Lower Cambrian arthropods from the Paseky Shale (Barrandian area, Czech Republic)

Spodnokambričtí arthropodi paseckých břidlic (Barrandien, Česká republika) (Czech summary)

(12 text-figs., 10 plates)

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The Lower Cambrian fauna of the Paseky Shale (Brdy Mts., central Bohemia) consists of three non-trilobite arthropods: the markedly dominant *Kodymirus vagans* Chlupáč et Havlíček, 1965, interpreted as the earliest representative of the class Eurypterida with some superficial resemblance with aglaspidids, the newly described and probably related *Kockurus grandis* n. gen. et sp., and the crustacean *Vladicaris subtilis* n. gen. et sp. This low diversity and endemic fauna inhabited a special non-marine or restricted marine, probably brackish and lagoonal environment, exceptional for the Cambrian Period.

Key words: Lower Cambrian, Chelicerata, Eurypterida, Phyllocarida, systematics, relationships, lagoonal brackish environment, Paseky Shale

The unique arthropod fauna of the Paseky Shale, found in the Brdy Mts. in the south-western part of the Barrandian area, central Bohemia, represents the oldest fauna so far known from the territory of the Czech Republic. The Paseky Shale fauna consists exclusively of non-trilobite arthropods. They are represented by the index and strongly dominant *Kodymirus vagans* Chlupáč et Havlíček, 1965, and two accompanying forms, namely *Kockurus grandis* gen. et sp. n. and *Vladicaris subtilis* gen. et sp. n.

This expressively low diversity fauna is exceptional in its composition (only merostomes and possible phyllocarids present), endemic character, and mode of occurrence in a single stratigraphic unit - the Paseky Shale Member embedded in a very thick sequence of coarse siliciclastic rocks of presumed continental origin. All this accentuates the exceptional and unique character of the described assemblage.

On the other hand, the Paseky Shale arthropods show in their peculiar character and in preservation of less mineralized parts (appendages) a certain analogy with Cambrian faunas of the Burgess Shale type as known from various parts of the world (reviewed e.g. in Briggs and Fortey 1992).

The present description is based on more than 1300 specimens the great majority of which was collected during the Project on investigation of the oldest fauna from Bohemia sponsored by the Ministry of Environment of the Czech Republic and carried out in 1992-1994.

The reference material is deposited mostly in the District Museum of Dr. B. Horák at Rokycany (inventory numbers prefixed by MR). The types and other fossils gathered during the first etape of investigations in 1964 and used in the first description of the Paseky Shale fauna (Chlupáč and Havlíček 1965) are housed in the collections of the Geological Survey, Prague (inventory numbers prefixed by ICh). A collection of selected instructive specimens was donated to the National Museum, Prague.

The line drawings were made using the video-camera and corresponding photographs. Dotted lines in drawings indicate secondary limits of organic remains caused by damage, broken surfaces of the rock etc.

Acknowledgements. The project was realized under the financial support of the Ministry of Environment of the Czech Republic and under kind cooperation with the District Office of the town of Příbram and District Museum of Dr. B. Horák at Rokycany. Numerous colleagues assisted in field collections, namely Mrs. O. Chlupáčová, Dr. O. Fatka, Dr. J. Frýda, Dr. J. Hladil, Mgr. E. Kadlecová, Dr. J. Kraft, Dr. P. Kraft, M. Kříha, Mgr. M. Kučera, Dr. M. Mergl, Dr. R. Mikuláš, Š. Rak and Mgr. J. Zusková. The majority of photographs was made by Mr. O. Malina.

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Systematic palaeontology

Phyllum Arthropoda
Subphyllum Chelicerata

Genus *Kodymirus* Chlupáč et Havlíček, 1965

1968 *Kodymirus,* Bergström, p. 494, 495, 497, 502
1971 *Kodymirus,* Bergström, p. 399
1979 *Kodymirus,* Whittington, p. 256
1979 *Kodymirus,* Bergström, p. 37, fig. 1.17C
1988 *Kodymirus,* Briggs and Collins, p. 795
1988 *Kodymirus,* Gray, p. 57

1989 *Kodymirus,* Hesselbo, p. 641

Type species: *Kodymirus vagans* Chlupáč et Havlíček, 1965

Diagnosis: Prosoma subpentagonal in outline, front projected anteriorly, reniform eyes elevated and placed anteromesially. Epistoma broadly linguiform, without differentiated border. Head appendages uniramous, strongly spinose, posterior pair similar to preceding ones, not transformed into swimming legs. Opisthosoma composed of twelve segments and a styliform telson. Segments with median ridges, protruded laterally into pleural spines increasing in length posteriorly. The last segment of horse-shoe outline. The dorsal surface of exoskeleton densely granulated.

Kodymirus vagans Chlupáč et Havlíček, 1965

Pl. I-VI; Text-figs. 1-7

1965 *Kodymirus vagans* n. sp., Chlupáč and Havlíček, p. 9-18, text-fig. 2, pl. 1, pl. 2, pl. 3, pl. 4, figs. 1-8, pl. 5, figs. 1-8, pl. 6, figs. 1, 2, 4, ?6, 7, 8 (non figs. 3, 5)

1979 *Kodymirus vagans,* Bergström, p. 37, fig. 1.17C

1989 *Kodymirus vagans,* Hesselbo, p. 641

Holotype: Incomplete opisthosoma with fragmentary prosoma ICh4541, figured by Chlupáč and Havlíček (1965, pl. I).

Locus typicus: Mt. Kočka, Brdy Mts., central Bohemia.

Stratum typicum: the Paseky Shale, Lower Cambrian.

Material: 57 articulated substantial parts of exoskeletons (mostly prosomas in connection with incomplete opisthosomas), 275 isolated prosomas, 57 isolated epistomas, 24 articulated appendages, 116 isolated podomeres of appendages, 115 articulated groups of segments, 188 groups of isolated segments and other parts, 390 selected isolated segments, 70 telsons (isolated or connected with the trunk).

Description. The primary description was given by Chlupáč and Havlíček (1965). A supplemented version is presented here.

Prosoma

The subpentagonal outline of the prosoma in dorsal view is marked by an obtusely angulate projection of the front, followed laterally by shallow and broad notches passing abaxially into arcuate anterolateral areas. The posterolateral angle is simply pointed, not protruded into a genal spine (exceptions see under ontogeny). The posterior margin is gently convex anteriorly in lateral parts and medially bent posteriorly. The prosomal length/width ratios shown in Text-fig. 1 range from 0.5 to 0.7 as a result of compaction in different orientations to bedding.

The convexity and relief of the prosoma is strikingly low which is evidenced by lacking or only exceptionally present compaction wrinkles. However, a low but distinct elevation of the axial area is perceptible in specimens less damaged by compaction. The most marked elevations are confined to eyes which are placed antemesially according to the terminology proposed by Tollerton (1989, fig. 7). Eyes exhibit a reniform shape with a marked abaxial curvature. The distance of eyes from the anterior margin of prosoma is less than the sagittal length of the eye elevation, although compaction causes common secondary differences.

Several well preserved specimens (Pl. I, figs. 2, 5, 6, 7, Pl. III, figs. 1, 2) show three blunt and low paired elevations differentiated by three slightly indicated depressions in the axial area of the prosoma. These structures, corresponding in position to lateral glabellar lobes and furrows of trilobites or to similar structures in the cardiophthalmic region of xiphosurids, may be interpreted as muscular markings.

The occipital band is not differentiated by a furrow. A short sagittally prolonged median ridge similar in shape to short axial ridges on opisthosomal segments (but less pronounced) is developed close to the posterior margin, but is commonly effaced by compaction.

The cuticle of the prosoma is thin. However, some thickening, marked by a darker colour, accentuates the outer prosomal contour indicating a narrow doublure.

The sculpture consists of a dense, uniform and fine granulation which covers the entire dorsal surface except the eyes. A less pro-

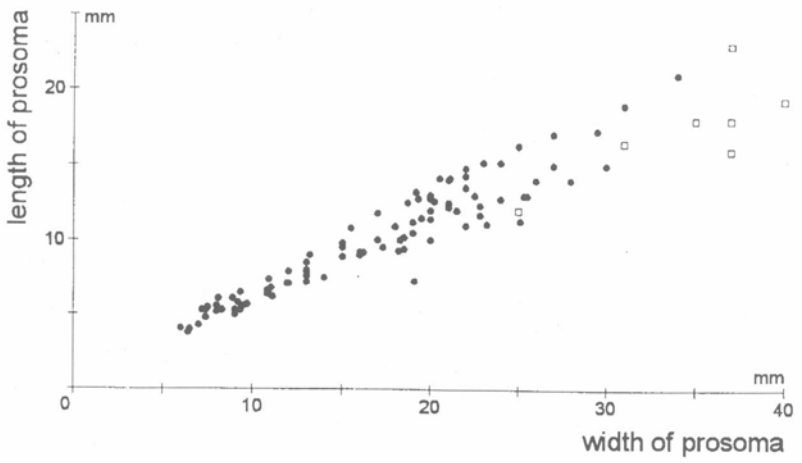

Fig. 1. Graph of sagittal lengths and transversal widths of prosomas of *Kodymirus vagans* (dots, 95 specimens measured) and *Kockurus grandis* (circles, 7 specimens measured)

nounced diminishing of granulae size close to margins is perceptible in specimens with well preserved surface (Pl. VI, figs. 2, 3, comp. also Chlupáč and Havlíček, 1965, Pl. IV, fig. 8).

Epistoma

Broadly linguiform plates found isolated or in association with remnants of *Kodymirus* are interpreted as epistomes (Pl. II., figs. 1-3).

They exhibit gently arcuate anterior margin, markedly developed anterolateral wings and a posteriorly tapering and rounded main lobe. The last shows a distinct convexity increase in the median region, accentuated by less conspicuous compaction wrinkles in some specimens. However, no distinct border and furrows dividing the main lobe are present.

The most striking feature are the anterolateral wings. They consist of a short and abaxially pointed proximal part which conforms in its ventral convexity with the main lobe, and a laterally widened distal part. The latter is directed dorsally, being often broken off or covered with the matrix. In the original description (Chlupáč and Havlíček, 1965, p. 13), these distal parts of wings were interpreted as separated by sutures, but this has not been confirmed by recent finds.

The whole configuration of the plate (and the wings in particular) strongly resembles the hypostoma of trilobites, though no border or furrows dividing the main lobe are present.

The interpretation as epistomas of *Kodymirus vagans* is primarily based on the association with detached *Kodymirus* remains of corresponding size. Several specimens, however, indicate the epistoma on its place beneath the frontal region of the prosoma: MR65784 (Pl. II, fig. 4) shows a linguiform pattern, fully corresponding in outline to isolated plates, imprinted into the frontomedian region of a compacted prosoma. MR65783 and MR65789 (Pl. III, figs. 1, 2, Text-fig. 5, 2, 3) exhibit a flattened epistoma beneath the compacted prosoma connected with the opisthosomal segments, and several other specimens show similar but less instructive examples.

