried alife in the sea sands, since, being rather agile forms, they were able easily to withdraw from the layer that was being deposited. The soft parts of the dead trilobite bodies decayed rapidly, while their exoskeletons, as well as the moults could not be preserved under the prevailing conditions, being swept away by waves and currents before the deposition of the material. A similar situation, i.e. lack of trilobite remains in spite of the characteristic ichnocoenosis left by these animals, also prevails in Cambrian sediments throughout the world. This will seem quite obvious on consideration that sediments containing such ichnocoenoses were formed under similar facial conditions (Fenton & Fenton, 1937; Seilacher, 1955).

TRILOBITE TRACES

Occurrence sites

The traces here discussed occur on the surfaces of sandy or silty layers and on lamination planes of very fine-grained siltstones, claystones and clays.

Types of traces

Two types of traces are generally recognized, namely: 1) traces on the upper side of layers, 2) traces on the under side of layers. The former are the true traces imprinted by the animals; in most cases they occur as grooves. Of this type the writers have found one rest trace on the surface of a sandstone layer, and a score or so of crawling traces on the lamination planes of fine-grained siltstones and claystones. The second type occurs as hieroglyphs formed by the burying of the grooves that were imprinted by the animal on the sediment. These forms bear the character of mounds on the underside of the layer that covers up the true trace. Of this type the writers have found such forms as *Rusophycus* Hall, 1852, *Cruziana* d'Orbigny, 1842, *Diplichnites* Dawson, 1873, *Dimorphichnus* Seilacher, 1955, and other forms.

Hieroglyphs are distinctly the predominant form within the ichnocoenosis here considered. Their characteristics will be described in detail. True traces are extremely rare.

A general classification of all the traces is given in table below.

Nomenclature of traces of various life activities of trilobites and their position on the sides of layers

Traces of trilobite life activities	
Upper sides of layers (sea bottom) G r o o v e s (true traces)	Lower sides of layers covering the sea bottom H i e r o g l y p h s* (counterparts of grooves)
Rest traces	Hieroglyphs of rest traces: *Rusophycus* Hall, 1852
Traces of changing the rest places	Hieroglyphs of the traces of changing the rest places
Traces of movements along the bottom or just above it = tracks	Track hieroglyphs
1) Crawling traces along the bottom and its digging up	1) Hieroglyphs of crawling traces: *Cruziana* d'Orbigny, 1842
2) Traces of striding on the bottom	2) Hieroglyphs of the traces of striding: *Diplichnites* Dawson, 1873
3) Traces of sideway movement	3) Hieroglyphs of the traces of sideway movement: *Dimorphichnus* Seilacher, 1955

* Undeformed structures and load-casted hieroglyphs — forms partly obliterated owing to loading processes.

Conditions of preservation of traces in sediments

A trace may persist only if the sediment surrounding it is sufficiently consolidated so that the groove burrowed by the animal is not filled up again by the loose material. In the environment here considered clayey sediment satisfied this prerequisite, while sand was loose enough to cause a rapid burying of grooves made by trilobites. Along with sufficient consolidation the qualitative differences of the sediment overlying the traces is an additional prerequisite for their preservation. Hence, the best preserved traces are hieroglyphs on the underside of sandy layers that covered up the grooves marked on the upper side of a clayey sediment. When a clayey, trace-bearing bottom became covered up by a clay layer subsequent processes of compaction and diagenesis almost completely obliterated the buried traces, so as to make them barely detectable. A similar situation occurred in the case of two consecutive sandy layers.

TRILOBITE HIEROGLYPHS IN THE ICHNOCOENOSIS

HIEROGLYPHS OF REST TRACES

Rusophycus Hall, 1852

Material. — The *Rusophycus* Hall (=*Rhysophycus* Eichw.) hieroglyphs are the most common constituent of ichnocoenosis. About 40 well preserved specimens were collected by the writers, while at least 50 more forms, not so well preserved or even partly damaged, were obtained from the outcrop.

Description. — Hieroglyphs of the *Rusophycus* type are generally shaped like a two-lobed mound, divided by a depression. Imprints of trilobite segments, pygidium and small pygidial spine (pl. II) are often preserved within the depression. The hieroglyphs range from 1.0 to 6.5 cm in length. The width of the particular forms represents about two thirds of the length. The state of preservation of morphological details in smaller forms (pl. II, fig. 1-3) agrees with that of the larger forms (pl. II, fig. 4-6), and thus suggests its independence from the size of the animal. The resemblance of variously sized forms reasonably suggests that all the traces were made by animals of one biocoenosis in which there existed a given ratio of the smaller (young) forms to the larger (adult) forms.

Origin. — The *Rusophycus* Hall hieroglyphs are interpreted as the counterparts of traces of the trilobites rest on the sea bottom (Fenton & Fenton, 1937; Lessertisseur, 1955; Seilacher, 1955, 1956, 1959, 1960, 1962). The hieroglyph mounds fit into the original grooves made by the animal or by parts of its body.

The *Rusophycus* hieroglyphs previously described in the literature are preserved mostly as two-lobed mounds and it is this type that predominates in the material from Wielka Wiśniówka (pl. II, fig. 1, 4). In addition to them, about 10 more completely preserved specimens were found (pl. II, fig. 2, 3, 5—8). They are composed of the two-lobed mound, the imprints of trilobite segments, pygidium and pygidial spine. There exist, however, transitions between these two types. The latest observations indicate that all the hieroglyphs in the shape of a two-lobed mound may be associated with the life activities of the same type of animals. Hence, it seems reasonable not to introduce a new name for forms shown in pl. II, fig. 2, 3, 5—8 though they differ considerably from those in fig. 1 and 4. Therefore, all the hieroglyphs here investigated are assigned to the *Rusophycus* type. The most representative forms among them are those bearing traces of trilobite segmentation. Forms in the shape of a two-lobed mound only belong to the *Rusophycus* type; their incomplete state of preservation results from original or secondary causes.

It may reasonably be supposed that the original factors, responsible for the formation of "incomplete" *Rusophycus* hieroglyphs, are the poor consolidation of the sea bottom sediments — conducive to the burying of traces — or the ununiform sinking of their infillings (i.e. of the hieroglyphs), possibly also the trilobites' agility, during their rest, which impedes the distinct imprinting of the animal's body parts in the sediment. It seems that the main factor here is the ununiform sinking of the hieroglyph. Most likely this process was started by the very existence of the hieroglyph on the underside of the layer overlying the sea bottom. By analogy to the names suggested by Kelling and Walton (1957) for other load structures, the writers propose to call such forms the load-casted hieroglyphs.

A secondary factor might be that some hieroglyphs are subject to more rapid weathering than the covering layer, this being due to the less advanced diagenesis of the hieroglyphs. The weaker diagenesis of the hieroglyphs is probably sometimes connected with lithological differences, i.e. their somewhat coarser granulation than that of the covering layer.

Before terminating the discussion on traces formed on the sea bottom by resting trilobites, it might be mentioned that the plasteline counterpart of the true trace of a resting trilobite which occurs on the upper side of the ripple-marked sandstone layer (pl. III, fig. 1) — and hence may be considered as its hieroglyph — closely resembles the incompletely preserved forms of the *Rusophycus* type. In this case unsatisfactory preservation is most likely due to the weak consolidation of the sand on which the trilobite was resting.

