Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic)

Ichnofosilie paseckých břidlic (spodní kambrium, Česká republika) (Czech summary)

(3 text-figs., 8 plates)

RADEK MIKULÁŠ

Geologický ústav Akademie věd ČR, Rozvojová 135, 165 00 Praha 6, Czech Republic

The Paseky Shale (Lower Cambrian, Central Bohemia) yielded the oldest known non-marine or brackish ichnoassemblage. It consists mostly of fodinichnia and repichnia of endemic arthropods *Kodymirus vagans* Chlupáč et Havlíček, 1965 and *Kockurus grandis* Chlupáč, 1995. These traces were attributed to ichnotaxa *Monomorphichnus biserialis* ichnosp. nov., *M. semilineatus* ichnosp. nov., *M. multilineatus* Alpert, 1976, *M. lineatus* Crimes et al., 1977, *M. bilinearis* Crimes, 1970, *?Rusophycus* ichnosp. A, *?R.* ichnosp. B, *?Dimorphichnus* ichnosp., and *Diplichnites* ichnosp. Presence of non-arthropod fauna is suggested only by finds of *?Bergaueria* ichnosp. and ?bromalites ichnogen. indet. Except for *M. lineatus* and *M. multilineatus*, ichnotaxa occurring typically in the Cambrian marine environments are not present.

Key words: Lower Cambrian, ichnofossils, arthropod traces, nonmarine settings, systematic ichnology, Barrandian area

Introduction

The project of investigation of the Paseky Shale (Early Cambrian) was motivated mostly by the peculiarity of the macrofauna being the oldest known from the Czech Republic and the oldest known of suspected non-marine environments at all (Chlupáč 1995, this volume). Besides the arthropods *Kodymirus vagans* Chlupáč et Havlíček, 1965, *Kockurus grandis* Chlupáč, 1995 and *Vladicaris subtilis* Chlupáč, 1995, microfossils (Fatka - Konzalová 1995) and trace fossils were also found. The aim of this paper is a systematic description of fossil traces and subsequent conclusions for a presumed sedimentary environment of the Paseky Shale.

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Geological setting and preservation of traces

The Paseky Shale is a thin but persistent unit within the thick Lower Cambrian siliciclastic sequence of inferred continental origin. Sharp lower limit of the Paseky Shale indicates a regional event marked by temporal dominance of aleuropelitic sedimentation under probable restricted marine influence (brackish lagoon) (Chlupáč et al. 1995, this volume).

Among the five outcrops of the Paseky Shale studied in detail (Chlupáč et al. 1986), only the locality Mt. Kočka yielded finds of trace fossils. Here, the finds are restricted to ca. 3 m thick layer of light green, olive-green and grey-green, markedly laminated shale, roughly 3-5 m above the base of the member. The same layer yielded also fauna with strongly prevailing *Kodymirus* (layers No. 1-3 in Fig. 5, Chlupáč et al. 1995, this volume).

Trace fossils are usually preserved as very low convex hyporeliefs (or their counterparts - concave epireliefs) on bedding planes of finely laminated shales to silty shales. Preservation of exichnial traces in such rather monotonous fine-grained sediments is given by an unusual coincidence of local factors - substrate cohesion, water dynamics, abrupt covering by a suitable material. Fine exichnia are practically absent from most marine, shale-dominated formations of the Barrandian Early Palaeozoic (such as Jince Formation of the Middle Cambrian, Klabava, Šárka, Bohdalec or Zahořany Formations of the Ordovician). On the contrary, limnic environment of the late Carboniferous in the Radnice Basin enabled preservation of similar delicate traces in very fine-grained sediments (Ovčín locality, Turek 1989).

In some cases, morphologically simple exichnia (*Monomorphichnus, Dimorphichnus*) can be hardly distinguished from inorganic traces (e.g. chevron marks) which are also common in places. Among the criteria for the recognition of the non-ethologic structures, as published by Ekdale et al. (1984), the following can be applied for the material from the Paseky Shale: resemblance to primary inorganic sedimentary structures; non-uniform size and/or shape of multiple structures; strict preferred orientation. But not all the structures can be distingiushed with certainty.

Systematic ichnology

Bergaueria Prantl, 1946
?Bergaueria ichnosp.

Pl. IV, figs. 1-8; Pl. V, figs. 1-2, 5-6

Material: 20 specimens.

Description: Circular depressions on bedding planes, usually very shallow, about 10 mm in diameter (6-15 mm). Subtle concentric ridges visible in specimen No. I 240 (Pl. IV, fig. 1); specimen No. I 241 (Pl. IV, fig. 2) shows low regular bulge in the centre. Surface smooth, without lining. Two specimens (I 249 and I 250; Pl. V, figs. 1 and 2) bear a delicate radial sculpture which, however, seems to be a result of compaction of the rock during diagenetic and anchimetamorphic processes.

Vertical sections necessary for study of the fill and of vertical dimensions were applied in six specimens. The fill is of the same character as surrounding rock, laminated, fine-grained, in some cases different in colour or in presence/absence of body fossil fragments. The section figured on Pl. V, fig. 6 shows that the colour of fill is identical with the colour of lamina underlying the trace. Therefore, passive filling of pits seems to be the most probable.

Original vertical dimension is difficult to determine. The orientated polished sections show that most specimens are preserved as convex hyporeliefs or concave epireliefs and the depth of the structures equals the depth of visible depressions (mostly less than 1 mm). In one case (I 254; Pl. V, fig. 6), however, the structure continues upwards to the rock and its total heigth is 4 mm. The above stated dimensions are undoubtedly much reduced by compaction during diagenesis; the degree of reduction is evidenced by planar preservation of body fossils. Therefore, the original vertical dimensions must be considered to have been several times larger than the measured dimensions.

Remarks: Preliminary placing of the structure to ichnogenus *Bergaueria* follows numerous papers discussing individual representatives of this ichnogenus (Prantl 1945, Crimes et al. 1977, Pickerill and Peel 1990, Fillion and Pickerill 1990) and the revision of "plug-shaped" traces by Pemberton, Frey and Bromley (1988). Most authors consider bergauerians as dwelling burrows or resting traces of anemones and related hydrozoans. *Bergaueria* occurs from Late Precambrian through all the Phanerozoic.

For relations to other problematica of the Paseky Shale see remarks of the following taxon ?bromalites ichnogen. indet.

? bromalites ichnogen. indet.

Pl. VII, figs. 1-8; Pl. VIII, figs. 1-4

Material: 26 finds.

Description: Oval to circular, often more or less irregular bodies filled with fragments of body fossils. Their diameter ranges usually between 10 and 30 mm, vertical dimension (after a strong diagenetic compaction) is very low (about 1 mm).

Remarks: Finds designated here as *?Bergaueria* ichnosp. and as ?bromalites form a morphologically continuous spectrum. One of its extremities is represented by shallow pits (or low protuberances in hyporeliefs) of circular outline, rarely with indication of concentric structures, filled by material corresponding to the overlying rock (typical *?Bergaueria* ichnosp.). The opposite end of the spectrum is formed by irregular, roughly oval clusters of minute fragments of body-fossils. These fragments are usually undeterminable, but in some cases larger parts can be determined as *Kodymirus vagans*, or, rarely, as *Vladicaris subtilis*.

In my opinion, continuity of this "spectrum" is a coincidence only; the "spectrum" itself is composed of two completely different ichnological phenomena. Using analogy with mostly younger finds from marine settings, the pits preserved as concave epireliefs (or their counterparts - convex hyporeliefs) can be classified as *?Bergaueria* ichnosp., i.e. as domichnia or cubichnia. Their tracemaker possibly had circular bases of bodies (as other makers of bergauerian-like traces, very probably hydrozoans). When left by the tracemakers, the pits were passively filled with available material. This material often contained fragments of arthropods, or a matter from floated clusters classified herein as bromalites. The pits were not strictly circular in all cases, some of them are oval; it makes them similar with the morphology of the presumed bromalites.

It is quite difficult to find criteria for the classification of larger, more or less irregular bodies filled with fragments of arthropods. Although the collected samples are not numerous enough for a statistical elaboration, it seems that larger "clusters" contain larger remains of arthropods in most cases. Another remarkable fact is the more or less uniform size of fragments within most of bodies. These facts lead to a hypothesis that a faecal material, mechanically crushed at the beginning of digestive process, is concerned. Dimesions of a tracemaker should influence both the size of "digestible" fragments and the overall volume of the excrement.