Prosomal appendages

New finds offer at least a partial picture of the configuration of prosomal appendages. Though complete appendages are not known, and the present remains are only rarely preserved in connection with other parts of the exoskeleton (comp. Pl. IV, Text-fig. 5), some conclusions are possible.

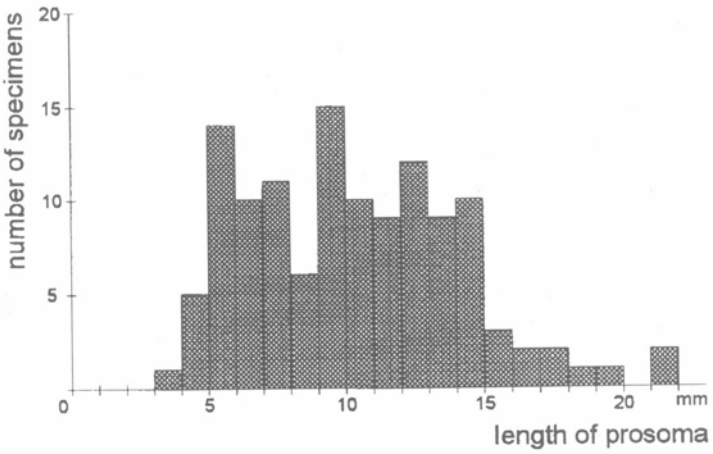

Fig. 2. Size frequency histogram of prosoma lengths of *Kodymirus vagans* (116 specimens measured)

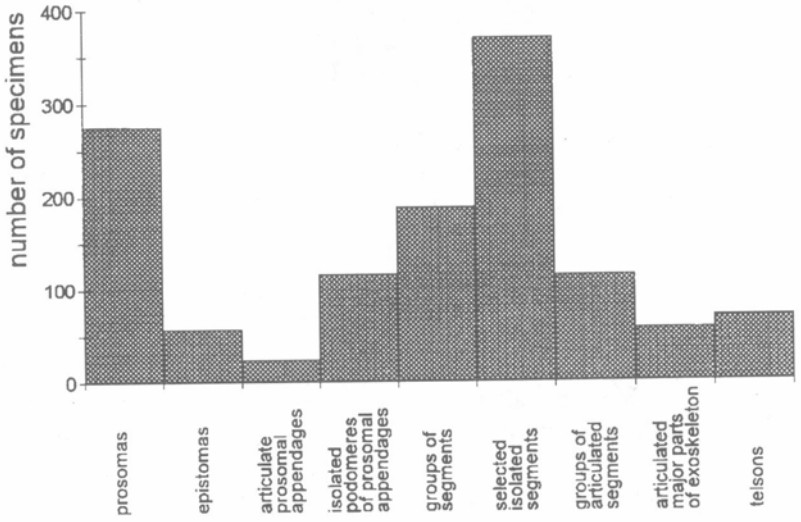

Fig. 3. Frequency histogram of collected exoskeletal parts of *Kodymirus vagans* (around 1200 specimens included)

The prosomal appendages are typically uniramous and markedly spinose. Large, probably movable spines and smaller fixed spines on individual podomeres are characteristic. The present finds exhibit a maximum of six articulated podomeres. The first podomere - the coxa - is not preserved in connection with any other more distant podomere and, therefore, the exact total number of podomeres in individual appendages is not known.

All prosomal appendages show some common features: Three proximal podomeres preserved in articulation and interpreted as the second to fourth podomeres of walking legs, exhibit on their posterodistal (in original position evidently ventrodistal) edge very marked and long, probably movable, spines. The more distal podomeres, interpreted as the fifth to eight ones, also show prolonged spines on their posterodistal (originally ventrodistal) edges, but these spines are markedly shorter and evidently fixed (their articulation with podomeres is not expressed). The posterior

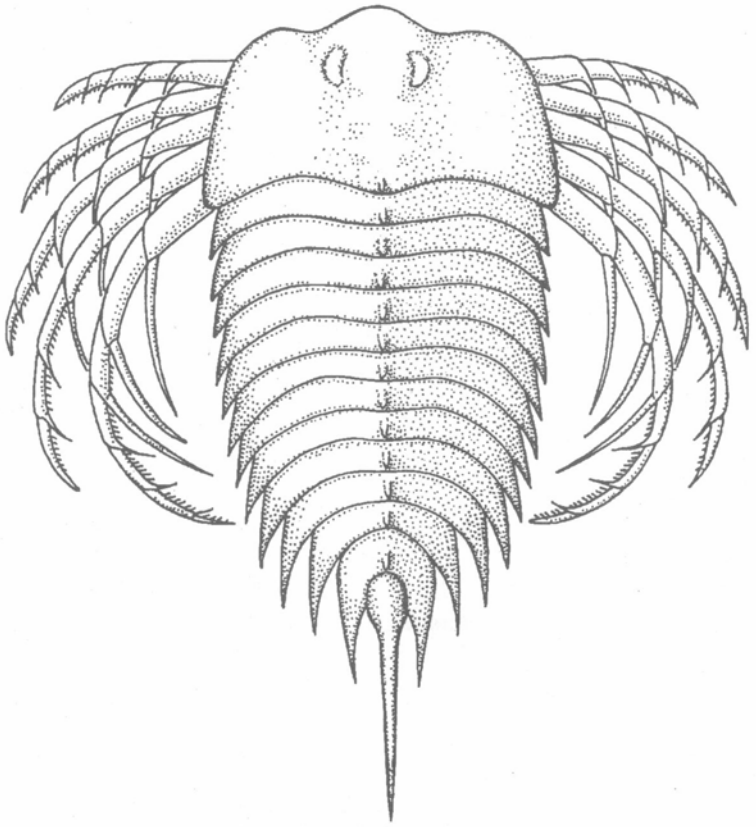

Fig. 4. *Kodymirus vagans,* reconstruction of the dorsal exoskeleton with prosomal appendages, total length around 80 mm

(in original position ventral) margin of these more distal podomeres bears a row of regularly arranged smaller fixed spines, in some cases alternating in size. The last and most distal podomere tapers markedly up to the curved spiniform edge.

Apart of these common features, individual appendages show marked differences, particularly in the length of podomeres. These differences point to a functional differentiation of appendages. In this respect, three types of appendages may be distinguished:

Type A. Three proximal podomeres are rather short, prolonged in posterodistal (ventrodistal) edges into long but mostly not curved spines. Three distal podomeres also short, with a row of simple fixed spines, gently increasing in size distally. Examples: MR65828 (Text-fig. 6, 1), MR65829 (Text-fig. 6, 2), possibly MR65794 (appendage on the right side of the Text-fig. 5, 5).

Type B. Three proximal podomeres longer than in the Type A, with long gently curved movable spines on posterodistal (ventrodistal) edges. Three distant podomeres markedly longer than in the Type A, with markedly thickened and prolonged spines on posterodistal (posteroventral) edges, but shorter than in proximal podomeres. A regular row of short fixed spines on posterior (ventral) margin, alternating in size in some specimens. Examples MR20489 (Text-fig. 6, 3), MR65826 (Text-fig. 6, 4), MR65767 (Pl. V, fig. 6, Text-fig. 6, 5), MR65797 (Pl. V, fig. 1, Text-fig. 6, 6).

Type C. Proximal and distal podomeres longer than in types A and B, three (or four?) proximal podomeres with very long and curved movable spines on posterodistal (posteroventral) edges, three distal podomeres prolonged and slender , with a regular row of fixed small spines on the inner (ventral) margin. The whole appendage markedly curved with adaxially trending distal podomeres. Examples: MR20490 (Pl. IV, fig. 1, Text-fig. 5, 3), MR65796 (Pl. IV, fig. 4, Text-fig. 5, 1), MR65795 (Pl. IV, fig. 3, Text-fig. 7, 1), probably MR20694 (Pl. VI, fig. 5, Text-fig. 7, 4).

The interpreted position of individual appendages is based on a presumption of backward increase in total length which is expressed in an increase in podomere length. This is supported by finds of appendages in contact with other parts of the exoskeleton, as shown especially in MR20490 (Pl. IV, fig. 1, Text-fig. 5, 4), MR65796 (Pl. IV, fig. 4, Text-fig. 5, 1) and MR65795 (Pl. IV, fig. 3).

Whilst the most anterior and chelae-bearing appendages of the first pair were probably small and remain unknown, the Type A appendages may be regarded as representing the second and/or third pair of head appendages. Consequently, the longer appendages of the Type B may be interpreted as the fourth and fifth pair, and the Type C as the last, sixth pair. In spite of differences in podomere lengths, all appendages show a substantial degree of resemblance and may be classified as "walking legs" sensu Stormer (1955) or "spiniferous legs" sensu Tollerton (1989).

The first podomeres or the coxae were found either in association with other exoskeletal parts of *Kodymirus*, or completely isolated but never in connection with articulated appendages. The specimen MR65829 (Text-fig. 6, 2) preserves an isolated coxa in close proximity to the articulated Type A appendage. The coxal gnathobase shows small teeth and the arcuate distal part exhibits a densely serrated margin, the diameter of which may indicate the correspondence with the articulated appendage in proximity. Another isolated coxa MR65801 (Pl. V, fig. 5; Text-fig. 7, 6) shows a strongly and unequally denticulated gnathobase and arcuate and non-serrated distal portion. The diameter of 4 mm corresponds to obvious dimensions of the *Kodymirus* appendages. The fragmentary coxa MR65799 is unusually large and its incomplete diameter of 15 mm markedly exceeds the common

measurements of corresponding parts of *Kodymirus* (its assignment to *Kockurus grandis* seems to be more probable, though without clear evidence).

The reconstructed position of prosomal appendages in Text-fig. 4 is based particularly on finds MR65796, MR20490, MR65795 and MR65783 (see Pl. IV, Text-fig. 5) which all show the appendages directed posterolaterally with spines turned backwards. However, the specimen MR65794 and MR65789 (Text-fig. 5, 3, 5; Pl. IV, fig. 2, Pl. III, fig. 1) show the appendages with spines turned anteriorly which would correspond the reconstructions of strongly spiniferous appendages of *Mixopterus* (Stormer 1934) and *Megalograptus* (Caster and Kjellesvig -Waering 1964). This difference is not fundamental, as the appendages exhibit a considerable radius of movement allowing the spines to be ventrally directed during the search food on the sediment surface.