Occurrence. — The *Rusophycus* hieroglyphs are known from the Cambrian deposits in Sweden, North America and Pakistan (Lessertisseur, 1955; Seilacher, 1955, 1960).

HIEROGLYPHS OF THE TRACES OF CHANGING THE REST PLACES

Among hieroglyphs imprinted by trilobites while changing their rest place the simplest ones are those which the trilobite made first: an irregular groove by digging up the sediment; then the trilobite moved on a little farther and quietly lay down to rest (pl. II, fig. 4; an indistinct hieroglyph without details which became obliterated by loading processes). Another type was formed when the trilobite changed its rest place more than once, slowly moving on in the same direction (pl. III, fig. 2; five partly overlapping consecutive rest places). The last type of hieroglyphs are transition forms grading to crawling traces without stops on the way (*Cruziana*).

HIEROGLYPHS OF CRAWLING TRACES

Cruziana d'Orbigny, 1842

After Lessertisseur (1955) and Seilacher (1960), the name *Cruziana* d'Orbigny is used by the writers for hieroglyphs that have a strongly elongated path-like shape, and are covered by minute herring-bone shaped ridges (*Crossochorda* Schimper, 1879, sensu Dżułyński & Żak, 1960).

Material. — Within the Wielka Wiśniówka ichnocoenosis the *Cruziana* type of hieroglyphs are three times less frequent than the *Rusophycus* type, and the excellently preserved specimens, encountered on the underside of the quartzitic sandstone layers (pl. IV-VII) are extremely rare. A total of only 20 specimens has been collected by the writers. Most of them are very incompletely preserved owing the same processes that impeded the preservation of the *Rusophycus* hieroglyphs. Forms on the lamination planes of siltstones are very indistinct and fragile, so that their extraction meets with considerable difficulty. In size and shape they resemble forms shown in pl. IV-VII.

Description. — The *Cruziana* type hieroglyphs vary in length. The longest specimen among those with two natural terminations (pl. IV) has a length of 16 cm, while the longest one of all the specimens collected is 24 cm in length. The latter form whose fragment with one natural termination is figured in pl. VII, was found on a slab on the heap; it lacks the other termination. Its entire length may be estimated at approx. 30 cm. The most common width ranges from 2.5 to 3.5 cm; it may change along the trackway hieroglyph. The smallest form is 5 cm long and approx. 1.5 cm wide.

The particular hieroglyphs are straight (pl. VI), slightly arched over a part (pl. V) or over the whole of length (pl. IV, VII). Plate VI shows two straight trackway hieroglyphs crossing each other; the preserved details suggest that the longer track is older. The hieroglyph height corresponds to the depth of the groove dug out by the animal; it also varies from a few millimetres to 1 cm, even along the same trackway hieroglyph. The greatest height (18 mm) is attained at midway of the track shown in pl. VII.

Origin. — The *Cruziana* type hieroglyphs are interpreted as counterparts of the crawling traces of trilobites on the sea bottom, accompanied by digging up of the material (Holm, 1887; Abel, 1935; Lessertisseur, 1955; Seilacher, 1960, 1962). Herring-bone shaped ridges along the trackway are counterparts of trilobite appendages, while smaller, often double ridges on their surface are counterparts of claw traces — seen best in pl. IV and V. The ends of the bigger ridges are occasionally thickened (right side of the track hieroglyph in pl. V) probably owing to the slime coating on the trilobites' claws and appendages (Seilacher, 1955). The appendage traces may reach to the very border of the trackway (pl. V) or break off before attaining it (pl. IV, VI, VII). This depends on the strength used in the digging up of the material. The borders of the particular tracks may be smooth (pl. IV) or more or less distinctly rimmed (pl. VI, VII, partly V). This rim is the counterpart of the groove imprinted by the protruding lateral processes of trilobite segments or by the lower portions of the cephalon — possibly also the limbus and the cheek lobes. The rim is generally encountered on higher hieroglyphs, while it vanishes on the lower or gradually lowering ones (centre of the right side border of the trackway in pl. V). The latter hieroglyphs correspond to the shallowing groove imprinted by the crawling trilobite when the animal's flanks no longer touched the sea floor.

The morphological details described above are variously indicated on the particular track hieroglyphs, moreover, they may also change along the same trackway. This is readily explained because the minor features of the shape of the original grooves were controlled by many factors resulting from the general character of the bottom sediment, its consolidation and, primarily, differences in the trilobite behaviour during crawling, the depth of burrowing and the speed of this process, as well as the weight and agility of the individual animals. The general resemblance of all the track hieroglyphs of the *Cruziana* sp. from Wielka Wiśniówka reasonably suggests that they were all imprinted by the same animals. On the other hand, the rather strong differentiation of these tracks warns us to exercise strong caution in the choice of nomenclature for trilobite traces, similarly as in the case of traces of other animals. This caution is indispensable because of differences observable even between the particular parts of the same trackway, so much so that, were they found as isolated specimens, they might be mistaken for quite separate forms and given different "specific" names.

No fragments of layers, containing both the *Rusophycus* and *Cruziana* types of hieroglyphs, have so far been found at Wielka Wiśniówka, but their occurrence in adjoining layers of a given series reliably indicates that the two types of traces were imprinted by the same trilobites. The largest tracks (pl. IV-VII) were probably made by such trilobites which, resting quietly on the sea bottom, left the grooves of the dimension of the *Rusophycus* hieroglyphs shown in fig. 4-7 of pl. II. The maximum width of the *Rusophycus* hieroglyph is 4.5 cm (pl. II, fig. 8). It is 1 cm wider than the widest *Cruziana* hieroglyph, and its shape suggests that it resulted from the infilling of a groove laterally much widened, probably owing to the sideway movement of the animal. The central portion of this trace — most sharply outlined — is 3.5 cm wide, thus agreeing in width with the *Cruziana* forms. The smallest and the narrowest *Cruziana* hieroglyph is 1.5 cm in width and could have been imprinted by an animal of the size corresponding to the *Rusophycus* hieroglyph shown in fig. 2 of pl. II. No narrower *Cruziana* hieroglyphs have so far been found corresponding to the smallest *Rusophycus* hieroglyph (pl. II, fig. 1).

Occurrence. — The *Cruziana* type hieroglyphs are reported from the Cambrian in England, Sweden, Spain, the United States of North America and Pakistan (Seilacher, 1960).

HIEROGLYPHS OF THE TRACES OF STRIDING

Diplichnites Dawson, 1873

Hieroglyphs of the *Diplichnites* type are characterized by the wide spacing of the isolated ridges which are arranged after an approximately herring-bone pattern. They are the infillings of grooves made by trilobites which strode on with outstretched appendages and did not drag their bodies on the sea floor nor dig up the bottom material. Such hieroglyphs are extremely rare at Wielka Wiśniówka. The best specimen was collected by Dżułyński and Żak (1960, pl. 25, fig. 1). The writers' material contains only small fragments of such hieroglyphs observable on minor slabs of layers.