Hunt et al. (1994) note that coprolites, and particularly the invertebrate coprolites, represent the least studied group of ichnofossils. Hunt (1992) introduced the term bromalites for all the fossil products of digestion; regurgiatalites (material evacuated anteriorly from the oral cavity), cololites (gut contents fossilized in situ) and coprolites (fossilized faeces) are inferior categories. Hunt (1992) stated numerous criteria for the recognition of coprolites from another formations. The discussed bodies from the Paseky Shale seem to fulfil the following criteria: inclusions of organic matter, probable viscosity of original body (it was not floated), and distortion of laminae of the surrounding shale (as proved by vertical section).

Because of insufficient kowledge of invertebrate coprolites (resp. all the bromalites) also in less exceptional fossil communities, it is impossible to find a well-documented analogy of this material at present. Future study of invertebrate bromalites should contribute also to the knowledge of the Paseky Shale remains.

If the faecal material is really concerned in the described "clusters", its tracemaker must have been a relatively large organism. Explanation of the bodies as coprolites seems to be much more probable than as regurgitalites, but no objective criterion of distinguishing between the two possibilities is at a disposal. However, a relatively common occurrence of the described bodies leads to the hypothesis that additional member of the Paseky Shale community existed, probably vagile benthic, feeding on dead bodies of arthropods. Another hypothesis, that *Kodymirus* and *Kockurus* themselves (feeding on exuvia and dead specimens of their own species) are the tracemekers seems to be less probable (primarily because of the large size of "clusters").

The locality Mt. Kočka provided also yet larger clusters of body fossil fragments, usually imperfectly bounded from the surrounding bedding planes. Their origin is probably inorganic (Chlupáč 1995, this volume).

Dimorphichnus Seilacher, 1955
Dimorphichnus ichnosp.

Pl. VI, fig. 2

Material: One well-preserved find, several other traces possibly classifiable as *Dimorphichnus* ichnosp. penetrate *Monomorphichnus*-like traces.

Description: The specimen No. I 256 (Pl. VI, fig. 2) consists of two rows of different imprints. Right row consists of 13 straight to gently sigmoidal grooves, subparallel, up to 9 mm long, at an angle of 60-70° to the axis of the trace. Left row is composed of shorter grooves: they are T-shaped at one end of the trace, and hardly visible, straight, longitudinally orientated at the opposite end. Total length of the preserved part is 70 mm, width 29 mm. Hyporelief is very low. No other surface structures are present on the bedding plane.

There are several finds from the Kočka locality, showing similar asymmetrical traces of small dimensions on slabs covered with grooves of *M. semilineatus*. Even a random character of their arrangement cannot be excluded.

Remarks: *Dimorphichnus* is typically produced by trilobites (grazing obliquely to direction of movement - see, e.g., Osgood 1970). In the Paseky Shale, no trilobite fauna was found. The origin of *Dimorphichnus*-like traces by specific activity of *Kodymirus vagans* or *Kockurus grandis* also seems possible (crawling with prosomal appendages, probably obliquely to direction of movement - see Fig. 1d). It should be emphasized that this trace is rare in the Paseky Shale compared with *Monomorphichnus*.

Diplichnites Dawson, 1873
Diplichnites ichnosp.

Pl. II, fig. 5; Pl. VI, fig. 1

Material: Two specimens.

Description: Two parallel rows of minute imprints (convex hyporeliefs resp. concave epireliefs). The specimen No. I 231 (Pl. II, fig. 5) is 8 mm wide and 30 mm long; individual imprints about 2 mm long, at intervals 3-4 mm, thin and sigmoidal on one end of the trace, wider and oval towards the opposite end. The second specimen (I 255; Pl. VI, fig. 1) is wider (22 mm) and composed only of S-shaped imprints.

Remarks: *Diplichnites* occurs most frequently in the Cambrian and Ordovician. It is usually interpreted as repichnion of arthropods including trilobites (e.g. Osgood 1970, Häntzschel 1975, Fillion and Pickerill 1990, Orlowski 1992) but Briggs et al. (1979) advocated a more restircted usage of the name to exclude trilobite trackways. In the Paseky Shale, exceptional origin of *Diplichnites*-like traces by activity of *Kodymirus vagans* or *Kockurus grandis* seems possible (crawling with prosomal appendages; Fig. 1c), but also the possibility that the trace is produced by another worm-like animal or arthropod cannot be excluded.

Monomorphichnus Crimes, 1970
Monomorphichnus semilineatus ichnosp. nov.

Pl. I, figs. 1, 3, 6; Pl. III, figs. 1, 2, 5; Pl. V, fig. 4; Pl. VI, figs. 3, 5

Holotype: Specimen figured on Pl. I, fig. 1 (B. Horák Museum, Rokycany, No. I 221).

Type horizon: Early Cambrian, Paseky Shale of the Holšiny-Hořice Formation.

Type locality: Mt. Kočka.

Material: About 40 well-developed specimens; more than 20 further finds crossed by other traces or by inorganic structures, or placed to the ichnospecies with some doubts only.

Description: Very variable, mostly short (3-10 mm), very thin (0.2 to 0.5 mm) grooves, formed in somewhat irregular series of two to ten, or single. Grooves are only exceptionally straight, often more or less arcuate or sigmoidal. Mass occurrence on bedding planes is characteristic. Individual series often intersect and penetrate each other; common arcuate shapes of grooves suggest a rotational movement of an organ producing them. Spacings between grooves and the general shapes of series are also very variable. The spacings usually reach several millimetres, therefore all the series are up to several centimetres wide despite a very small length of grooves.

"Regular" traces corresponding with morphology of *Monomorphichnus lineatus* and *M. bilinearis* occur rarely on the same bedding planes as the described structure.

Remarks: Traces of the described morphology represent most of the ichnofossils found at Mt. Kočka. They are the most common and therefore probably ethologically well-defined type of trace, although their morphology seems to be chaotic or random. Logical explanation of this morphology is given by the new reconstruction of the arthropod *Kodymirus vagans* presented by Chlupáč (1995, this volume). After this reconstruction, six pairs of prosomal appendages were present, five of which were substantially long, classifiable as "walking legs" or "spiniferous legs", bearing long spines at distances corresponding to the usual distance of grooves of *M. semilineatus*. Therefore the prosomal appendages of *K. vagans* appeared to be the organ forming *M. semilineatus* at our locality, most probably when the tracemaker searched for food on the bottom. After this explanation, *M. semilineatus* is a fodinichnion, not a repichnion as other representatives of *Monomorphichnus*. This possibility is supported by the irregularity of the described trace, by uniqueness of series of the same shape, and by a planar (not linear) character of the trace. The arthropod *Kockurus grandis*, very probably closely related to *Kodymirus*, may have been another tracemaker of *M. semilineatus*.

Typically developed *M. semilineatus* can be clearly distinguished from *M. lineatus* Crimes et al, 1977, *M. bilinearis* Crimes, 1970, and *M. multilineatus* Alpert, 1976. Specimens of these ichnospecies occur as solitary or parallelly repeating series, while *M. semilineatus* covers the bedding planes more or less evenly by numerous irregular series of grooves of various directions (or by solitary grooves). Grooves of other ichnospecies of *Monomorphichnus* are mostly straight, those of *M. semilineatus* typically arcuate or sigmoidal, resulting from presumed "swinging" movement of appendages of the tracemaker (Fig. 1a). *M. lineatus* and other formerly stated representatives (described and figured, e.g., by Mathur et al. 1988, Crimes et al. 1977, Orlowski 1992, Pickerill and Peel 1990, Fillion and Pickerill 1990) show the groove width/groove spacing ratio mostly much greater (about 1: 4 to 1:1) compared to the same ratio in *M. semilineatus* (about 1:3 to 1:10). The groove length/series width ratio is very variable in *M. semilineatus*, often being very low (about 1:10). The values of these ratios resemble to the ichnogenus *Dimorphichnus* Seilacher, 1955, which, however, is formed by two different types of impressions (e.g., Häntzschel 1975). Similar ratios are also shown by the trace of probably trilobite origin, described by Briggs and Rushton (1980) from the Upper Cambrian of northern Wales. In that case, however, the series are strictly repeating (obliquely to the direction perpendicular to the grooves), therefore, the trace is a typical repichnion.

Monomorphichnus biserialis ichnosp. nov.

Pl. I, fig. 5; Pl. II, fig. 3; Pl. VI, fig. 4

Holotype: Specimen figured on Pl.II, fig. 3 (B. Horák Museum, Rokycany, No. I 229).

Type horizon: Early Cambrian, Paseky Shale of the Holšiny-Hořice Formation.

Type locality: Mt. Kočka.

Material: Three specimens from the type locality.

Description: Two long series of four to six grooves parallel to each other (I 225; Pl. I, fig. 5, and I 229; Pl. II, fig. 3). Roughly in a half of series, individual grooves intersect, so inner grooves turn into outer ones and vice versa. Length of grooves up to 60 mm, spacings between them 1-3 mm.