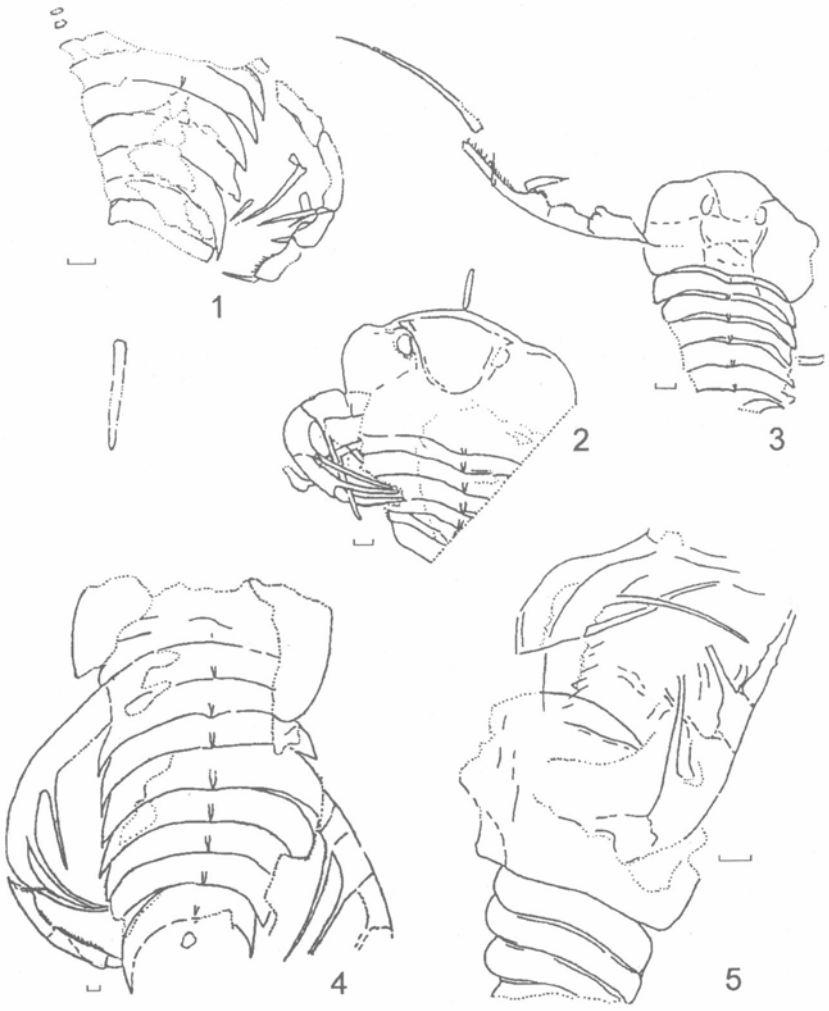

Fig. 5. *Kodymirus vagans*, selected finds of prosomal appendages in connection with other parts of the exoskeleton. Paseky Shale, Mt. Kočka
1 - smaller specimen MR65796, opisthosomal segments, prosomal appendage and telson, (comp. Pl. IV, fig. 4, 2); *2* - prosoma with imprinted epistoma and one appendage, MR65783; *3* - prosoma, head appendage and anterior opisthosomal segments, MR65789, (comp. Pl. III, figs. 1, 2); *4* - fragmentary prosoma, opisthosoma and posterior prosomal appendages, MR20690, ventral view (comp. Pl. IV, fig. 1); *5* - obliquely flattened prosoma, anteriorly shifted prosomal appendages and anterior opisthosomal segments, MR65794 (comp. Pl. IV, fig. 2). Scale bars=1mm

Opisthosoma

The opisthosoma or trunk consists of twelve segments (tergites) and a telson.

The anterior six to seven segments retain an approximately equal transverse width and sagittal length. The successive posterior segments (tergites) markedly taper by decreasing in transverse width backwards, whilst their sagittal length gently increases (particularly in the last two segments). The shape of segments changes accordingly: the first six tergites are analogous and exhibit transversely wide pleural regions, the successive posterior tergites are marked by progressively backwardly deflected pleural regions up to the horse-shoe-shaped last segment - the pretelson. The posterolateral tips of all segments are prolonged into backwardly directed spines the length of which gradually increases posteriorly in contrast to the transversal width.

Segments show a gently developed trilobation expressed in the increase of convexity in the axial region and in the posterior curvature of the flat pleural regions. A characteristic feature of the opisthosoma is a longitudinal row of median ridges (nodes). Each ridge is placed medially on the tergite and forms a sagittaly prolonged ridge-like elevation terminated by a pointed apex close to the posterior margin of the segment.

Narrow articulation facets are indicated as sculptureless gently convex bands along the anterior segment (tergite) margin. The overlapping of successive tergites occurred in an area markedly longer sagittally than the articulating facets (Pl. III, fig. 5, the overlap marked by darker bands). The overlap varies according to the position of the opisthosoma and may be strongly asymmetrical in laterally curved specimens (comp. also the gently curved holotype, Pl. I in Chlupáč and Havlíček 1965).

The telson is styliform, rather long and straight. Its proximal part - the telson head - is widened and prolonged anteriorly (Pl. VI, figs. 7-9). It is partly covered by the last tergite where it is preserved articulated (Pl. III, fig. 5).

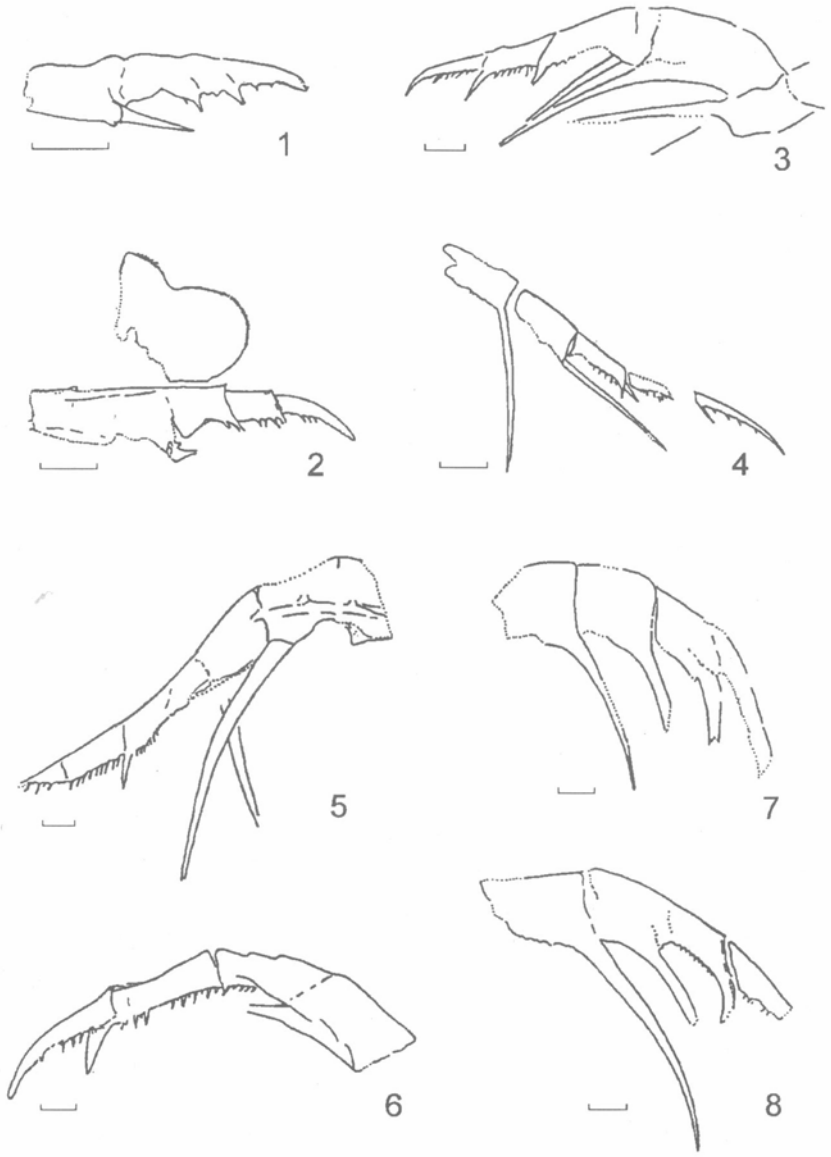

Fig. 6. *Kodymirus vagans*, isolated head appendages. Paseky Shale, Mt. Kočka
1 - appendage of the type A, MR65828; *2* - appendage of the type A, isolated coxa, MR65829; *3* - appendage of the type B with five podomeres in connection, MR20489; *4* - appendage of the type B with five podomeres, MR65826; *5* - appendage of the type B, distal podomere incomplete, MR65767; *6* - appendage of the type B with four podomeres, MR65797; *7* - proximal part of appendage (probably type B), MR65827; *8* - proximal part of the appendage (probably type B), MR20483. Scale bars=1mm

Whilst the telson head is convex dorsally, its ventral side shows a corresponding cavity open anteriorly and ventrally. The posterior part of the telson forms a lanceolate process gradually tapering backwards to a sharp termination. The lack of longitudinal ridges or furrows points to a rounded cross-section, probably subtriangular (its form is fully effaced by flattening). The length of the telson is about one fifth or one sixth of the total length of the exoskeleton.

The sculpture of the opisthosoma corresponds to that of the prosoma: dense and fine. Rather uniform granulation covers the dorsal side of segments and the telson except the articulating facets, tips of pleural spines and the proximal part of the telson head. A decrease in size of granulae in proximity of segment margins is demonstrable in specimens with a well preserved surface.

Ontogeny

The smallest opisthosoma MR65793 with eleven preserved segments and the telson head (Pl. III, fig. 8) is 8 mm long and belongs to an individual of calculated total length around 11 mm (without telson).It shows a well developed longitudinal row of median nodes and segments similar in shape to adult forms (only the pleural regions and spines seem to be transversely shorter and the whole opisthosoma more slender, but effects of compaction cannot be excluded).

Another small specimen MR65792 (Pl. III, fig. 7) is slightly ventrally curved and laterally compressed showing the left side of the opisthosoma (12 segments and the proximal part of the telson) and obliquely compacted prosoma. This specimen also exhibits a well-marked longitudinal row of median ridges and short pleural spines. Its total length without telson is calculated to around 12 or 13 mm.

The smallest prosomas (length 4 to 6 mm, width 6 to 9 mm) do not show any marked differences, especially in the length/width ratio, from the adult forms (cp. Text-fig. 1). However, some ontogenetic changes in the relative size and position of eyes and/or anterior prosoma outline are to be expected, though effects of compaction hinder their evaluation. The posterolateral angles of the prosoma are characteristically pointed but not extended into genal spines. This is evidenced in individuals of different size but exceptions do exist: two specimens which exceed in larger dimensions from the common average (Pl. VI, figs. 5, 6) exhibit distinctly developed sharp and posteriorly directed genal spines. As the whole configuration of the prosoma otherwise agrees with *Kodymirus vagans*, the presence of genal spines is regarded as a gerontic feature.