HIEROGLYPHS OF THE TRACES OF SIDEWAY MOVEMENT

Dimorphichnus Seilacher, 1955

The generic and specific name of *Dimorphichnus obliquus* was introduced by Seilacher (1955) for tracks imprinted by the sideway movement of trilobites, similarly as in the case of some living crustaceans, e.g. crabs. These track hieroglyphs, described by Seilacher from the

Lower Cambrian of Pakistan, are characterized by several sets of ridges, regularly repeated along the trackway.

The material from Wielka Wiśniówka contains only track hieroglyphs consisting of one or more sets of ridges (Harksiegel; Seilacher, 1962) which occur sporadically on the underside of some layers. The best preserved specimen is shown in fig. 1 of pl. VIII where two track hieroglyphs are observable. Most likely they were imprinted by two trilobite individuals advancing sideway just above the sea floor which they occasionally grazed. The first trackway (central upper part of figure) consists of only one set of ridges slightly spread to the right. These extensions represent the counterparts of grooves grazed by claws that were probably coated with slime. The thinning out of the extensions to the left of the ridges indicates that the trilobite moved from right to left (see Seilacher's reconstruction, 1955, fig. 3). The other trackway on the specimen (pl. VIII, fig. 1 — left bottom of figure) consists of 4 sets of ridges, the most left set being upcurved. This curve represents the trace of the animal as it turned away from the formerly followed course. Another, somewhat similar trackway of a trilobite, changing its former course as it advanced sideway, is shown in pl. VIII, fig. 2.

Specimens of track hieroglyphs of trilobites moving sideway, which were found at Wielka Wiśniówka, differ from the tracks of *Dimorphichnus obliquus* Seilacher from Pakistan in that they are much more fragmentary. Hence they are here identified as *Dimorphichnus* sp.

OTHER TRILOBITE TRACK HIEROGLYPHS

The most common forms here are tiny isolated ridges occurring en masse as counterparts of grooves imprinted by appendages of trilobites. These track hieroglyphs that are arranged at random often cover a considerable area of the surface of layers. They were formed in places crowded with trilobites where these animals were swimming just above the sea floor now and then touching the bottom with their appendages.

Some other traces, also mostly appendage imprints, were likewise made while the animal swam very close to the sea bottom, sometimes touching it or even resting down. These forms sometimes resemble rudimentary hieroglyphs of the *Cruziana*, *Diplichnites* or *Dimorphichnus* type. The resemblance is obviously due to affinities in the mode of the animal's movements. A number of irregular hieroglyphs somewhat resemble forms described by Fenton and Fenton (1937). They were probably imprinted in the sediment by trilobites burrowing for food or to lay their eggs.

NON-TRILOBITE COMPONENTS OF THE ICHNOCOENOSIS

Within the Wielka Wiśniówka ichnocoenosis, besides the trilobite traces, there are structures due to the activity of other animals, preserved mostly as hieroglyphs. Among them are: *Bergaueria perata* Prantl, *Diplocraterion* sp. and numerous minute enigmatic forms.

Bergaueria perata Prantl, 1945

Description of material. — The *Bergaueria perata* Prantl hieroglyphs occur sporadically on the underside of relatively thin quartzitic sandstone layers. So far two fairly well preserved isolated specimens (pl. IX, fig. 1, 2) have been found on slabs of layers; a few other available specimens are badly preserved. Of the two satisfactorily preserved specimens the larger one, 20 mm in diameter (pl. IX. fig. 1), has its end damaged, while the smaller one, 16 mm in diameter and 8 mm in height (pl. IX. fig. 2) is nearly complete.

The hieroglyphs collected by the late Professor Jan Samsonowicz several years ago from the Upper Cambrian deposits at Marcinkowice near Opatów (eastern part of the Holy Cross Mountains) were much better preserved, but they were never described. This specimen, housed at the Museum of Geological Institute in Warsaw, was figured by Kotański (1959, p. 318, fig. 121) as sandstone with bagshaped hieroglyphs of enigmatic origin. Thanks to the courtesy of Dr Z. Kotański the photograph of the above specimen is published in the present paper (pl. IX. fig. 3).

The Marcinkowice specimen, with *Bergaueria perata* Prantl hieroglyphs, is a 9 × 12 cm fragment of the underside of a quartzitic sandstone layer. This fragments bears on its surface 12 characteristic hieroglyphs, shaped like small bags or bulbs, well rounded off at the ends. One half of them are incomplete, their ends being badly damaged. The average diameter of the hieroglyphs is 20 mm, the average height of the completely preserved forms is 10 mm. The individual hieroglyphs are circular in section, with the surface generally smooth, bearing rather faint concentric rings and a shallow, occasionally irregular, terminal depression. Some forms have several indistinct ribs radiating from or slightly oblique to the vertical axis of the hieroglyph. Within the preserved slab of the layer, the hieroglyphs occur singly, though in two places it may be observed that two hieroglyphs join by means of a flat, centrally constricted mound.

The morphological details of the Wielka Wiśniówka forms resemble those of the Marcinkowice specimens, but they are less clear owing to a worse state of preservation.

Origin. — The *Bergaueria perata* Prantl hieroglyphs are very rare. Their origin has been more fully investigated by Pranti (1945). According to that author, the hieroglyphs he studied were formed by the infilling of bag-shaped holes, probably made by some anthozoans whose mode of life resembled that of the living sea anemones or other recent anthozoan sand burrowers, or possibly also by other similarly constructed animals, which led a similar life. Some of the living sea anemones make holes which, if infilled, might result in a type of hieroglyphs strongly resembling *Bergaueria perata*. Such sea anemones in the first place contain representatives of the genus *Cereus* (cf. Lessertisseur, 1955, fig. 17A, and p. 31) encountered i.a. in shallow water off the French coasts. Recently, Seilacher (1956) has also accepted that interpretation of the *Bergaueria perata* hieroglyphs. *Kulindrichnus langi* Hallam from the Sinemurian beds of Dorset in England, which are relatively large forms, up to 75 mm in diameter and 130 mm in length, have been also similarly interpreted (Hallam, 1960).

A closer morphological analysis of the *Bergaueria perata* Prantl hieroglyphs suggests that their faintly marked concentric rings may correspond to traces of sea anemones due to the alternating contraction and dilatation of their bodies. The shallow depression at the ends of hieroglyphs probably fit into the traces of the device by which the anemones are attached to the sea floor. The fact of the preservation of the above details on hieroglyphs from the Holy Cross Mountains and from other areas, might reasonably indicate that the sand layer did not bury the holes that persisted after the death of the animal but the animals themselves alife in their holes and thus caused their death. After the decay of the organic remains the holes were gradually filled in by the sand. It is to be noted here that forms from the Holy Cross Mountains and from the Ordovician of Bohemia (Prantl, 1945) are encountered in more fine-grained silt or clay sediment than that which forms and covers the hieroglyphs.