Remarks: *Kodymirus,* as reconstructed by Chlupáč (1995, this volume), possibly produced the parallel striae on the bottom by spines of prosomal appendages when swept by currents, or possibly during more or less active locomotion (Fig. 1a, 1c). This possibilty seems to be very suggestive in the case of long paired series of *M. biserialis*: one series should be formed by left appendages, the second series by right ones (Fig. 2). Morphology of a presumed tracemaker, *Kodymirus vagans* (or possibly also *Kockurus grandis*), as reconstructed by Chlupáč (1995) explains why the individual grooves intersect and change their position. *Kodymirus* probably used its prosomal appendages for active locomotion and the three found specimens of *M. biserialis* represent a record of individual "paces". The tracemaker drew up its prosomal appendages (particularly the greatest last pair with the longest spines) to the opisthosoma; this increased the desirable lifting force and the organism moved forwards above the bottom. When the spines touched the bottom surface, the tracemaker withdrew its appendages, so ends of spines changed their position (Fig. 2). Subsequently, further active "pace" interrupted the record on the bottom surface. Specimen No.I 229 also shows extension of the trace in a direction of presumed locomotion caused by withdrawing the appendages. Two remaining specimens do not show such an extension. Hence it follows that the locomotion of the tracemaker was mostly more complicated. The appendages might have moved not

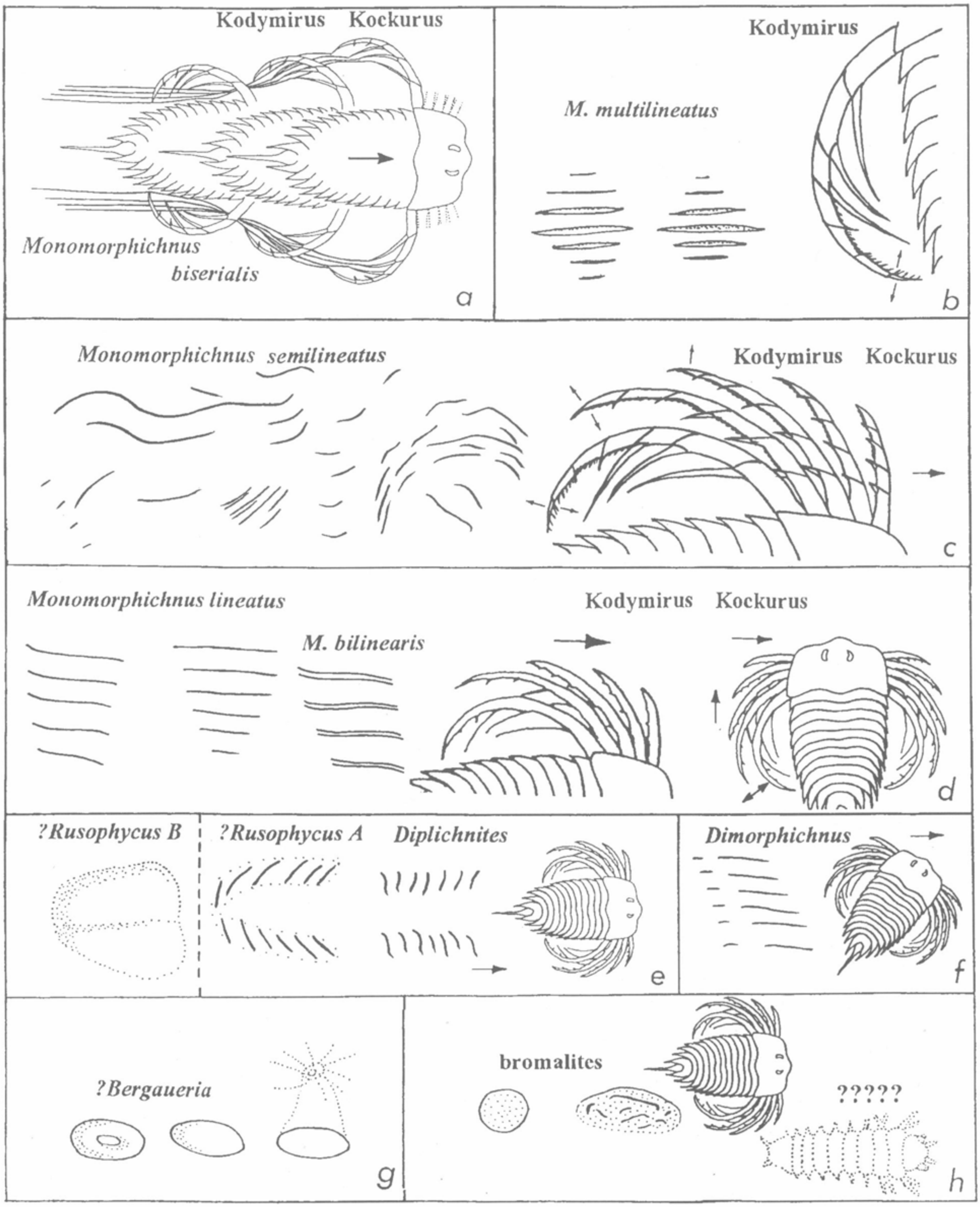

Fig. 1. Trace fossils of the Paseky Shale and their presumed tracemakers. Arrows: directions of locomotion or movements of the tracemakers. a - *Monomrphichnus biserialis*, tracemaker *Kodymirus vagans* (or *Kockurus*), x1.5. b - *Monomorphichnus multilineatus,* tracemaker *Kodymirus* (*Kockurus*), x2.5. c - *Monomorphichnus semilineatus,* tracemaker *Kodymirus vagans* (or *Kockurus*), x2.5. d - *Monmorphichnus lineatus* and *M. bilinearis*, tracemaker *Kodymirus* or *Kockurus,* x1.5. e - ?*Rusopyhycus* and *Diplichnites*, tracemaker *Kodymirus* or *Kockurus,* x1.0. f - *Dimorphichnus*, tracemaker *Kodymirus* or *Kockurus*, x1.0. g - *?Bergaueria,* tracemaker unknown, possibly coelenterate, x1.0. h - bromalites, tracemaker: unknown benthic vagile organism or *Kodymirus* (*Kockurus*), x1.0

only in the horizontal plane, but also up and down; individual spines were also probably movable. This caused a certain variability of the trace. Nevertheless, *M. biserialis* is the most suggestive trace fossil from the Paseky Shale, confirming the position and the purpose of prosomal appendages of *Kodymirus vagans.*

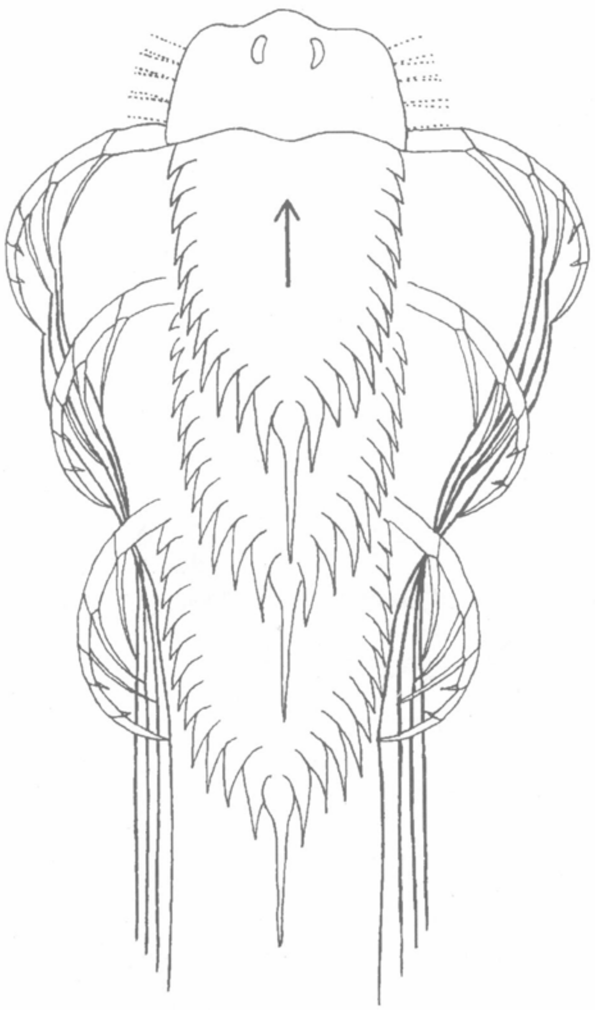

Fig. 2. *Kodymirus vagans* during active locomotion, forming the trace *Monomorphichnus biserialis* ichnosp. nov. Reconstruction of *Kodymirus* after Chlupáč (1995, this volume). Enlarged 3 x

Monomorphichnus bilinearis Crimes, 1970

Pl. III, figs. 3, 4

Material: Four well-preserved specimens, some other questionable.