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Measurements

The total length of the smallest known specimens is calculated to around 11 to 13 mm (see the ontogeny). The length/width dimensions of measured prosomas (Text-fig. 1) and their comparison with articulated specimens result in calculated total exoskeleton lengths between 14 and 80 mm (without telson, i.e. around 17 to 100 mm with the telson). Some isolated segments may point still to larger dimensions exceeding the total length 100 mm.

Larger values calculated by Chlupáč and Havlíček (1965) are not plausible, as they were based on remnants of *Kockurus grandis* erroneously regarded as segments of *Kodymirus* (Pl. VI, fig. 8 in the paper cited).

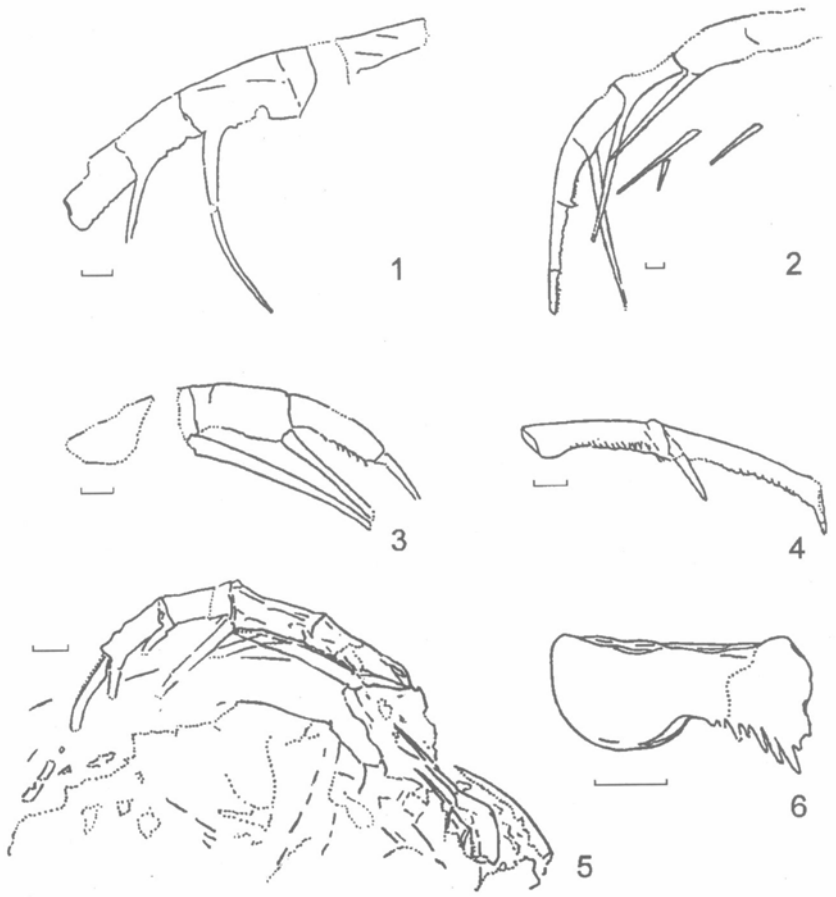

Fig. 7. *Kodymirus vagans*, isolated prosomal appendages, Paseky Shale, Mt. Kočka
1 - appendage of the type C with four incomplete podomeres, MR65795; *2* - appendage of the type B or C, MR65798; *3* - appendage of the type B or C with four incomplete podomeres, MR65830; *4* - distal part of the appendage, probably type C, MR20494; *5* - isolated coxa MR65801; *6* - isolated fragmentary coxa MR65800. Scale bars=1mm

Affinities and systematic position

Kodymirus vagans was originally placed with aglaspidids (Chlupáč and Havlíček 1965) and referred to merostomes. Its position was discussed particularly by Bergström (1968) who assigned it, mainly on the basis of the 12 opisthosomal segments and the presence of epistoma, with eurypterids (comp. also Bergström 1979). This was not followed by Whittington (1979) and *Kodymirus* was omitted from reviews of eurypterids presented by Tollerton (1989) and Selden (1993).

Evaluating the systematic position of *Kodymirus*, some basic features should be reported:

1. The gross morphology of the exoskeleton, particularly the configuration of opisthosomal somites with gently developed trilobation and wide pleural regions tapering backwards only gradually, agrees with aglaspidids as monographed by Raasch (1939) and revised by Hesselbo (1992).
2. The sculpture (dense granulation) and phosphatic composition of the cuticle (confirmed by spectroscopic investigation) agree with aglaspidids.
3. The number of opisthosomal segments - 12 in *Kodymirus* and 11 in aglaspidids, suggests an affinity with eurypterids.
4. The presence of epistoma, which is unknown in aglaspidids, also strenghtens the eurypterid relationships. However, the epistomas of eurypterids are unlike that of *Kodymirus* which strongly resembles the hypostoma of trilobites.
5. The decisive features for the systematic evaluation are in the configuration of appendages. These are basically different in *Aglaspis* excluding this crucial genus from chelicerates (Briggs - Bruton - Whittington 1979). The strongly spiniferous prosomal appendages of *Kodymirus* show some analogy with the *Ctenopteruss* or *Mixopterus* B types in Tollerton's (1989) review, but they also differ substantially from these types in development of spinosity both in proximal and distal podomeres.

The functional differentiation of individual pairs of prosomal appendages of *Kodymirus* is much less advanced than in the great majority of stratigraphically younger eurypterids whose sixth pair is commonly transformed into a swimming organ (swimming leg paddle).

The gross configuration of prosomal appendages which in *Kodymirus* may be all assigned as spiniferous walking legs, shows some resemblance with the superfamily Stylonuroidea (oldest representatives in late Ordovician). However, the differences in *Kodymirus* appendages are so marked that affinities to established families of eurypterids remain obscur. Within the class Eurypterida, *Kodymirus vagans* corresponds, particu-

larly in the presence of epistoma, spiniferous prosomal appendages, lost of marked trilobation and in the styliform telson, to the theoretical ancestor of "protostylonuroid" eurypterids as postulated by Waterston (1979). The general morphology of the exoskeleton allows *Kodymirus vagans* to be designated as an "aglaspidid-like eurypterid".

The above conclusions result in assignment of *Kodymirus vagans* to chelicerates.

The oldest known chelicerate so far is *Sanctacaris uncata* Briggs et Collins, 1988 from the Middle Cambrian Stephen Formation of British Columbia. This peculiar arthropod, thoroughly described by Briggs and Collins (1988), exhibits some similarity with *Kodymirus* in the configuration of trunk segments and anterior projection of the front of prosoma, but it exhibits a different position of eyes, eleven opisthosomal segments without prolonged pleural spines, two longitudinal rows of ridges on the trunk and a paddle-like telson. The head appendages are fundamentally different: *Sanctacaris* exhibits five pairs of rather short spinose raptorial limbs flanked by antenna-like rami, Briggs and Collins (1988, Text-figs. 1A, 1B, 2A), all markedly differing from the extremely long appendages of *Kodymirus* (comp. Text-fig. 4).

Like many Cambrian arthropods, *Kodymirus* cannot be ranged within the known hierarchic scheme of superfamilies and families of arthropods. Consequently, - as the "aglapidid-like eurypterid" - it may be regarded as belonging to "non aligned" arthropods, representatives of which are known e.g. from the Burgess Shale or Chengjiang faunas (see reviews in Conway Morris 1986, Whittington 1985, Briggs and Fortey 1989, Gould 1989, Briggs 1990, Hou Xianguang et al. 1991, Hou Xianguang and Bergström 1991).

Occurrence. *Kodymirus vagans* strongly dominates the fauna of the Paseky Shale in all localities. It is very common at Mt. Kočka, frequent at Mt. Tok, markedly less common at Medalův mlýn. A single fragment is known from the locality N of Nepomuk (see Chlupáč et al., this volume).

Genus *Kockurus* n. gen.

Type species: *Kockurus grandis* gen. et sp. n., here described.

Derivatio nominis: named according to the type locality, Mt. Kočka in the Brdy Mts.

Diagnosis. Prosoma semicircular in outline, gently convex in axial region. Eyes allantoid in outline, placed centrimesially. Posterolateral angles protruded into genal spines.

Comment. The diagnosis is so far based on the prosoma only, as the epistoma and other parts of the exoskeleton were not found in direct connection with prosomas undoubtedly belonging to *Kockurus*. Species:

Kockurus grandis sp. n.

Kockurus grandis sp. n.

Pl. VII, VIII; Text-fig. 8

partim 1965 *Kodymirus vagans* n. sp., Chlupáč and Havlíček, pl. 6, fig. 5 and possibly 6 (non cetera)

Holotype: Incomplete prosoma MR65777 figured on Pl. VII, fig. 3.

Locus typicus: Mt. Kočka, Brdy Mts., central Bohemia.

Stratum typicum: the Paseky Shale, Lower Cambrian.

Derivatio nominis: from Latin *grandis* - large.

Material: 41 incomplete prosomas, 8 epistomas. The conspecifity of other parts (opisthosomal segments, telsons) is very probable but not completely established.

Description. Prosoma semicircular in outline, the length/width ratio ranges between 0.6 and 0.7. The anterior margin simply arcuate, the posterior margin transverse and straight. Posterolateral angles protruded into short genal spines, directed posterolaterally and pointed distally. Eyes allantoid in outline, rather narrow, gently curved abaxially. The increased convexity of the axial region of the prosoma is indicated by subconcentric compaction wrinkles marked in some specimens (Pl. VII, figs. 1, 7, 8; Pl. VIII, fig. 3.). The border is not differentiated but a narrow darker band accentuating the outer outline indicates a gentle thickening of the cuticle along the anterior margin. A smnall median node pointed posteriorly is placed in the axial part of the posterior margin.

The sculpture consists of a very fine granulation which becomes denser and more expressed in proximity of the prosoma margins and on the genal spines (comp. Text-fig. 9).

Isolated epistomas (Pl. VII, fig. 4) regarded as conspecific particularly because of their correspond-

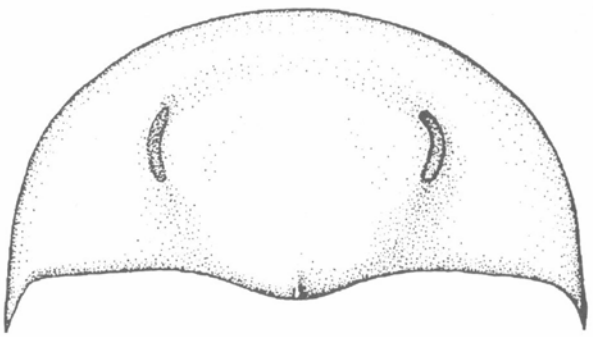

Fig. 8. *Kockurus grandis*, reconstruction of the prosoma according to finds from the Mt. Kočka

ence in size to the co-occurring prosomas, are distinguished by markedly convex and arcuate anterior margin and a strongly curved and parabolical posterior margin. Anterolateral wings are directed posterolaterally, following the curvature of the anterior margin. The convexity is effaced by flattening but the change of direction between the proximal and distal parts of wings is indicated by a fold perceptible in some specimens.