Occurrence. — The *Bergaueria perata* Prantl hieroglyphs are known from the Lower Cambrian of northern Spain (Seilacher, 1962, personal comm.), the Middle Cambrian of the Grand Canyon, Colorado Bright Angel Shale (McKee, 1945; Seilacher, 1956) and from the Upper Llandeilo (Ordovician) Chrustenice beds of Bohemia (Prantl, 1945). The specimens so far recorded from the Cambrian of the Grand Canyon (McKee, 1945) and from the Holy Cross Mountains, approx. 20 mm in diameter, are smaller than the Ordovician forms which have a diameter from 35 to 45 mm (Prantl, 1945).

The facial development of the Upper Cambrian beds in the eastern part of the Holy Cross Mountains, near Opatów (Samsonowicz, 1934, 1956; Radwański & Roniewicz, 1962), comprising the *Bergaueria perata* hieroglyphs locality at Marcinkowice, very much resembles the facial conditions prevailing in the vicinity of Wielka Wiśniówka in the western part of the Holy Cross Mountains. Owing, however, to lack of palaeontological evidence, the contemporaneity of sediments in these two regions is still an open question (Radwański & Roniewicz, 1962). *Cruziana, Planolites* and *Arenicolites* are organic hieroglyphs previously reported from the vicinity of Opatów (Samsonowicz, 1934).

Diplocraterion Torell, 1870

Description of material. — The *Diplocraterion* Torell hieroglyphs are common forms whose mass occurrence may be observed on the surface of some layers (pl. X, fig. 1). They occur mostly in minor series of thin quartzitic sandstone layers alternating with dark, nearly black claystones and clays. They are much rarer within the lighter deposits where they occur singly, sometimes jointly with *Bergaueria perata* Prantl (pl. IX, fig. 1). The *Diplocraterion* hieroglyphs are in the shape of a small rope-like elevation that issues from and re-enters the underside of the sandstone layer.

Origin. — The formation of the *Diplocraterion* type of hieroglyphs is probably due to the filling in by sand of U-shaped channels burrowed by slime-eaters, possibly the annelids, which searched for food in dark sediments abounding in decayed organic remains. These channels are relatively shallow since they represent only the lower fragments of U-shaped loops whose upper parts together with the funnel aperture had been destroyed by paenecontemporaneous erosion prior to being infilled by sand. A similar process of the erosion of the upper portions of *Diplocraterion* was traced by Goldring (1962) on the forms from clastic Famennian deposits in North Devon, England.

Occurrence. — The *Diplocraterion* sp. hieroglyphs are known from the Cambrian strata in the United States of North America (Seilacher, 1956), Sweden (Westergård, 1931) and Spain (Seilacher, 1962, personal comm.).

Enigmatic forms

These are minute, extremely diverse and locally numerous hieroglyphs, a few millimetres to 1 cm in length. They are the counterparts of isolated depressions, possibly the feeding places of some more closely unidentifiable animals, occurring in sediments with decaying organic remains or in the faecales of other animals. Several very characteristic forms, shaped like an elongated and slightly twisted drop, are shown in pl. X, fig. 2.

RECAPITULATION

An analysis of the forms described above points to the strong diversity of the traces of the life activities of trilobites encountered within the Upper Cambrian sediments at Wielka Wiśniówka in the Holy Cross Mountains. These traces primarily represent hieroglyphs of the traces of rest (*Rusophycus* sp.), of crawling along the sea floor and digging up the bottom material (*Cruziana* sp.), of striding on the sea bottom (*Diplichnites* sp.), and of sideway walking and swimming just above the bottom occasionally grazed by the trilobite (*Dimorphichnus* sp.), finally very faint traces of burrowing. Illustrations in the present paper show the strong shape variations of these forms. Apart from subsequent sinking processes the causes of the shape variability are probably differences in the animals' behaviour during their particular life activities. Hence, it seems that trilobite traces, similarly as those of other animals, must not be considered statically by means of specific and generic assignments or the introduction of new names, but in the light of the extent of all their variations and mutual gradations. During the description of the material the writers tried to avoid the use of such names, even in the case of forms strongly differing in shape (*Rusophycus* sp.). The special names (*Rusophycus* sp., *Cruziana* sp., *Diplichnites* sp., *Dimorphichnus* sp.) have been used not so much for the 4 types of traces with strictly determined shape, as for the 4 groups of traces connected with the 4 above named life activities of trilobites which may now be interpreted on fossil material. The writers look on their material as on one entity — a trace assemblage or ichnocoenosis. An ichnocoenosis evidently results from those life activities only whose traces persisted in the sediment. In turn this depends not only on the nature of the life activities, but likewise on the character of the sediment. Hence, several various ichnocoenoses may result from one and the same biocoenosis depending on the facial variability of sediments.

On the basis of the trilobite ichnocoenosis from Wielka Wiśniówka some suggestions may be made concerning the trilobite mode of life within the Upper Cambrian sea of the Holy Cross Mountains. On the one hand we observe an abundance of the traces of rest and the relative scarcity of the traces of crawling, together with traces made by trilobites swimming just above the sea bottom and sporadically grazing it; on the other hand, there is a lack of distinct traces of burrowing on the sea floor. Both observations probably indicate that the trilobites here considered were free-swimming forms which settled down on the sea floor mainly for the rest. It may also be inferred that for their places of rest, the trilobites selected areas of the sea bottom without decaying organic substances. This is suggested by the fact that the dark sediments so characteristically marked by traces of slime-eaters (*Diplocraterion* sp. hieroglyphs) were obviously avoided by trilobites. Though it is hardly possible to determine whether these trilobites are referable to different species, genera or families it is reasonably supposed that these forms displayed similar mode of life and life-conditions which may be largely due to the adaptation to the prevailing environment. Future investigations at Wielka Wiśniówka may lead to a better knowledge concerning the composition, variability and dependence on facial conditions of the trilobite ichnocoenosis there. These data will in turn help to clear up some interesting trilobite problems.

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ANDRZEJ RADWAŃSKI & PIOTR RONIEWICZ

GÓRNOKAMBRYJSKA ICHNOCENOZA TRYLOBITOWA Z WIELKIEJ WIŚNIÓWKI W GÓRACH ŚWIĘTOKRZYSKICH

Streszczenie

Osady górnego kambru Wielkiej Wiśniówki w Górach Świętokrzyskich, które były przedmiotem opracowań sedymentologicznych Dżułyńskiego i Żaka (1960) oraz autorów (Radwański & Roniewicz, 1960), zawierają charakterystyczny zespół bardzo różnorodnych śladów związanych z działalnością trylobitów i innych zwierząt. Niektóre z tych śladów zostały już pokrótce opisane przez wymienionych autorów. Niniejsza praca jest próbą szczegółowego rozpatrzenia zagadnień związanych z licznym występowaniem całego zespołu śladów ogranicznych, czyli ichnocenozy (Dawitaszwili, 1945). Rozpatrzono również zagadnienia dotyczące trybu życia trylobitów, których ślady są najbardziej charakterystycznym składnikiem tej ichnocenozy, jak również warunki umożliwiające zachowanie się wszystkich śladów zwierzęcych w osadzie.