Description: Paired parallel grooves (convex hyporeliefs), mostly very thin, forming series of various dimensions: length of grooves up to 30 mm, spacings between them 2-4 mm. Each series consists of 2-6 pairs of grooves. Lateral repeating of series was not observed.
Remarks: Trace fossils of the same morphology and dimensions were described and figured as *M. bilinearis* by Crimes (1970) and by Fillion and Pickerill (1990) from the Early Palaeozioc marine environments. For further remarks see *M. lineatus*.

Monomorphichnus lineatus Crimes, Legg, Marcos, and Arboleya, 1977

Pl. I, figs. 2, 4; Pl. II, figs. 2, 4, 6; Pl. VI, fig. 6

Material: Seven well-developed specimens, some other questionable.

Description: Series of simple parallel thin grooves (convex hyporeliefs), straight to very slightly sinuous. Grooves of each series are roughly of the same wide and high, and mostly also of a roughly equal length. Series are repeating laterally only exceptionally (specimen No. I 228; Pl. II, fig. 2). Length of grooves up to 50 mm, spacings between them usually 3-8 mm.
Remarks: Traces of equal morphology were described by numerous authors, mostly from the Early Palaeozoic marine environments (e.g., Crimes et al. 1977, Mathur et al. 1988, Orlowski 1992, Fillion and Pickerill 1990).

Traces of the ichnogenus *Monomorphichnus* consisting of thin shallow striae (or grooves in hyporeliefs) - *M. lineatus* and *M. bilinearis* - were believed to be trilobite fodinichnia (Crimes 1970). Later Osgood (1970, 1975) interpreted them to be made by trilobites swept by curretns. Fillion and Pickerill (1990) accepted the Osgood's hypothesis but presumed that some specimens may represent grazing traces. In the Paseky Shale the trilobite fauna is not present and *Kodymirus* resp. *Kockurus* can be suggested as tracemakers. As stated above, *Kodymirus* may have produced the parallel striae on the bottom by spines of prosomal appendages when swept by currents, or possibly during more or less active locomotion (Fig. 1b).

Monomorphichnus multilineatus Alpert, 1976

Pl. II, figs. 7, 8

Material: Two specimens.

Description: Series of parallel grooves, preserved as convex hyporeliefs. Specimen No. I 234 (Pl. II, fig. 8) occurs in a bedding plane with no other traces. It consists of four grooves. One of inner grooves is much longer (18 mm) wider and higher than others (they are 10-13 mm long). Specimen No. I 233 (Pl. II, fig. 7) is composed of five grooves with variable spacings, showing an indication of paired arrangement; central grooves are longer and more conspicuous than lateral ones.
Remarks: Alpert (1976) and Fillion and Pickerill (1900) diagnosed *M. multilineatus* as the trace composed of parallel dig marks, the central marks being deeper than the outer marks. *M. multilineatus* was described so far only from the marine Cambrian to Early Ordovician sediments (Fillion and Pickerill 1990). It originated presumably by powerful digging strokes of trilobite appendages (probably exites) - see Bergström (1976).

In the Paseky Shale, this trace represents somewhat deeper digging compared to *M. semilineatus, M. lineatus* and *M. bilinearis*, e.g. to the traces formed very probably by *Kodymirus* and possibly also *Kockurus* (see above). It is a very rare trace; therefore, it is difficult to decide whether it was produced by unusual activity of *Kodymirsus* or *Kockurus* (stronger digging by prosomal appendages) or whether it resulted from the activity of a so far unknown tracemaker.

Rusophycus Hall, 1852
?Rusophycus ichnosp. A

Pl. II, fig. 1

Material: Sole find.

Description: Straight to very slightly sigmoidal grooves arranged in a very shallow depression of horseshoe shape. Grooves orientated at an angle of 20-40° to the axis of the trace. Width and length of the trace are 25 mm. Individual grooves 5-10 mm long, spacings 1-3 mm.
Remarks: Overall morphology of the trace is close to *Rusophycus*, typically a trilobite cubichonion (for descriptions and discussions see, e.g., Osgood 1970, Osgood and Drennen 1975) but known also from non-marine settings (Bromley and Asgaard 1979). In the Paseky Shale, interpretation of *?R.* ichnosp. as a resting trace of *Kodymirus vagans* seems to be possible; *Kodymirus* was possibly able to make shallow depressions with prosomal legs (Fig. 1c, Fig. 3). Because the find is sole, the animal activity leading to the origin of the described trace was exceptional and should be rather random.

A rusophyciform trace made by Cambrian aglaspidid arthropods, *Raaschichnus gundersoni*, was described by Hesselbo (1988). It clearly differs from the traces described herein as *?Rusophycus* from the Paseky Shale, e.g., by the presence of marks of tail spine. In the material from the Paseky Shale, no mark interpretable as a trace of telson of *Kodymirus vagans* (or *Kockurus*) was found either among presumed grazing traces, or among suspected fodinichnia and cubichnia. This can be, however, hardly considered as evidence that *Kodymirus* is not the maker of these traces; more probably, the telson of *Kodymirus* was directed upwards and did not leave any marks on the bottom.

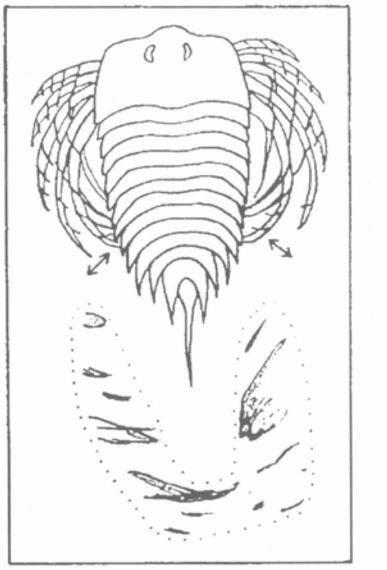

Fig. 3. *Kodymirus vagans* forming the cubichnion *?Rusophycus* ichnosp. A by "swinging" movements of prosomal appendages. The trace drawn after specimen No. I 227, the tracemaker adapted after Chlupáč (1995, this volume). Arrangement of striae of the trace correspond to disposition of the longest sipnes when the appendages are drawn on the opisthosoma. Enlarged 1.5 x

?Rusophycus ichnosp. B

Pl. V, fig. 3

Material: Sole find.

Description: Shallow, smooth bilobate pit, preserved as concave epirelief and its counterpart - convex hyporelief. Dimension in direction of axis is 21 mm, in perpendicular direction 22 mm.
Remarks: Overall morphology of the trace resembles the ichnogenus *Rusophycus* (see the preceding ichnotaxon). Sole occurrence and lack of morphological features does not enable to determine the tracemaker; because of the smooth surface, its origin as cubichnion of *Kodymirus* or *Kockurus* seems to be less probable (Fig. 1c).

Conclusions

In the ichnoassemblage of the Paseky Shale, numerous minute exichnia were ascertained, produced very probably by endemic arthropods *Kodymirus vagans* and *Kockurus grandis*. Morphologically variable ichnofossil *Monomorphichnus semilineatus* ichnosp. nov. is interpreted as the trace of feeding with prosomal appendages of the tracemaker. *Monomorphichnus biserialis* ichnosp. nov. is a trace of active locomotion of *Kodymirus* (*Kockurus*) close above the bottom. Traces comparable with existing ichnotaxa (e.g., produced by trilobites) are rare (*Monomorphichnus lineatus* Crimes et al. 1977, *M. bilinearis* Crimes, 1970, *?M. multilineatus* Alpert, 1976, *?Rusophycus* div. ichnosp.). The most probable maker of these traces is also *Kodymirus* (*Kockurus*), producing them by various modes of locomotion and by a resting on the bottom.

Besides these exichnia, problematical traces *?Bergaueria* ichnosp. and ?bromalites ichnogen. were found. Their tracemakers are probably not *Kodymirus* and *Kockurus*; they can be attributed to organisms which were not able to fossilize at the given setting. *?Bergaueria* may represent dwelling burrows, most probably of sessile coelenterates, while suspected bromalites seems to be faecal material of vagile benthic "worms".