No opisthosomal segments were found in direct connection with prosomas undoubtedly belonging to *Kockurus grandis*. However, some isolated segments, marked by large dimension and lack of dense granulation, are probably conspecific.

Among more complete specimens, two finds deserve special attention.

The specimen MR65811 (Pl. VIII, figs. 1, 2) shows seven opisthosomal segments, similar in configuration to *Kodymirus*, in connection with a fragmentary prosoma indicating a subcircular outline of the anterior margin analogous to *Kockurus* but lacking distinct genal spines. The epistoma preserved below and imprinted into the dorsal prosomal exoskeleton, exhibits a parabolic to gently pointed posterior outline characteristic of epistomas associated with *Kockurus*. Though conspecifity with *Kockurus grandis* is very probable, it cannot be so far regarded as completely established.

Another remarkable specimen is MR65812 (Pl. VIII, fig. 4). It represents a strongly curved and obliquely flattened entire exoskeleton. The fragmentary prosoma indicates a semicircular outline and short genal spine characteristic of *Kockurus*. The opisthosomal segments are analogous as in *Kodymirus* and show even a marked longitudinal row of median ridges in axial parts. The number of segments, however, seems to be unusually high, namely 14 to 16. Though the substantial degree of overlap and imprints of overlapping segments during compaction may obscure the real number of segments,the possibility of more than 12 demands evaluation, having no analogy in eurypterids or aglaspidids. The exoskeleton terminates in a styliform telson with a longitudinal ridge behind the broadened telson head.The specimen is preserved together with a fairly large specimen of *Vladicaris subtilis* and several indeterminable fragments as a rounded cluster of organic remains as commonly occurring in the Paseky Shale (comp. also R. Mikuláš in this volume).

The specimens MR65811 and MR65812 support the conclusion that the opisthosomal segments of *Kockurus grandis* are very similar to *Kodymirus vagans*, being hardly distinguishable if found isolated. Some large segments with short pleural spines and suppressed granulation may thus belong to *Kockurus* rather than to *Kodymirus* (e.g. Pl. VI, fig. 6 in Chlupáč and Havlíček 1965). The same is true of several isolated telsons, some of which exhibit fairly large dimensions (the length exceeds 22 mm, Pl. VIII, figs. 5, 6). In contrast with telsons found in connection with opisthosomas of *Kodymirus*, they show a distinct gentle curvature and indices of longitudinal ridges which may point to an angulate cross-section behind the telson head.

Measurements. The holotype shows the sagittal length of prosoma to be 19 mm and the extrapolated width around 40 mm. The length of other prosomas ranges between 10 and 20 mm, width 25 to 40 mm. Some fragmentary specimens indicate still larger dimensions (extrapolated prosomal width around 50 mm).

Remarks. *Kockurus grandis* differs from *Kodymirus vagans* particularly in the simply arcuate anterior, and transverse posterior margins of the prosoma (without anterolateral notches), invariable presence of genal spines, allantoid shape and centrimesial position of eyes, and finer sculpture (less dense granulation on most parts of prosoma except the border regions).

The epistomas assigned to *K. grandis* differ from those assigned to *Kodymirus* in a markedly curved anterior margin, posterolaterally directed wings and especially in the posterior outline of the main lobe which is narrower and parabolic.

The general configuration of the exoskeleton and particularly the opisthosomal segments,were most likely analogous to those in *Kodymirus*. However, as suggested by MR65812, the number of opisthosomal segemnts might be larger and the detailed configura-

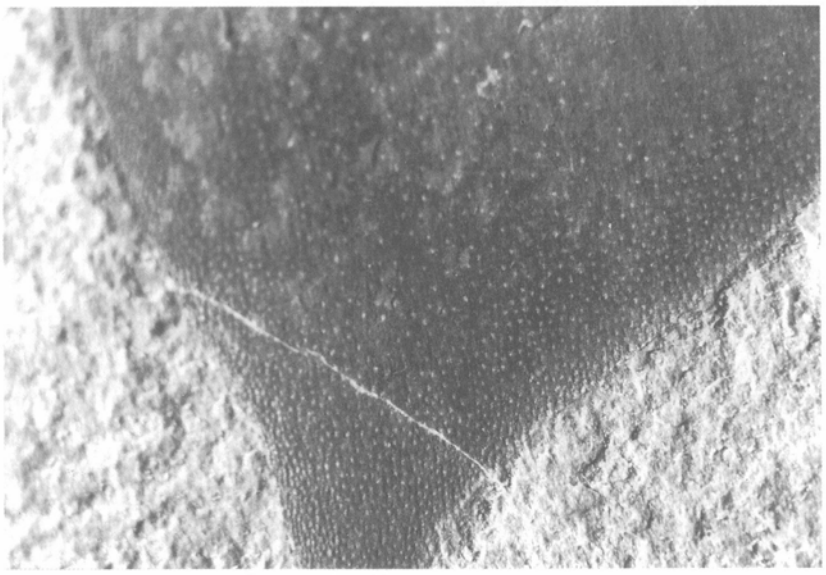

Fig. 9. *Kockurus grandis*, strongly enlarged posterolateral part of prosoma at the genal spine showing the fine granulation becoming denser close to margins

tion of the telson different. Future discoveries are necessary to elucidate the true relationships of *Kockurus grandis*.

Occurrence. *K. grandis* is much rarer than *Kodymirus vagans* but it occurs at the same localities and in the same layers (Mt. Kočka, Mt. Tok, Medalův mlýn in the Litavka river valley)

Subphyllum Crustacea
Class Malacostraca Latreille, 1806
Subclass Phyllocarida Packard, 1879
Family Perspicarididae Briggs, 1978

Genus *Vladicaris* gen. n.

Type species: *Vladicaris subtilis* sp. n., Paseky Shale, Lower Cambrian, central Bohemia.

Derivatio nominis: named in honour of Dr. Vladimír Havlíček, the discoverer of the Paseky Shale fauna.

Diagnosis. Carapace valves suboval, smooth, very thin. Trunk slender, relatively small (compared to the carapace), telson subtriangular in dorsal view, pointed posteriorly, caudal furca not spinose.

Comment. The genus is tentatively referred to Phyllocarida, mainly on the basis of the bivalved carapace, configuration of the telson and furcal spines. The relationships are discussed under the type species.

Species: *V. subtilis* gen. et sp. n.

Vladicaris subtilis sp. n.

Pls. IX, X; Text-figs. 10, 11, 12

Holotype: specimen MR65773 preserved in lateral aspect, figured on Pl. IX, figs. 1, 2; Pl. X, fig. 2; Text-fig. 11, 3.

Locus typicus: Mt. Kočka, Brdy Mts., central Bohemia.

Stratum typicum: the Paseky Shale, Lower Cambrian.

Derivatio nominis: from Latin subtilis - subtle.

Material: 16 clusters composed of several specimens, 16 specimens preserving the carapace and the trunk in connection or in close proximity, 60 isolated carapaces, 34 isolated trunks (mostly abdominal parts), several isolated segments.

Description. Carapace very thin, bivalved. Both carapace valves are commonly almost perfectly overlapping and the bivalve nature of the carapace may be deduced merely from the doubled ventral margin with its thickened narrow border (Pl. IX, figs. 1, 2, 7, 8; Text-fig. 11, 3) or from carapaces preserved as two separate layers in the rock (Pl. X, fig. 3). The other evidence that the carapace is bivalved is two valves of corresponding size found in contact in parallel position (MR65831, 65833) or closely associated (Pl. IX, fig. 3).

Carapace valves suboval in outline, slightly tapering anteriorly and expanding posteriorly. The anterior margin is rounded, and narrower than the posterior one. The outline of individual carapace valves is markedly influenced by the orientation of the valves to bedding during compaction : diverse shapes from narrowly suboval (Pl. IX, figs. 1, 2; Pl. X, figs. 2), anteriorly pointed (Pl. X, fig. 4), up to broadly suboval (Pl. IX, figs. 7, 8; Pl. X, fig. 1) are represented. The hinge line proper is only seldom clearly evident. It is straight in parallel aspect, and, as deduced from laterally compressed valves, gently curved dorsally. The original convexity of valves was evidently low and no marked concentric folds appear in laterally compressed valves. A thickening of the carapace along the ventral margin indicating a narrow ventral border is marked by a darker colour band or accentuated by a low ridge parallel with the margin (Pl. IX, figs. 6, 7; Pl. X, fig. 1). The surface of valves is smooth.

The trunk consists of inferred 17 (or even more?) segments. The full and exact number of segments is not known due to unclear preservation of the anterior part of the trunk, usually within the carapace valves. Isolated trunks found outside the carapaces exhibit in maximum 14 to 16 segments (Pl. X, figs. 5, 6, 7). The lack of distinctly preserved appendages prevents a clear distinction between thoracic and abdominal segments which all show no perceptible differences (7 posterior somites are classed as abdominal according to general configuration in phyllocarids).

The trunk gradually tapers posteriorly. This is evident particularly in the posteriorly decreasing transverse width of segments, whilst the sagittal length of individual segments remains unchanged, particularly in the abdominal part (Pl. X, figs. 5 to 10).

The last abdominal segment (pretelson) is equal in length with the preceding ones and it is not prolonged as is the case in many phyllocarids. Inter-segment boundaries are straight, without denticles. Only the posterolateral corners of segments are pointed but not prolonged into spines. The transverse cross-section of at least the abdominal segments was subcircular or elliptical, as evidenced from isolated segments found in proximity of carapaces (Pl. IX, fig. 7).

The telson is longer sagittally than the pretelson segment. Its outline in parallel aspect is subtriangular or subpentagonal with markedly pointed posterior edge, not protruded into a spine (comp. e.g. Pl. X, figs. 5). The telson outline in lateral aspect is subquadrate with pointed and somewhat prolonged posterodorsal edge (Text-fig. 11, 1).

The furca consists of two rather long and slender rami. They taper gradually posteriorly and are straight in both parallel and lateral aspects. The angle of divergence of furcal rami is 70 to 90 degrees as measured in specimens preserved in parallel aspect (comp. also Pl. X, fig. 10). The angle of divergence in specimens

preserved in lateral aspect varies according to flattening. The details of articulation of furcal rami and the telson are obscured by compaction. However, several specimens suggest that the furca was articulated with the telson (see Pl. X, fig. 5 as an example). Both furcal rami were probably firmly connected on the ventral side below the telson (Pl. X, fig. 10).

The trunk was evidently flexible, particularly in the dorsoventral direction: it is commonly gently curved ventrally and also some lateral flexibility is indicated (Pl. IX, fig. 6).