Najczęstszymi śladami związanymi z działalnością trylobitów są hieroglify (terminologia poszczególnych śladów, w zależności od ich położenia na dolnych lub górnych powierzchniach ławic, została podana na tabeli, s. 264), wśród których wyróżniono: hieroglify śladów spoczynku — *Rusophycus* sp. (pl II), śladów pełzania po dnie połączonego z jego rozgrzebywaniem — *Cruziana* sp. (pl. IV—VII), śladów stąpania po dnie — *Diplichnites* sp., śladów kroczenia lub pływania bokiem tuż ponad dnem, w czasie którego trylobit dotykał dna — *Dimorphichnus* sp. (pl. VIII), oraz niewyraźnych śladów grzebania. Wymienione ślady, jak widać z ilustracji, miały bardzo zmienne kształty, co — pominąwszy późniejsze deformacje, głównie pogrzęzanie — wywołane było różnym zachowaniem się zwierząt w czasie wykonywania poszczególnych czynności. Z tego też względu autorzy stosują nazwy specjalne: *Rusophycus* sp., *Cruziana* sp., *Diplichnites* sp., *Dimorphichnus* sp. — w dość szerokim zakresie, nie tyle dla czterech rodzajów śladów o ściśle zdefiniowanym kształcie, co dla czterech grup śladów związanych z czterema wyżej wymienionymi czynnościami życiowymi trylobitów, które można obecnie interpretować na podstawie materiału kopalnego. Zebrany materiał autorzy traktują jako jedną całość — czyli ichnocenozę, którą nazywają ichnocenozą trylobitową ze względu na dominujący udział śladów pozostawionych przez trylobity. Obok tych śladów, w obrębie ichnocenozy spotyka się ślady związane prawdopodobnie z działalnością ukwiałów (hieroglify *Bergaueria perata* Prantl; pl. IX, fig. 1, 2) oraz zwierząt mułożernych, być może pierścienic (hieroglify *Diplocraterion* sp., pl. X, fig 1). Istnieją także drobne hieroglify zagadkowego pochodzenia (pl. X, fig. 2).

Na podstawie ichnocenozy trylobitowej z Wielkiej Wiśniówki można spróbować wyciągnąć pewne wnioski co do trybu życia trylobitów w morzu górno-kambryjskim Gór Świętokrzyskich. Fakt występowania dużej ilości śladów spoczynku, a stosunkowo mniejszej śladów pełzania, oraz obecność śladów pozostawionych przez trylobity pływające tuż ponad dnem i chwilami zawadzające o nie, z drugiej zaś strony brak wyraźnych śladów grzebania w osadzie, — zdają się wskazywać, że trylobity tutaj żyjące należały raczej do form pływających, a przebywających na dnie przede wszystkim w celu spoczynku. Można również zauważyć, że jako miejsce spoczynku trylobity wybierały dno nie zanieczyszczone gnijącymi substancjami organicznymi, gdyż wyraźnie unikały ciemnych osadów, w których tak charakterystyczne są ślady żerowania zwierząt mułożernych (hieroglify *Diplocraterion* sp.). Aczkolwiek nie można rozstrzygnąć, czy były to trylobity należące do różnych gatunków, rodzajów i rodzin, można z dużym prawdopodobieństwem przypuścić, że były to formy o podobnym trybie życia i podobnych wymaganiach życiowych, co oczywiście w znacznej mierze wywołane było przystosowaniem do panujących warunków środowiskowych. Być może, że przyszłe badania w Wielkiej Wiśniówce pozwolą dokładniej ustalić warunki występowania ichnocenozy trylobitowej, jej skład, zmienność i zależność od warunków facjalnych, co z kolei może rzucić większe światło na interesujące problemy dotyczące samych trylobitów.

OBJAŚNIENIA DO ILUSTRACJI

Pl. I

Ogólny widok fragmentu serii osadów górno-kambryjskich, odsłaniających się w kamieniołomie Wielka Wiśniówka k.Kielc.

Pl. II

Fig. 1—8. Hieroglify *Rusophycus* sp. (objaśnienia w tekście).

Pl. III

Fig. 1. Ślad spoczynku trylobita na górnej powierzchni ławicy piaskowca pokrytej ripplemarkami.

Fig. 2. Hieroglif śladu miejsca spoczynku trylobita. Widać 5 kolejnych miejsc spoczynku, częściowo nakładających się na siebie.

Pl. IV

Hieroglif *Cruziana* sp. z dwoma naturalnymi zakończeniami.

Pl. V

Hieroglif *Cruziana* sp. o zmiennej wysokości, odpowiadającej pogłębianiu się lub spłycaniu bruzdy tworzonej przez pełznącego trylobita.

Pl. VI

Dwa hieroglify *Cruziana* sp. krzyżujące się wzajemnie.

Pl. VII

Fragment dolnej powierzchni ławicy piaskowca z dwoma hieroglifami *Cruziana* sp.

Pl. VIII

Fig. 1. Fragment hieroglifu *Dimorphichnus* sp.

Fig. 2. Fragment hieroglifu utworzonego przez trylobita skręcającego w czasie poruszania się bokiem.

Pl. IX

Fig. 1. Hieroglif *Bergaueria perata* Prantl oraz 3 hieroglify *Diplocraterion* sp.

Fig. 2. Inny hieroglif *Bergaueria perata* Prantl, o mniejszej średnicy; × 1,25.

Fig. 3. Grupa hieroglifów *Bergaueria perata* Prantl, znaleziona przez prof. J. Samsonowcza w osadach górnego kambru w Marcinkowicach k.Opatowa. (Okaz w zbiorach Inst. Geolog. w Warszawie).

Pl. X

Fig. 1. Hieroglify *Diplocraterion* sp.

Fig. 2. Nieokreślone bliżej hieroglify organiczne.

Okazy wielkości naturalnej, z wyjątkiem pl. IX, fig. 2

АНДРЖЕЙ РАДВАНЬСКИ и ПЁТР РОНЕВИЧ

ВЕРХНЕ-КЕМБРИЙСКИЙ ТРИЛОБИТОВЫЙ ИХНОЦЕНОЗ ИЗ ВЕЛЬКОЙ ВИСЬНЮВКИ В СВЕНТОКРЖИСКИХ ГОРАХ (ПОЛЬША)

Резюме

Отложения верхнего кембрия Велькой Висьнювки в Свентокржиских Горах, которые были предметом седиментологических исследований Джулыньского и Жака (1960), а также авторов настоящей статьи (Радваньски и Роневич, 1960), содержат характерный комплекс весьма разнообразных следов связанных с деятельностью трилобитов и других животных. Некоторые из них уже вкратце описаны упомянутыми авторами. Настоящая работа является попыткой подробного рассмотрения вопросов связанных с многочисленным выступанием целого комплекса органических следов или ихноценоза (Давиташвили, 1945). Рассмотрены также вопросы касающиеся образа жизни трилобитов, которых следы являются наиболее характерной частью этого ихноценоза, равным образом как и условия позволяющие на сохранение следов животных в отложениях.