Trace fossils typically occurring in the marine Cambrian sediments (e.g. *Planolites*, various tubes with meniscate filling, *Teichichnus, Phycodes* - see Crimes 1987 and many others) are completely missing in the Paseky Shale. Therefore, the described trace fossil assemblage is quite different compared to all other so far known Cambrian ichnoassemblages. Sedimentological, palynological and palaeogeographical data from the Paseky Shale and endemic character of the fauna (Kukal 1995, Fatka - Konzalová 1995, Chlupáč et al. 1995, Chlupáč 1995, all in this volume) lead to the conclusion of non-marine or restricted marine (brackish, lagoonal) environment and the described ichnoassemblage is in a good agreement with this result. It is the oldest known ichnoassemblage from these settings [Donovan (1994) stated that the oldest similar ichnoasseblage is of the Ordovician age; similarly Johnson et al. (1994) considered the traces from the subaerial Borrowdale Volcanic Group, Lake Distrct of England, to be the earliest]. If the presumed bromalites really contain the faecal material, they are also the oldest known (cf. Hunt et al. 1994).

Presented March 1, 1995 *Translated by the author*

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Ichnofosilie paseckých břidlic (spodní kambrium, Česká republika)

V ichnospolečenstvu paseckých břidlic byla zjištěna četná exichnia (povrchové stopy), jejichž předpokládaným původcem je *Kodymirus vagans* (nebo příbuzný *Kockurus grandis*) při získávání potravy z povrchu dna pomocí pohyblivých hlavových okončetin. Tato morfologicky variabilní ichnofosilie je popsána jako *Monomorphichnus semilineatus* ichnosp. nov. *Monomorphichnus biserialis* ichnosp. nov. představuje stopu po plavání původce (*Kodymirus*, příp. *Kockurus*) těsně nade dnem pomocí hlavových končetin. Vzácné jsou ichnofosilie paralelizovatelné s existujícími ichnotaxony, jejichž předpokládanými původci jsou obvykle trilobiti. I v těchto případech je nejpravděpodobnějším původcem *Kodymirus* při různých životních činnostech (variabilní lezení a plavání u dna, odpočinek). Jedná se o ichnotaxony *Monomorphichnus lineatus* Crimes et al. 1977, *M. bilinearis* Crimes, 1970, *?M. multilineatus* Alpert, 1976, *?Rusophycus* div. ichnosp. Dále byly ve společenstvu nalezeny problematické ichnofosilie *? Bergaueria* ichnosp. a *bromalites* ichnogen. indet. Původci jsou pravděpodobně jiní než *Kodymirus* resp. *Kockurus* a je možno je přičíst organismům neschopným v daném prostředí fosilizace: *Bergaueria* může představovat obydlí, nejpravděpodobněji láčkovců (a tedy přisedlý bentos), *bromality* se jeví nejpravděpodobněji jako fekální materiál pohyblivého bentosu.

Zcela naopak chybějí typická endichnia, známá v mořském prostředí už od svrchního proterozoika - *Planolites*, různé trubice s meniskátní výplní, spreiten-struktury (první z nich je *Teichichnus*) a jiné požerky (běžný ve stejně starých horninách je např. *Phycodes*) - viz souhrnná práce Crimese (1987) a řada dalších.

Popsané ichnospolečenstvo se tedy výrazně vymyká dosud popsaným ichnospolečenstvům spodního kambria, u kterých je předpokládán původ v normálním mořském prostředí. Nepřítomnost řady jinak běžných ichnotaxonů a naopak neobvyklý charakter nalezených stop dovolují předpoklad brakického či limnického prostředí. V takovém případě se jedná o nejstarší dosud známé nemořské ichnospolečenstvo na světě (viz Donovan 1994; ten uvádí nejstarší podobné ichnospolečenstvo až z ordoviku). Jestliže předpokládané bromality obsahují skutečně fekální materiál, jedná se i o nejstarší bromality na světě (srov. s údaji Hunta et al. 1994).

Explanation of plates

All the figured specimen come from the locality Kočka. **I** before the inventory number: collection of ichnofossils in the Horák's Museum, Rokycany. *Photos by R. Mikuláš*

Plate I

1, 3, 6: *Monomorphichnus semilineatus* ichnosp. nov.; I 221, I 223, I 226. 2, 4: *Monomorphichnus lineatus* Crimes et al., 1977; I 222, I 224. 5: *Monomorphichnus biserialis* ichnosp. nov.; I 225. All x1.5

Plate II

1. *?Rusophycus* ichnosp. A; I 227; x1.8. 2, 4, 6: *Monomorphichnus lineatus* Crimes et al., 1977; I 228, x1.7; I 230, x1.0; I 232, x1.5. 3: *Monomorphichnus biserialis* ichnosp. nov.; I 229; holotype; x1.5. 5: *Diplichnites* ichnosp.; I 231; x2.8. 7, 8: *Monomorphichnus multilineatus* Alpert, 1976; I 233 and I 234; x1.5

Plate III

1, 2, 5: *Monomorphichnus semilineatus* ichnosp. nov.; I 235, x1.5; I 236, x1.5; I 239 x2.2. 3, 4: *Monomorphichnus bilinearis* Crimes, 1970; I 237, x1.5; I 238, x2.3

Plate IV

1-8: *?Bergaueria* ichnosp.; I 240, I 241, I 242, I 243, I 244, I 245, I 246, I 247; x1.8 (Fig. 4: x2.6). 9: *?Bergaueria* ichnosp. and relict of a bioturbate texture or bromalite; I 248; x0.7

Plate V

1, 2: *?Bergaueria* ichnosp.; specimens with slight radiate sculpture (probably of secondary origin); 1 - x3.1; I 249; 2 - x2.2; I 250. 3: *?Rusophycus* ichnosp. B; x2.2; I 251. 4: *Monomorphichnus* cf. *semilineatus* ichnosp. nov.; specimen resembles (?randomly) the ichnogenus *Multipodichnus* Bergström and Ineson, 1988; x2.3; I 252. 5, 6: *?Bergaueria* ichnosp. (vertical sections); 5 - I 253; x2.1. 6 - I 254; x3.0

Plate VI

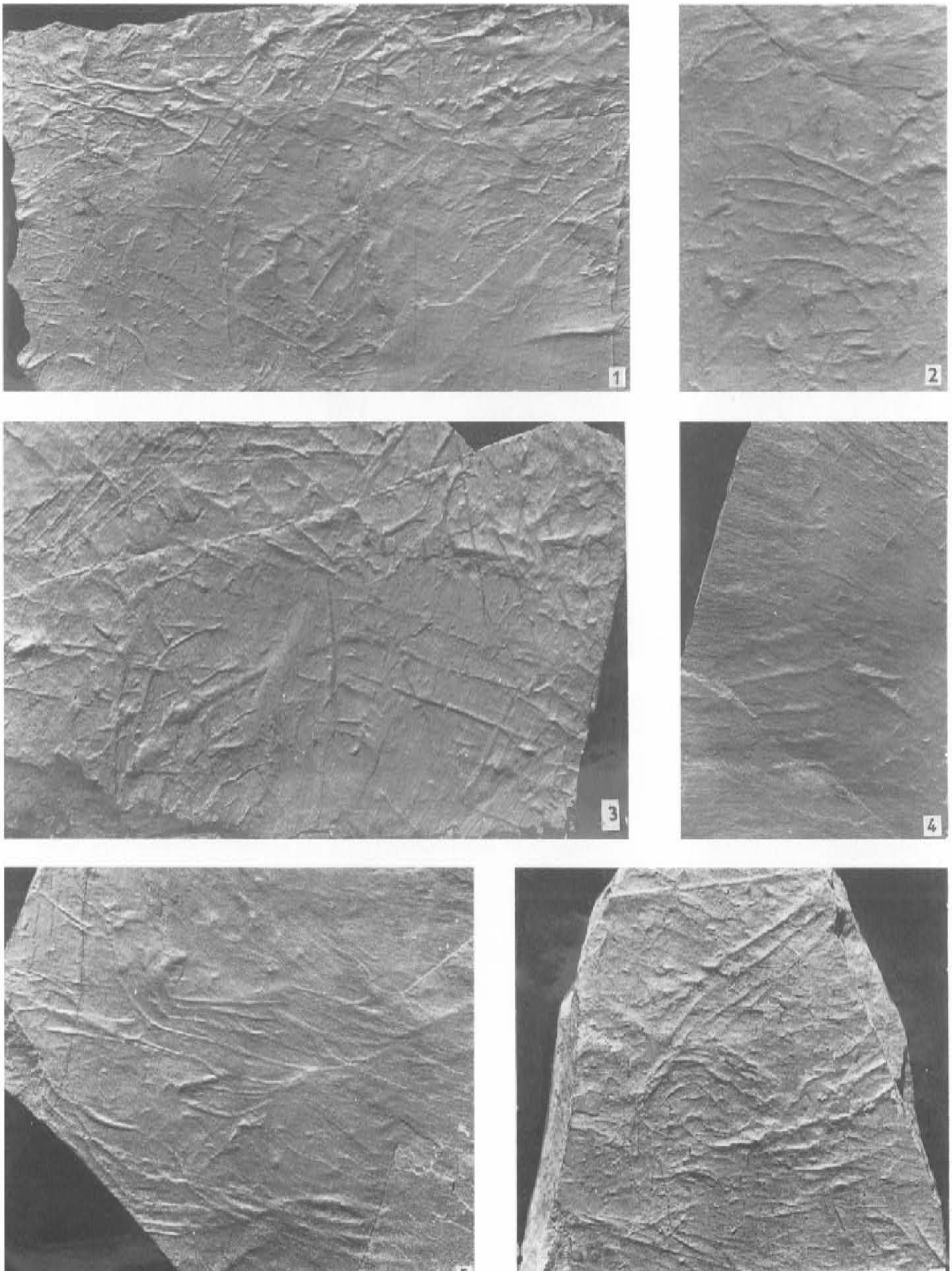
1: *?Diplichnites* ichnosp.; I 255x; 1.5. 2: *Dimorphichnus* ichnosp.; I 256; x1.2. 3, 5: *Monomorphichnus* cf. *semilineatus* ichnosp. nov.; 3 - I 257; x3.2; 5 - I 259; x2.1. 4: *Monomorphichnus biserialis* ichnosp. nov; I 258; x2.1. 6: *Monomorphichnus lineatus* Crimes et al., 1970; 4-6 - I 260; x2.3