The relative position of the carapace and the trunk is markedly variable and influenced by distortion during burial and compaction, or possibly by the moulting process. Whilst the holotype shows abdominal segments uncovered by the carapace and directed posteroventrally, i.e. in the inferred primary position (Pl. IX, figs. 1, 2; Pl. X, fig. 2), most other specimens show different positions of trunk segments in relation to the carapace: the trunk may be fully impressed into the carapace (Pl. IX, fig. 6), partly extended from the carapace or shifted outwards close to the ventral carapace margin (Pl. IX, fig. 4; Text-fig. 11, 2). These relations suggest displacements of abdomens observed in malacostracans and explained by post-mortem shift or moults.

Head and trunk appendages are not well demonstrable in *Vladicaris*. Some specimens, however, show dark parallel lines in different parts of compacted carapaces which may indicate remnants of pereiopods and/or pleiopods: the holotype (Text-fig. 11, 3.) shows a row of anteroventrally directed dark lines in the ventral area of the carapace and similar rows are found e.g. in MR65815 (Text-fig. 11, 2) and other individuals from the locality Mt. Kočka (comp. e.g. the specimen in the NW part of the cluster MR20920 figured on Text-fig. 12 b).

A longitudinal row of dark spots on trunk segments of MR65826 (Pl. X, fig. 6) probably indicates the trace of the alimentary canal (less expressed in several other specimens).

Measurements. *V. subtilis* is distinguished by a rather small size. The carapace length, which is generally less affected by secondary deformations, ranges in measurable specimens between 4 and 18 mm (comp. Text-fig. 10) but some fragmentary carapaces point even to higher values (calculated carapace length up to 25 mm). The histogram

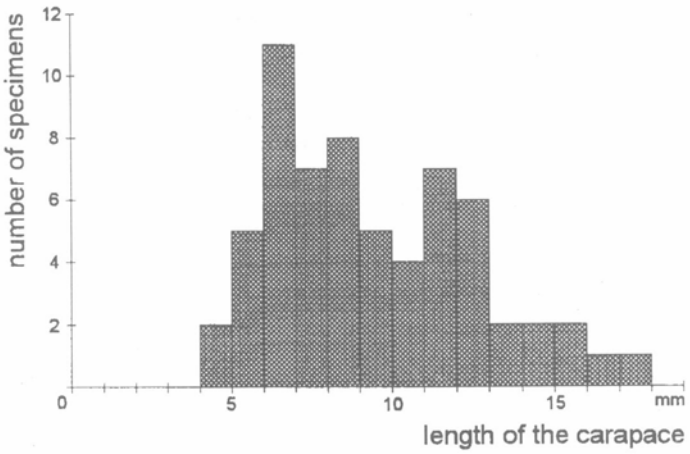

Fig. 10. Size-frequency histogram of carapace lengths of *Vladicaris subtilis* from the Paseky Shale (63 specimens measured)

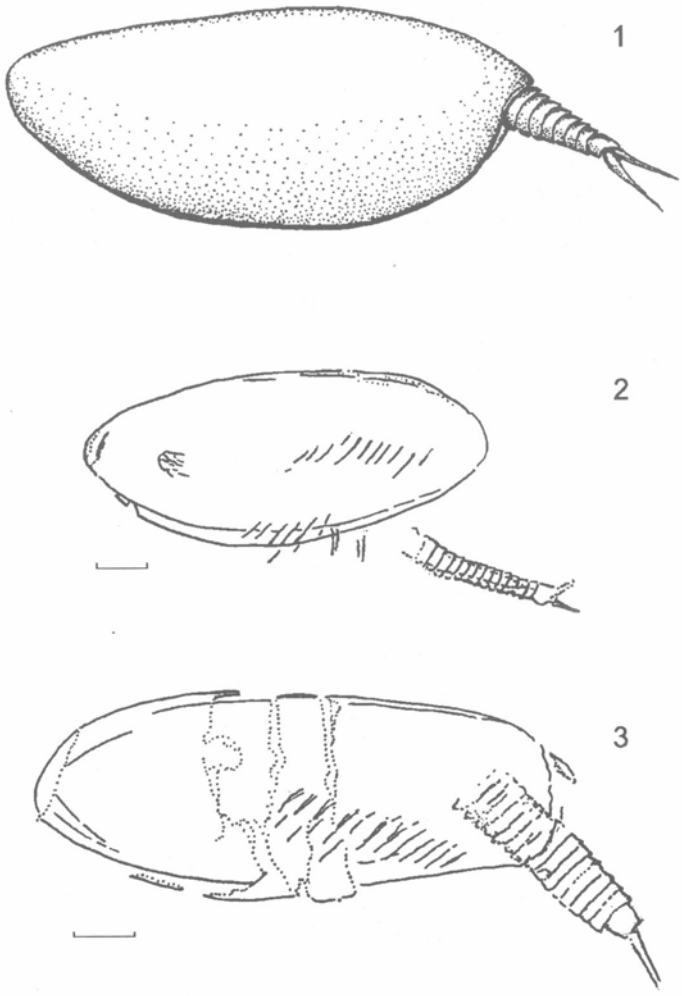

Fig. 11. *Vladicaris subtilis* gen. et sp. n. from the Paseky Shale
1 - reconstruction of the exoskeleton in lateral view, length around 12 mm; *2* - laterally flattened carapace with detached trunk, lines inside the carapace and close to its ventral margin indicate thoracal appendages, MR65815; *3* - laterally flattened specimen with traces of thoracal appendages inside the carapace, the holotype MR65773. Scale bars=1mm

on the Text-fig. 10 shows the maximum frequency of carapace lengths between 5 and 13 mm. The length of preserved trunks usually varies between 3 and 6 mm but also here some markedly larger specimens greatly exceed the average. The holotype exhibits a total length 11 mm, the length of the carapace is 8.6 mm.

Relationships. Among Cambrian arthropods, representatives of four genera show some similarity with *Vladicaris,* namely *Perspicaris* Briggs, 1976, *Canadaspis* Novozhilov, 1960, *Protocaris* Walcott, 1884 and *Branchiocaris* Briggs, 1976.

Most similarities are shown with *Perspicaris* from the Middle Cambrian Burgess Shale of British Columbia. Its type species *P. dictynna* (Simonetta et Delle Cave, 1975) as thoroughly described by Briggs (1977) shows a smooth bivalved carapace, subtriangular telson and prominent furcal rami but it differs from *Vladicaris* in a markedly shorter telson, furcal rami with rows of posteriorly directed spines, spinose posterior margins of trunk segments and generally larger proportions of the trunk in relation to the carapace. Less important differences concern the shape of carapace valves, the distinct hinge-line and probably thicker carapace cuticle.

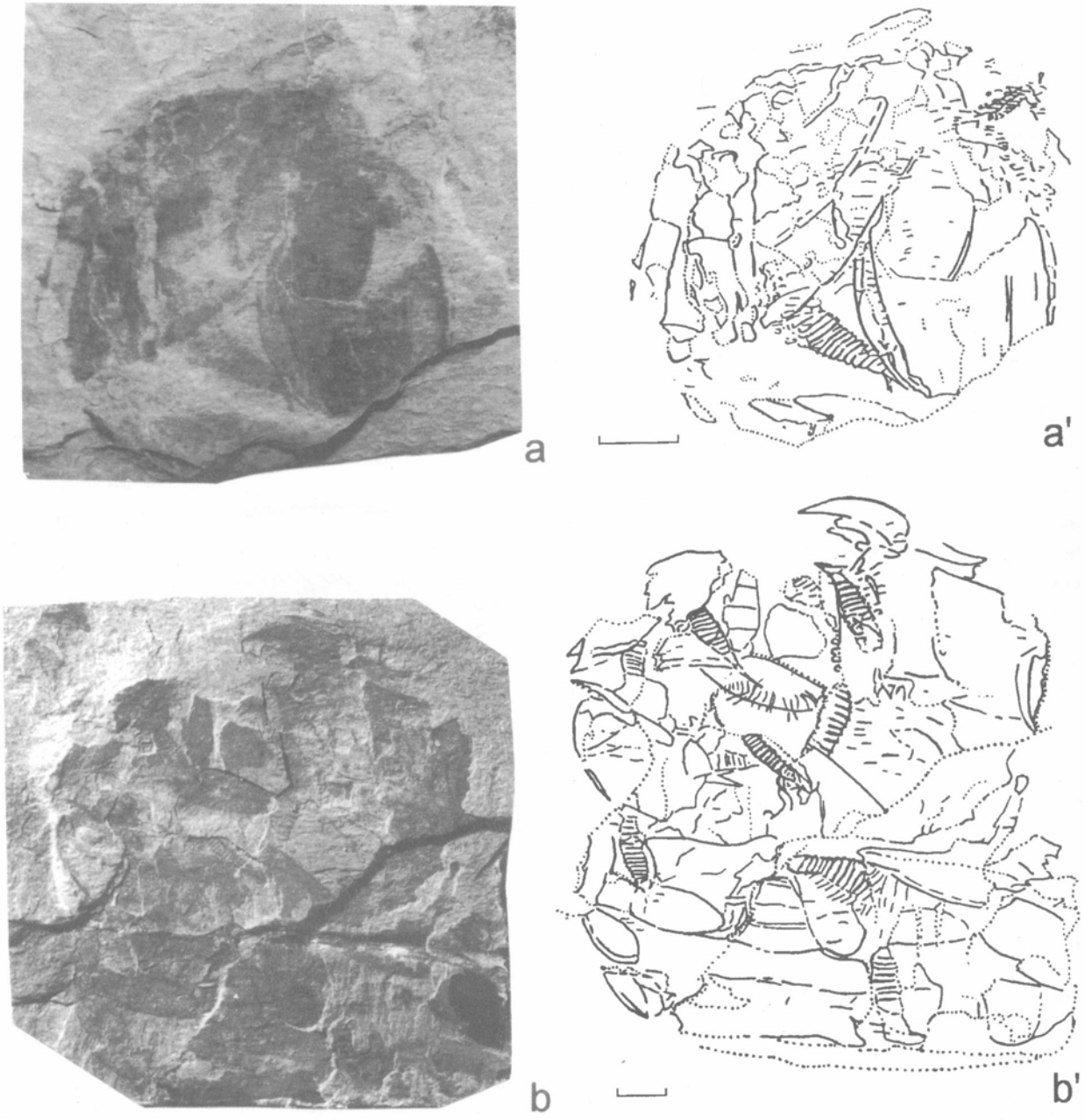

Fig. 12. Clustered carapaces and trunks of *Vladicaris subtilis* gen. et sp. n. from the Paseky Shale, Mt. Kočka
a - cluster of the characteristic circular outline, ICh7000, diameter 11.5 mm; *b* - cluster MR20920 with less regular outline, diameter around 25 mm. Scale bars indicate in drawings the length of 2 mm

Canadaspis, with the type species *C. perfecta* (Walcott, 1912) from the Burgess Shale, is following the study of Briggs (1978), one of the best known Cambrian crustaceans. It differs from *Vladicaris* in markedly shorter outline of carapace valves, stout and generally larger trunk, and basically different configuration of the pretelson somite which bears on its ventral side groups of unequal spinose projections. The telson of *Canadaspis* is shorter and posterior margins of segments are spinose. *Protocaris*, based on the single specimen of the type species *P. marshi* Walcott, 1884 from the Lower Cambrian of Vermont (see Briggs 1976), shows some similarity in smooth carapace valves, telson and furca, but its trunk is clearly multisegmented (the total segment number estimated to more than 65) and the curved furcal rami converge posteriorly.