Наиболее часто встречаемыми следами связанными с жизнедеятельностью трилобитов являются иероглифы (терминология отдельных следов в зависимости от их расположения на нижних или верхних поверхностях пластов показана на таблице, стр. 264), среди которых выделено: иероглифы следов покоя — *Rusophycus* sp. (пл. II), следов ползания по дну с его разгребанием — *Cruziana* sp., (пл. IV-VII), следов ступания по дну — *Diplichnites* sp., следов шагания или плавания боком непосредственно над дном, во время которого трилобит касался дна — *Dimorphichnus* sp. (пл. VIII), и неотчетливых следов рытья. Перечисленные следы, как видно на иллюстрации, имели очень изменчивую форму, что кроме позднейших деформации, главным образом связанных с увязанием, было вызвано разным поведением животных при выполнении разных действий. Потому авторы применяют особые названия: *Rusophycus* sp., *Cruziana* sp., *Diplichnites* sp., *Dimorphichnus* sp. в довольно широких границах, не для четырех видов следов точно определенной формы, но для четырех групп следов связанных с четырьмя выше перечисленными проявлениями жизнедеятельности трилобитов, которые можно теперь интерпретировать на ископаемом материале. Собранный материал рассматривается авторами как целое или ихноценоз, который называют трилобитовым в виду преобладания следов оставленных трилобитами. Рядом с этими следами, в пределах ихноценоза встречаются следы связанные по всей вероятности с деятельностью актиний (иероглифы *Bergaueria perata* Prantl — пл. IX, фиг. 1, 2,) и мулоедов, вероятно аннелид (иероглифы *Diplocraterion* sp. — пл. X, фиг. 1). Существуют тоже небольшие иероглифы загадочного происхождения (пл. X, фиг. 2).

На основании трилобитового ихноценоза из Велькой Висьнювки можно попытаться сделать некоторые выводы относительно образа жизни трилобитов

в верхне-кембрийском море Свентокржиских Гор. Наличие большого количества следов покоя, а относительно менее многочисленных следов ползания, далее — присутствие следов оставленных трилобитами плавающими тут же над дном и иногда прикасающимися к нему, а с другой стороны отсутствие отчетливых следов рытья в осадке, указывает повидимому на то, что живущие тут трилобиты были плавающими формами пребывающими на дне прежде всего для отдыха. Можно также заметить, что для отдыха трилобиты выбирали дно незагрязненное гниющим органическим веществом, так как несомненно избегали темных осадков, в которых характерными являются следы просверленные животными поедающими донный осадок (иероглифы *Diplocraterion* sp.). Хотя невозможно решить, были ли это трилобиты принадлежащие разным видам, родам или семействам, очень правдоподобно предположение, что были это формы со сходным образом жизни и сходными жизненными требованиями, что конечно в большой степени было вызвано приспособлением к господствующим условиям среды. Возможно, что дальнейшие исследования в Велькой Висьнювке позволят установить более подробно условия выступания трилобитового ихноценоза, его состав, изменчивость и зависимость от фациальных условий, что в свою очередь может бросить больше света на интересные вопросы касающиеся самих трилобитов.

PLATES

Pl. I

Fragment of a series of Upper Cambrian sediments cropping out in the Wielka Wiśniówka quarry, near Kielce.

Phot. P. Roniewicz


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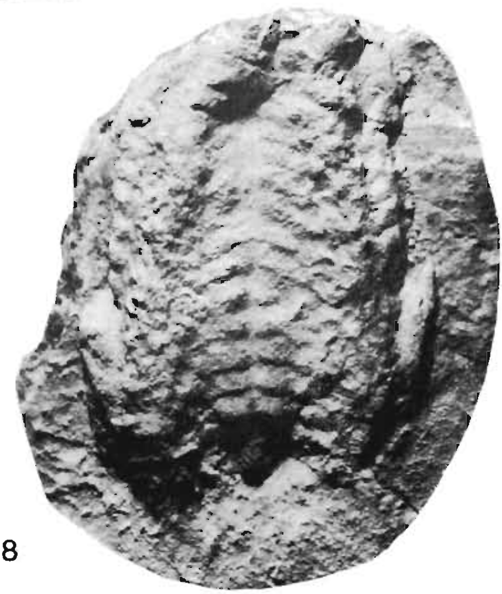
8

Fig. 1 — 4 *phot. B. Drozd* Fig. 5 — 8 *phot. J. Błaszyk*

Pl. II

Fig. 1-8. *Rusophycus* sp. hieroglyphs (explanations in the text); nat. size.

Pl. III

Fig. 1. True trace of a trilobite resting on the upper side of a ripple-marked sandstone layer; nat. size.

Fig. 2. Hieroglyph of the trilobite trace in change of the rest place, showing 5 consecutive partly overlapping rest places; nat. size.

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Fig. 1 — *phot. J. Błaszyk* Fig. 2 — *phot. S. Wdowiak*