Plate VII

1-9: ?bromalites ichnogen. et ichnosp. indet.; 1 - I 261; x2.1, 2 - I 262; x2.3, 3 - I 263; x4.1, 4 - I 264; x3.0, 5, 6 - I 265 a I 266; x4.0, 7 - I 267; x3.8, 8 - I 268; x3.0

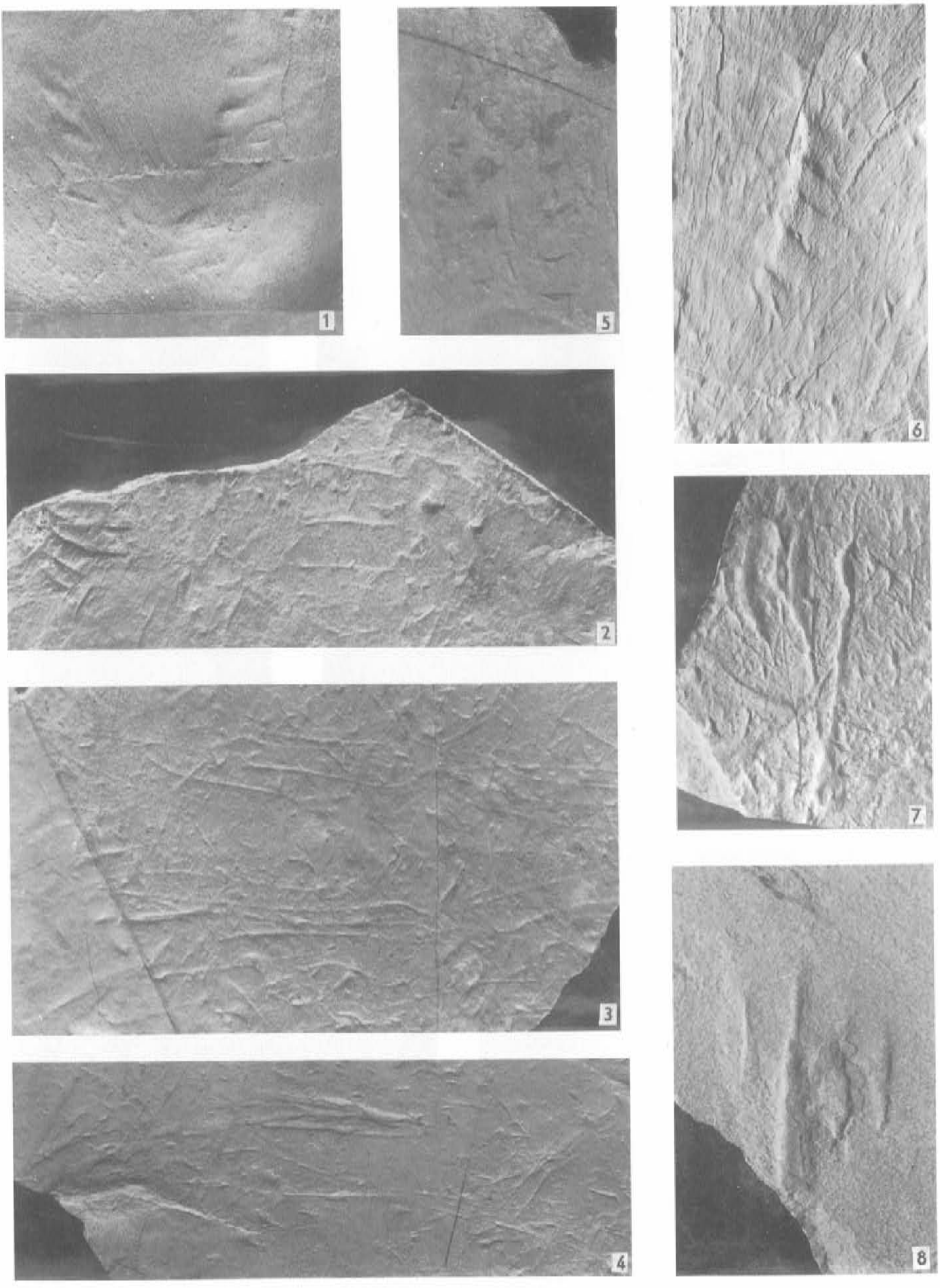
Plate VIII

1-4: bromalites ichnogen. et ichnosp. indet.; 1 - I 269; x2.5, 2 - I 270; x2.2, 3 - I 271; x1.2, 4 - I 272; x2.2