Branchiocaris, with the type species *B. pretiosa* (Resser, 1929) from the Burgess Shale (description: Briggs 1976), is also distinguished by a multi-segmented trunk with more than 46 segments, the furcal rami forming broad lanceolate processes, strongly different from those in *Vladicaris*.

The Cambrian-Ordovician genus *Hymenocaris* Salter, 1853, to which the type species of *Canadaspis* was formerly referred, differs from *Vladicaris* in markedly larger trunk in relation to the carapace, absence of the hinge line, and in three pairs of caudal spines terminating the trunk (cp. Jones and Woodward, 1888, Rolfe in Moore, ed. 1969, p. R314-315).

Occurrence. *Vladicaris subtilis* is fairly common at Mt. Kočka together with *Kodymirus vagans* and less frequent *Kockurus grandis*. Very rare (single finds) from Mt. Tok, Medalův mlýn and Nepomuk.

Palaeobiological and taphonomical remarks

The faunal assemblage of the Paseky Shale, particularly at the localities Kočka and Tok which display frequent fossil occurrences, should be regarded as generally autochthonous.

This is supported in *Kodymirus* especially by a frequent representation of specímens with articulated even larger parts of exoskeleton (Text-fig. 2), by a common representation of individuals of different growth stages in the same layers, and by the frequent co-occurrence with traces assignable to the activities of *Kodymirus* (comp. R. Mikuláš in this volume).

In *Vladicaris*, the autochthonous origin is suggested by frequent specimens preserving the trunk either connected with the carapace, or in close proximity. This contrasts e.g. with the mode of occurrence of the worldwide distributed Ordovician phyllocarid genus *Caryocaris*, resembling in size and form *Vladicaris*, which is almost invariably found as separated carapaces and abdominal parts.

The presumption of autochthoneity does not exclude a short post-mortem transport of organic remains caused e.g. by vawe action. As shown by Allison (1986), carcasses of arthropods with slightly skeletized and flexible cuticle may withstand a transport without disarticulation and substantial damage, and some degree of transportation is evident from frequent occurrence of cuticle debris found in the Paseky Shale at several localities.

The mode of preservation of *Kodymirus* and *Vladicaris* point to a low-energy environment. However, the burial took place rather quickly: the progress of decay commonly reached only the Stages 2 (Ruptured) and 3 (Hollow) as stated by Briggs and Kear (1994) in Recent shrimps under laboratory conditions.

The mode of life of the Paseky Shale arthropods may be inferred from their morphology.

Kodymirus with strongly spinose and long limbs which likely served raptorial, locomotory and feeding functions, was most probably a nektobenthic predator. Long spines on its legs, particularly the posterior ones, possibly had also a sensory function in search and capturing the prey. *Kodymirus* was most likely a more active bottom dweller than swimmer, though it was adapted to search its food both on the bottom surface and within the water column immediately above it. Common traces, attributable to these activities of *Kodymirus* (comp. R. Mikuláš in this volume), support this interpretation.

Vladicaris with its thin carapace and delicate trunk was probably less dependent on the bottom feeding. It may be plausibly regarded as a nektonic animal which fed on suspensed organic particles or other so far unknown planktonic or nektonic organisms.

The arthropod remains of the Paseky Shale commonly occur in clusters. These may be composed of remnants of one taxon, or, more frequently, of more taxa, namely *Kodymirus* associated with *Vladicaris* or even with *Kockurus*. Within the clusters, the remains are frequently articulated or only incompletely disarticulated, commonly flexed to conform the circular outline of the cluster. This mode of occurrence almost excludes any longer transport and suggests that clusters originated at the primary biotope of the Paseky Shale arthropods.

The origin of clusters may be diverse. Less regular clusters may originate by sedimentary processes, e.g. wave action in a very shallow-water environment. In clusters of regular circular outline, an organic origin is plausible (accumulations in domiciles or bromalites of some unknown organisms, comp. R. Mikuláš in this volume).

The clustered remains of *Vladicaris* strongly suggest rather common cases of clustering in Palaeozoic bivalve arthropods as shown e.g. in the Lower Cambrian Chengjiang fauna (Hou Xianguang and Bergström 1991), in Canadaspis from the Middle Cambrian Burgess Shale (Briggs 1978: 445, 447) and in the

world-wide distributed Ordovician genus *Caryocaris* (Chlupáč 1970). This mode of occurrence may suggest a gregarious habitat.

A substantial part of the Paseky Shale arthropods may be regarded as moults. The gradual size increase demonstrated in prosomas of *Kodymirus* (Text-fig. 1) suggests that the size differences between moult stages were small, not resulting in clearly defined groups of points in the diagram. The representation of moults in *Vladicaris* may be inferred from the relative position of the carapace and the trunk, frequently displaced but in close proximity. However, taphonomic processes of inorganic origin may result in a similar configuration (comp. Schäfer 1951, Rolfe 1962).

The size diagram of *Vladicaris* (Text-fig. 10) indicates several peaks in carapace lengths between 5 and 13 mm which may indicate molt stages, but the number of available specimens is not sufficient for conclusive statements.

The assemblage of arthropods of the Paseky Shale is distinguished by its low diversity, the abundance of its dominant components (*Kodymirus, Vladicaris*), and the consistent composition at diverse localities. This conforms to the geological distribution and lateral persistence of the fossiliferous Paseky Shale Member as documented in the geological part (Chlupáč et al., this volume).

The spread of the Paseky Shale fauna with *Kodymirus* may be explained as a time-limited invasion of arthropods into the restricted marine or non-marine, most likely brackish lagoonal realm. These arthropods, with originally marine ancestors, evolved here as an endemic and special community. This conclusion corresponds to the geological evidence, lithology (see Z. Kukal in this volume) and the special character of the ichnofacies and microbiota (see R. Mikuláš and O. Fatka - M. Konzalová in this volume).

Conclusions

The Lower Cambrian arthropod fauna of the Paseky Shale, known exclusively from the Brdy Mts. area of central Bohemia, is unique and unusual in its composition and character. It consists of non-trilobite arthropods represented by strongly dominant and frequent *Kodymirus vagans* with demonstrable eurypterid affinities, *Vladicaris subtilis* gen. et sp. n. tentatively ranged with phyllocarids, and the so far imperfectly known *Kockurus grandis* gen. et sp. n. The endemic character of the assemblage and its composition reflect unusual life environment for the Cambrian Period.The representation of arthropods with eurypterid and crustacean affinities which during their later evolutionary history showed trends of invading non-marine and restricted marine environments (cp. review in Gray 1988), makes a conclusion on a non-marine or at least not "normal-marine" (brackish) environment of the Paseky Shale fauna most plausible.

However, restricted marine influences should be considered. Ancestors of the Paseky Shale fauna are to be sought in marine realms which were inhabited as early as in the early Cambrian by rich arthropod assemblages (the best known example is the Chengjiang fauna, which is older than the famous Middle Cambrian Burgess Shale fauna).

The Paseky Shale fauna might fit the concept of significance of non-marine environments for the evolution of arthropods as expressed by Bergström (1979, 1980), but the origin of the Paseky Shale arthropods should be sought rather in marine realms.

A temporary invasion of arthropods from the shelf sea into the restricted-marine or even non-marine, most likely lagoonal and brackish environment, and a subsequent development of a special low diversity assemblage seem to be the appropriate explanation for the Paseky Shale fauna.

The Paseky Shale fauna is at present the oldest known fauna of suspected non-marine or restricted marine environment. It is also the oldest fauna known from the territory of the Barrandian and the Czech Republic proper. Owing to its unique character, it deserves further studies and protection of its localities as geological and palaeontological sites of international interest.

Submitted January 12, 1995 *Translated by the author*

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Spodnokambričtí arthropodi paseckých břidlic (Barrandien, Česká republika)

Nejstarší česká fauna, známá ze spodnokambrických paseckých břidlic centrálních Brd, je jedinečná svým složením i charakterem. Sestává výlučně z členovců, mezi nimiž výrazně dominuje *Kodymirus vagans* Chlupáč et Havlíček, 1965, který je nejstarším známým zástupcem podkmene Chelicerata a přes podobnost s aglaspididy vykazuje afinitu k eurypteridům. Vzácnější je korýš *Vladicaris subtilis* n. gen. et sp. se vztahy k phyllocaridům a zatím neúplně známý větší členovec *Kockurus grandis* n. gen. et sp., patrně systematicky blízký rodu *Kodymirus*.

Fauna paseckých břidlic obývala pro kambrium zcela neobvyklé prostředí, které lze interpretovat nejspíše jako brakickou lagunu s omezenou komunikací s mořem. I když je třeba hledat fylogenetické předky fauny paseckých břidlic v prostředí mořském, které již ve spodním kambriu hostilo značně diverzifikovaná společenstva arthropodů, je faunistická asociace paseckých břidlic zatím nejstarším příkladem invaze fauny do nemořského či omezeně mořského prostředí. Výskyt této fauny výrazně zvyšuje význam Brd pro geologické i biologické vědy a akcentuje nutnost ochrany paleontologických lokalit.

Explanation of plates

Plate I

1-8 - *Kodymirus vagans* Chl. et Havl., Paseky Shale, Mt. Kočka
1 - prosoma MR65758, sagittal length 9.2 mm; 2 - prosoma with indicated muscular markings and two opisthosomal segments, MR65762, length of prosoma 14 mm; 3 - prosoma of a younger specimen MR65778, length 5.3 mm; 4 - prosoma of a younger specimen MR65779, length 8.8 mm; 5-6 prosoma with muscular markings in different lights, MR65780, length 10.8 mm; 7 - prosoma with gently differentiated central part, MR65781, length 11.7 mm; 8 - prosoma of a young specimen MR65782, sag. length 6.2 mm.

Plate II

Kodymirus vagans Chl. et Havl., Paseky Shale, Mt. Kočka and Mt. Tok (fig. 4 only).
1 - epistoma MR65783. sag. length 7.1 mm; 2 - epistoma MR65763, length 7mm; 3 - epistoma MR20300, length 7 mm; 4 - anterior part of prosoma with imprinted epistoma MR65784, width 23 mm; 5 - the forelast opisthosomal segment MR65785, preserved width 19.8 mm; 6 - anterior opisthosomal segment MR65765, width 32.2 mm; 7 - medium opisthosomal segment MR65786, width 15.8 mm; 8 - last opisthosomal segment (pretelson) MR65787, sag. length 6.9 mm; 9 - anterior opisthosomal segemnt MR65788, width 20.4 mm.