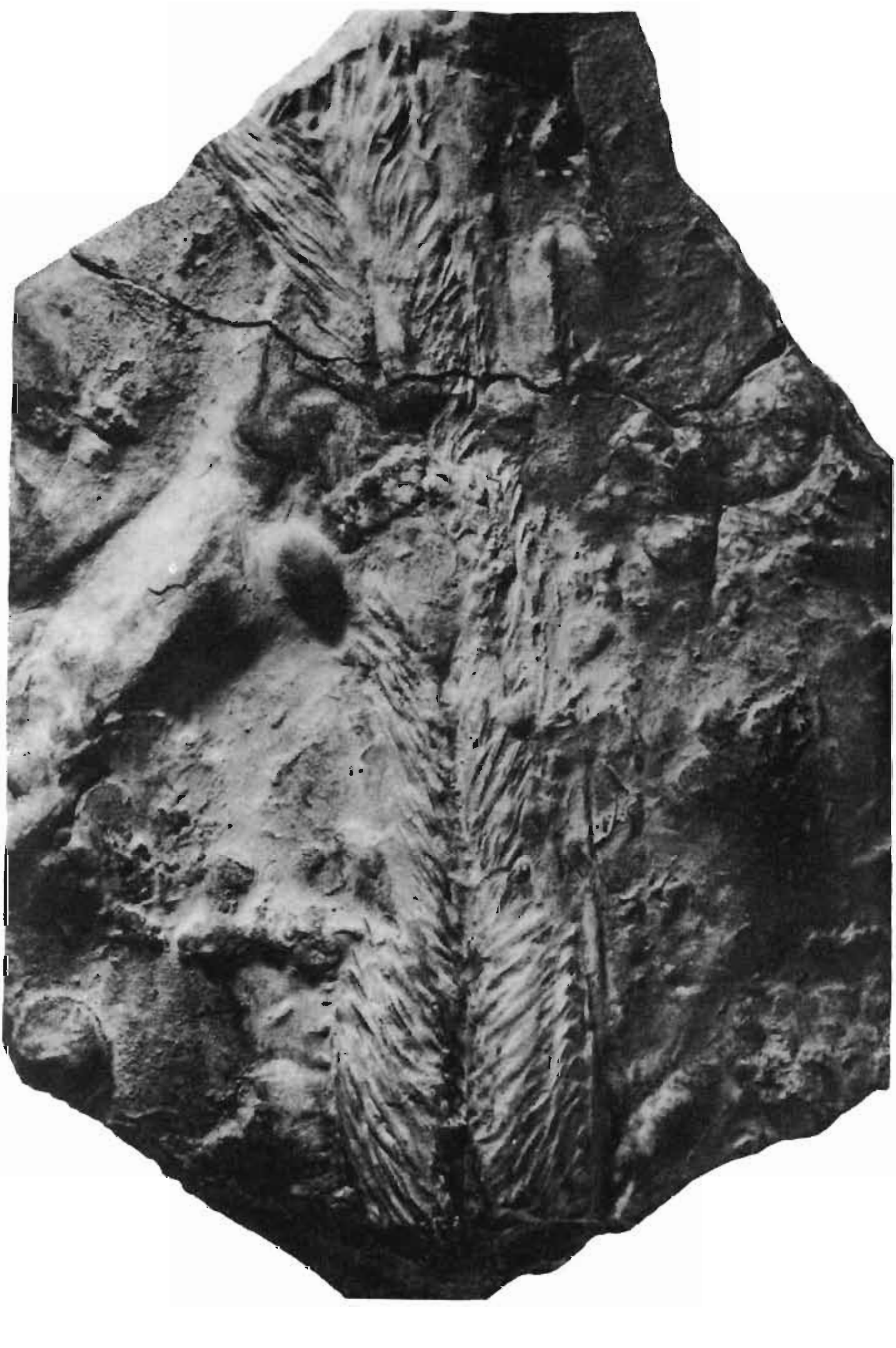
Phot. B. Drozd

Pl. IV

Cruziana sp. hieroglyph provided with two natural terminations; nat. size.

Pl. V

Cruziana sp. hieroglyph showing varying height, fitting into the shallower or deeper groove, imprinted by the crawling trilobite; nat. size.



Phot. J. Błaszyk

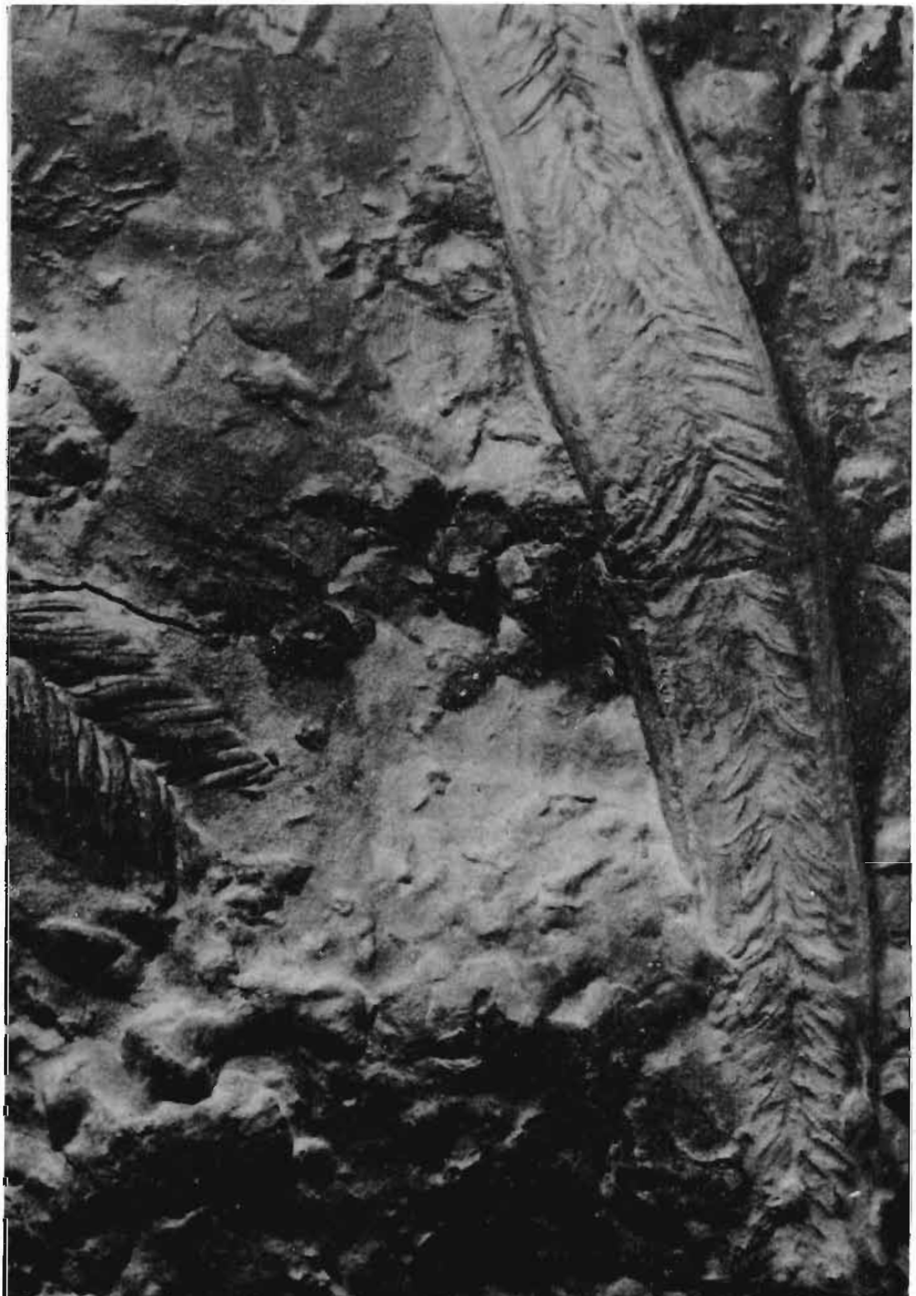
Phot. J. Błaszyk

Pl. VI

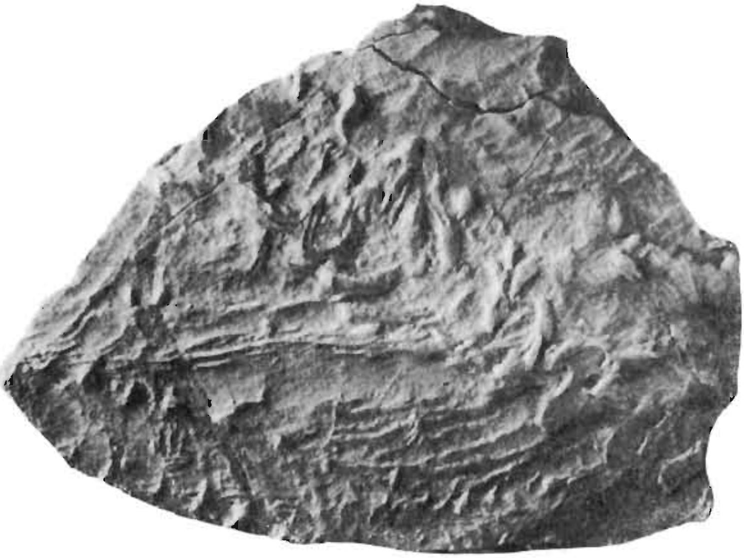
Two *Cruziana* sp. hieroglyphs, crossing each other, the longer track is older; nat. size .