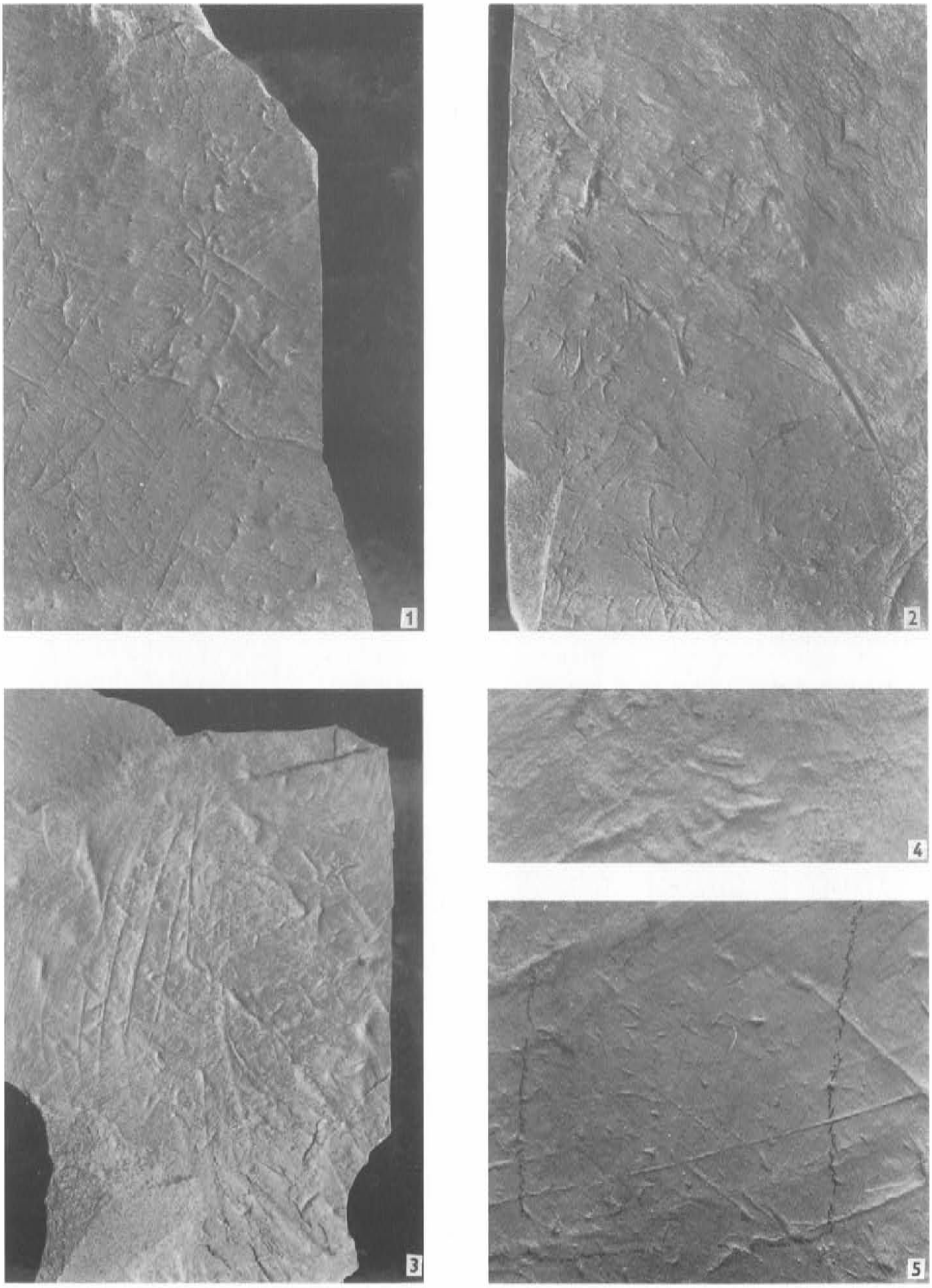


For explanation see p. 45

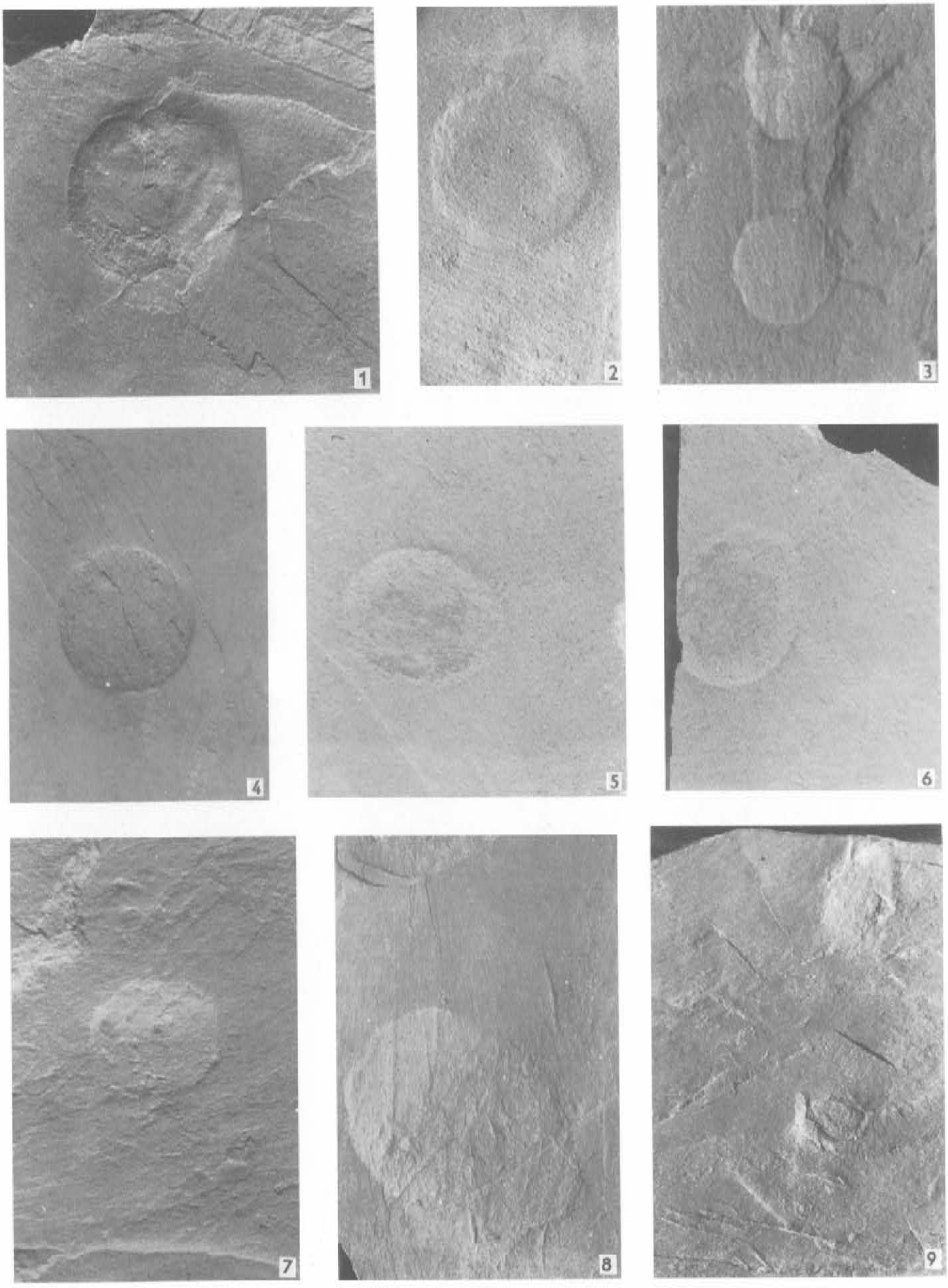
R. Mikuláš: Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic) (Pl. II)

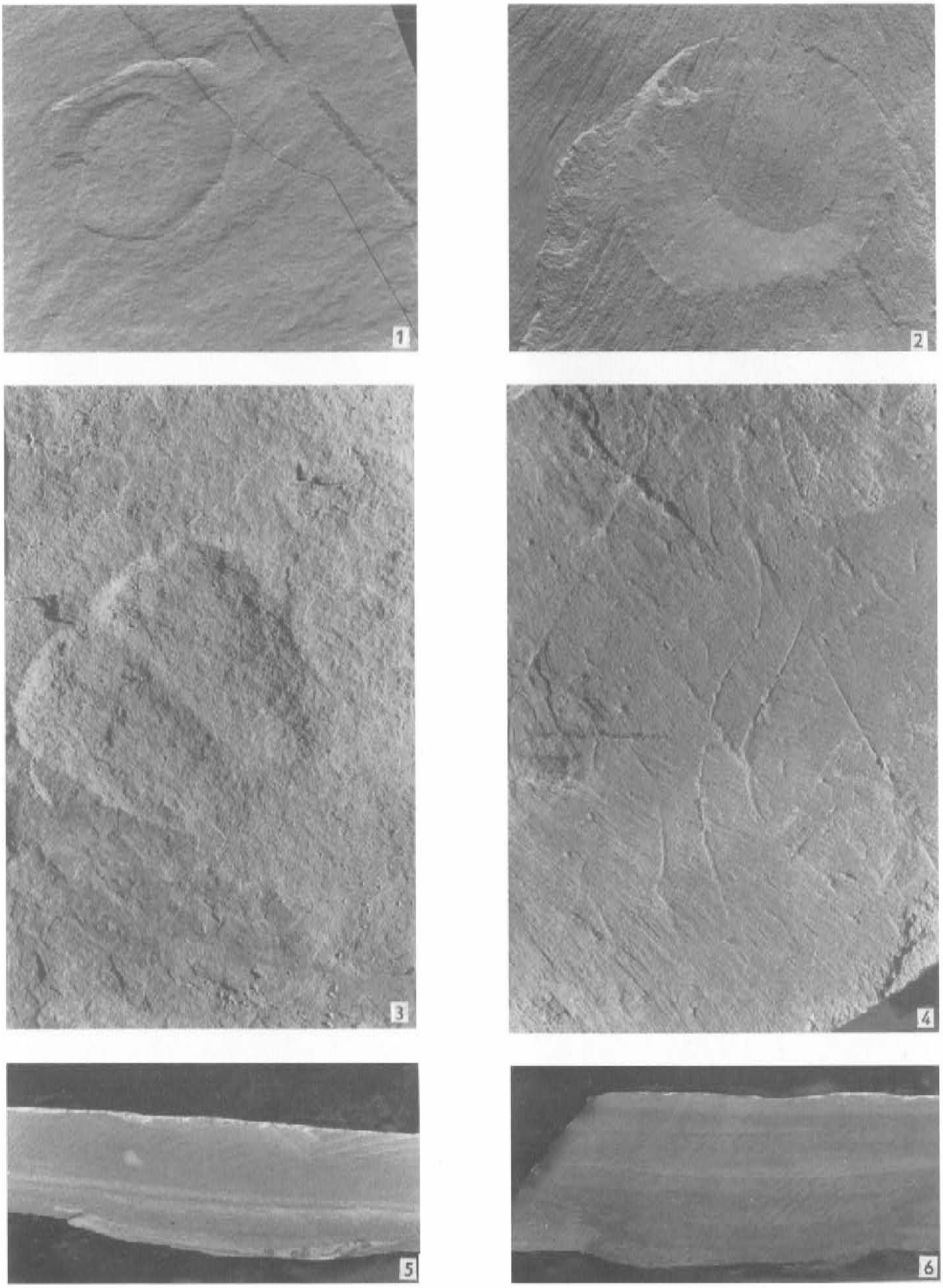


R. Mikuláš: Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic) (Pl. III)

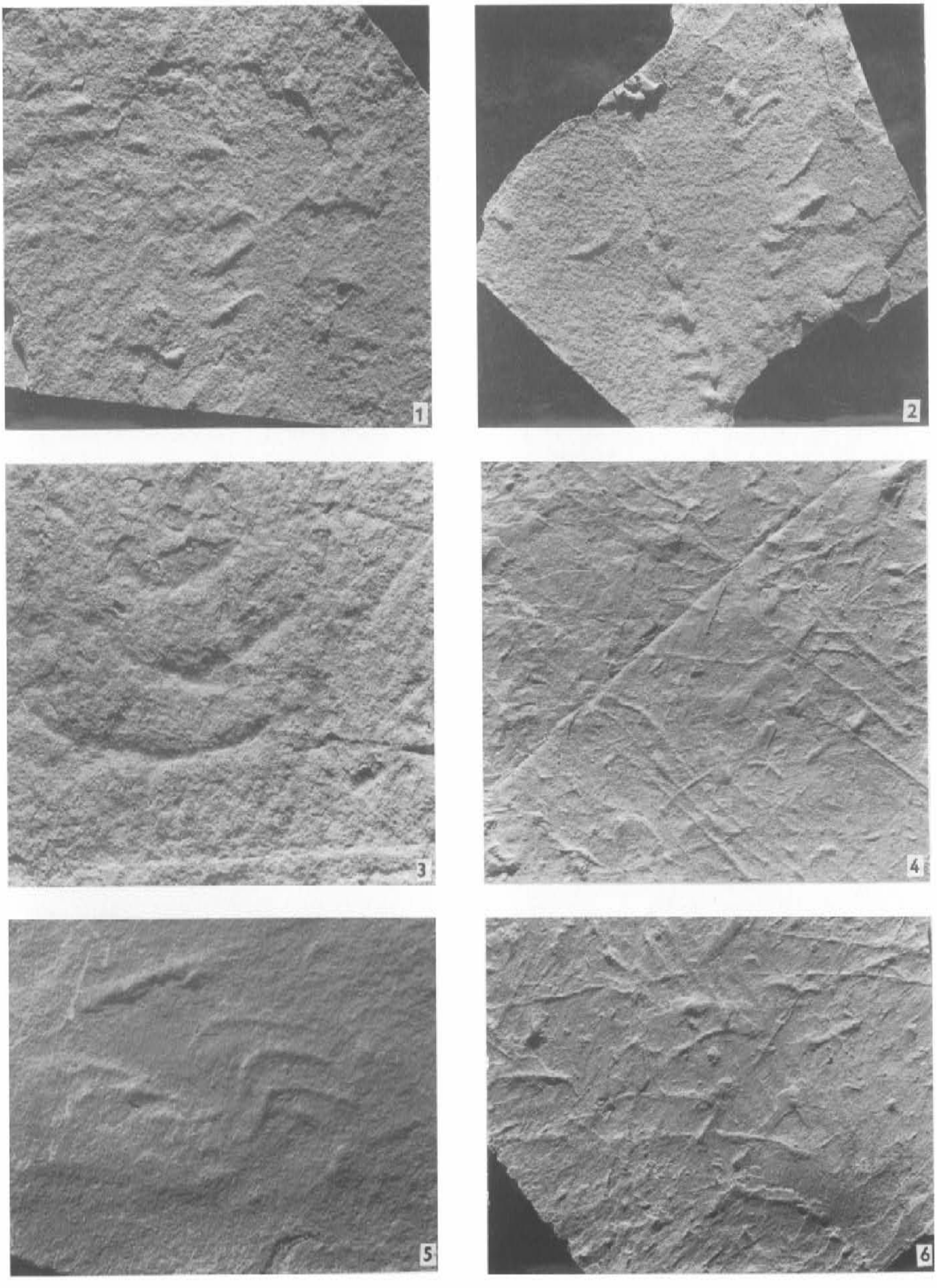


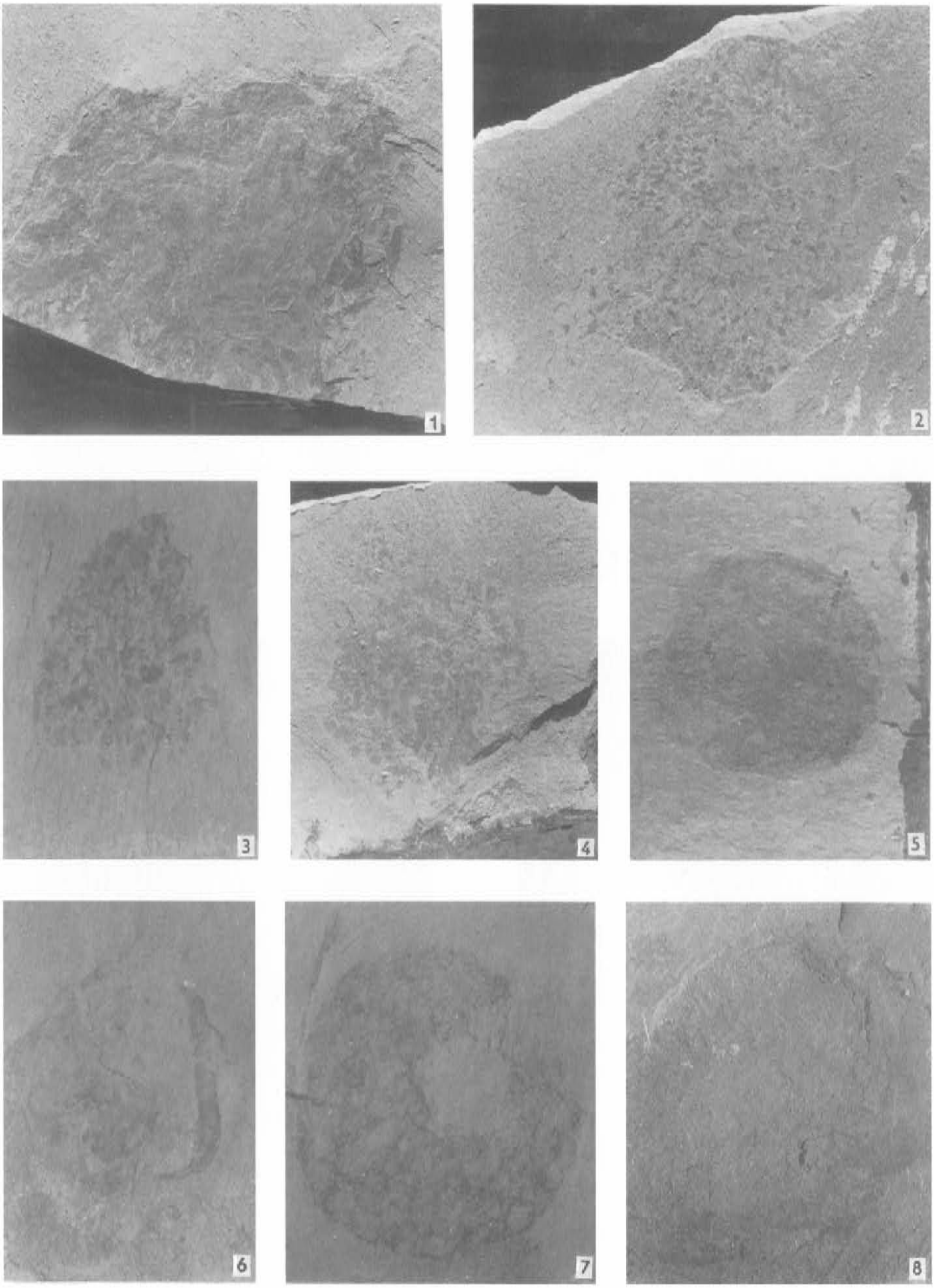
R. Mikuláš: Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic) (Pl. IV)





R. Mikuláš: Trace fossils from the Pasecky Shale (Early Cambrian, Czech Republic) (Pl. VI)

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R. Mikuláš: Trace fossils from the Paseky Shale (Early Cambrian, Czech Republic) (Pl. VIII)