Pl. VII

Fragment of the underside of a sandstone layer with two *Cruziana* sp. hieroglyphs; nat. size.



Phot. J. Błaszyk



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Phot. J. Błaszyk

Pl. VIII

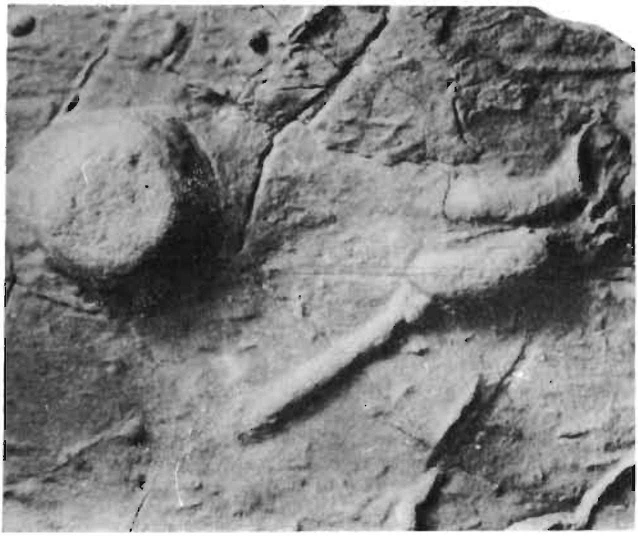
Fig. 1. Fragment of a *Dimorphichnus* sp. hieroglyph; nat. size.
Fig. 2. Fragment of a track hieroglyph of a trilobite changing its course during sideway movement; nat. size.

Pl. IX

Fig. 1. One *Bergaueria perata* Prantl hieroglyph and three *Diplocraterion* sp. hieroglyphs; nat. size.

Fig. 2. Another *Bergaueria perata* Prantl hieroglyph, smaller in diameter; × 1.25.

Fig. 3. A group of *Bergaueria perata* Prantl hieroglyphs found by Prof. J. Samsonowicz in Upper Cambrian sediments at Marcinkowice, near Opatów; nat. size. (From the collection of the Polish Geological Institute in Warsaw).



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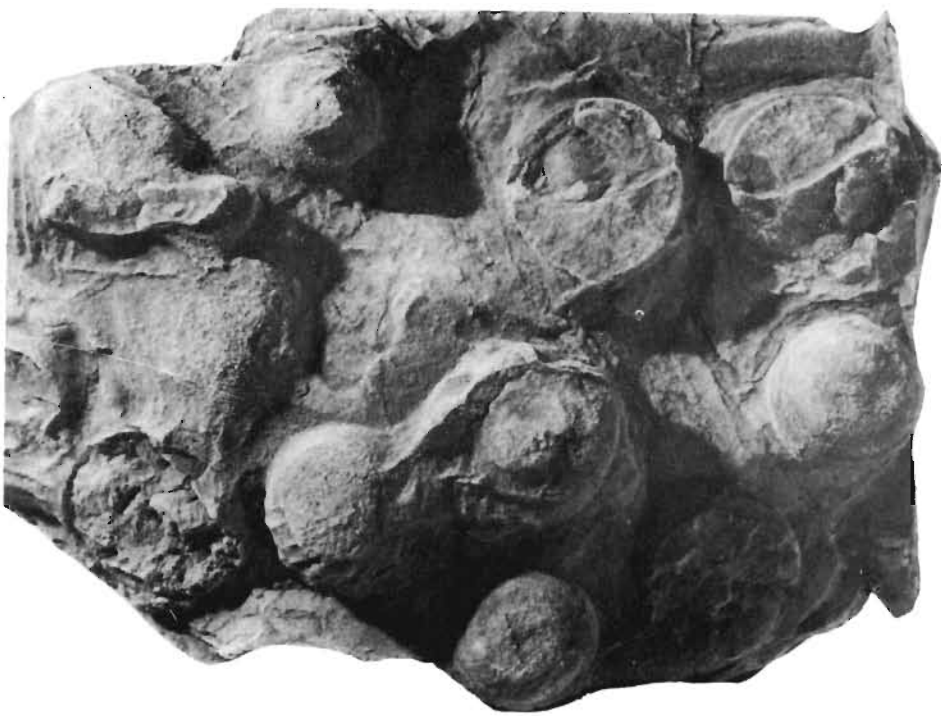

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Fig. 1, 2 — *phot. M. Mazek*

Fig. 3 — *phot. J. Błaszyk & M. Czarnocka*

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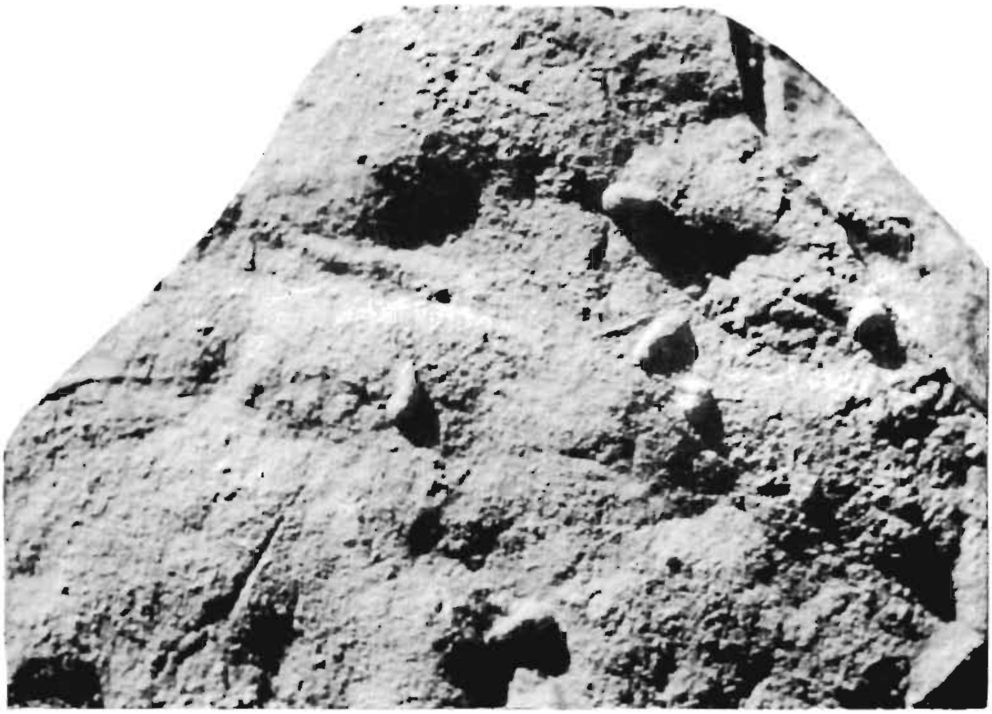

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Fig. 1 — *phot. J. Błaszyk* Fig. 2 — *phot. S. Wdowiak*

Pl. X

Fig. 1. *Diplocraterion* sp. hieroglyphs; nat. size.
Fig. 2. Enigmatic forms of hieroglyphs; nat. size.