Plate III

Kodymirus vagans Chl. et Havl., Paseky shale, Mt. Kočka.
1, 2 - prosoma, anterior part of opisthosoma and one head appendage shifted from the original position, MR65789, sag. length 13 mm, fig. 2 whitened with ammonium chloride; 3, 4 - prosoma and incomplete opisthosoma MR65790, sag. length 30 mm; 5 - opisthosomal segments and telson MR65766, length 23 mm; 6 - incomplete opisthosoma of a younger specimen MR65791, length 16,8 mm; 7 - younger specimen obligue-laterally flattened, MR65792, total preserved length 15 mm; 8 - the smallest opisthosoma MR65793, length 8.2 mm.

Plate IV

Kodymirus vagans, Paseky Shale, Mt. Kočka.
1 - fragmentary prosoma, opisthosoma and posterior head appendages MR20490, ventral view, sag. length 22.5 mm; 2 - obliquely flattened prosoma with incomplete and anteriorly upturned appendages and anterior opisthosomal segments, MR65794, smaller specimen (length 17 mm); 3 - opisthosomal segments, shifted head appendage and telson MR65795, sag. length 28.5 mm; 4 - opisthosomal segments, right head appendage and detached telson, MR65796, smaller specimen (length of the exposed segmented part 7.5 mm); 5 - isolated head appendage MR20496, length 11.1 mm.

Plate V

Kodymirus vagans Chl. et Havl., Paseky Shale, Mt. Kočka.
1 - isolated head appendage MR 65797, length 11 mm; 2 - damaged head appendage MR65798, length 18 mm; 3 - coxa MR65799, preserved width 15 mm; 4 - incomplete gnathal part of coxa MR65800, length 2.3 mm; 5 -isolated coxa MR65801, width 4 mm; 6 - incomplete head appendage MR65767, length 13mm (distal part broken off); 7 - distal part of head appendage MR20483, length 9 mm; 8 - incomplete head appendage MR65802, preserved length 10 mm; 9 - isolated spine of a head appendage MR65768, length 11.5 mm; 10 - proximal part of a head appendage with coxa, MR65803, length 10 mm.

Plate VI

Kodymirus vagans Chl. et Havl., Paseky Shale, Mt. Kočka, Mt. Tok (fig. 3), Medalův mlýn (fig. 6).
1 - enlarged surface of an opisthosomal segment with typical granulation, MR65764, sag. length 3.2 mm; 2 - sculpture of the posterior part of prosoma ICh444a showing diminishing granulae close to the post. margin, (about 6x); 3 - enlarged sculpture on the anterior part of prosoma MR65784, about 20x; 4 - negative counterpart of an opisthosomal segment showing the median ridge and articulating facets, ICh477, (5x); 5 - incomplete prosoma of a large specimen MR65760 showing the short genal spine, sag. length 20 mm; 6 - incomplete prosoma with the genal spine and fragmentary opisthosoma, length 29 mm; 7 - telson MR65805, length 15.6 mm; 8 - incomplete telson MR 65806, length 10 mm; 9 - telson MR65807, length 10 mm.

Plate VII

Kockurus grandis gen. et sp. n., Paseky Shale, Mt. Kočka, Mt. Tok (fig. 6).
1 - incomplete prosoma of a smaller specimen MR65808, width 25.3 mm; 2 - lateral part with the genal spine MR65776, length 18.5 mm;

3 - incomplete prosoma MR65777, holotype, sag. length 19 mm; 4 - isolated epistoma MR65809, tr. width 23 mm; 5 - prosoma MR20297, width 37.5 mm; 6 - right part of prosoma with the eye tubercle MR65810, length 14 mm; 7 - prosoma MR65772, wrinckles indicate the elevated central part, sag. length 18 mm; 8 - the same, negative counterpart showing the ganal spine.

Plate VIII

Kockurus grandis gen. et sp. n., Paseky Shale, Mt. Kočka.
1, 2 - fragmentary prosoma, epistoma and anterior part of opisthosoma probably belonging to this species, MR65811, sag. length 21.4 mm; 3 - incomplete prosoma obliquely flattened, with accentuated median elevated part. MR65778, sag. length 18 mm; 4 - strongly obliquely flattened and flected specimen possibly belonging to *Kockurus grandis*, MR 65812, diameter 11.4 mm; 5 - isolated telson MR65813, length 22.6 mm; 6 - isolated telson MR65814, length 24 mm.

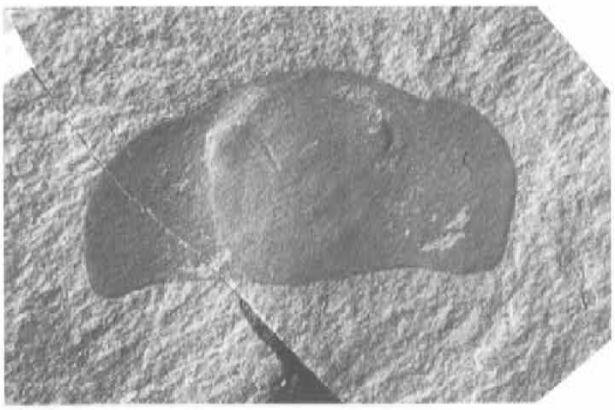
Plate IX

Vladicaris subtilis gen. et sp. n., Paseky Shale, Mt. Kočka, Mt. Tok (fig. 5).
1 - laterally flattened specimen MR65773, holotype, length 11 mm; 2 - counterpart of the same specimen; 3 - two carapace valves MR65769, length 9 mm; 4 - isolated carapace valves of four specimens, trunk detached, MR65815, length of the largest valve 8.4 mm; 5 - isolated carapace valve MR65816, length 11.4 mm; 6 - carapace with the trunk inside the valves, MR65817, length 11 mm; 7 - carapace and isolated trunk segment in cross-section, MR65818, preserved length of the valve 12 mm; 8 - carapace of a large specimen MR65819, length 17.6 mm.

Plate X

Vladicaris subtilis gen. et sp. n. Paseky Shale, Mt. Kočka.
1 - carapace MR65771, length 16 mm; 2 - laterally flattened specimen MR65773, holotype, length 11 mm; 3 - Carapace showing two overlapping valves, MR65820, length 9 mm; 4 - carapace of a smaller specimen MR65827, length 6 mm; 5 - isolated trunk MR65824, length 4.5 mm; 6 - isolated trunk with traces of the alimentary canal, MR65826, length 4 mm; 7 - isolated trunk with furca, MR65821, length 5 mm; 8 - trunk of a larger specimen MR65822, length 6.3 mm; 9 - carapace with the trunk preserved inside the valves, MR65774, length 13.4 mm.; 10 - posterior part of the trunk with the furca, MR65825, length 5 mm.

I. Chlupáč: Lower Cambrian arthropods from the Paseky Shale (Barrandian area) (Pl. I)



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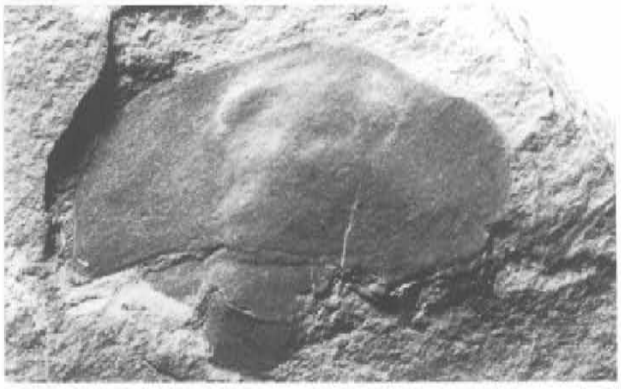

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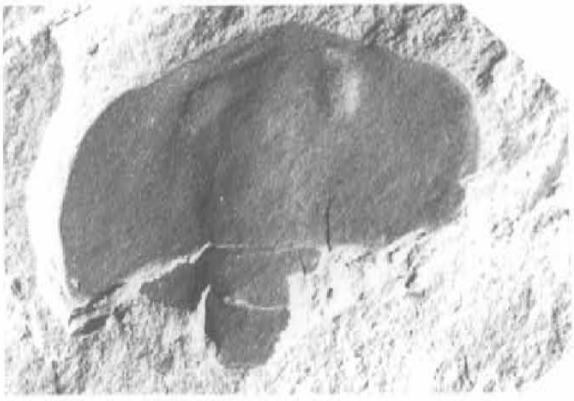

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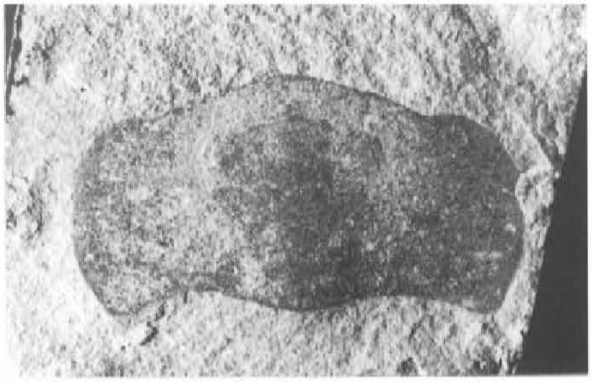

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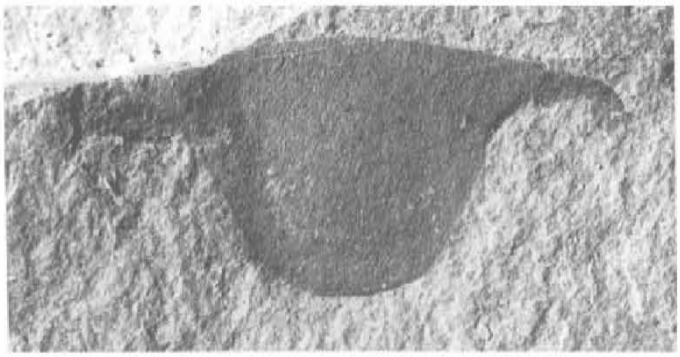
For explanation see p. 24-25



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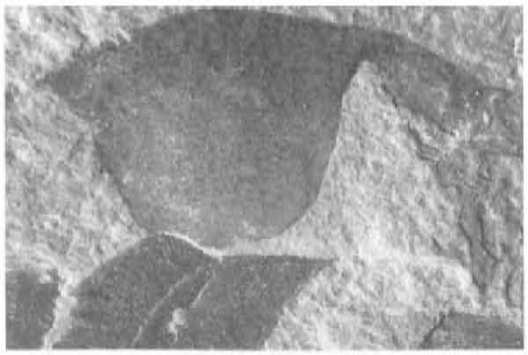

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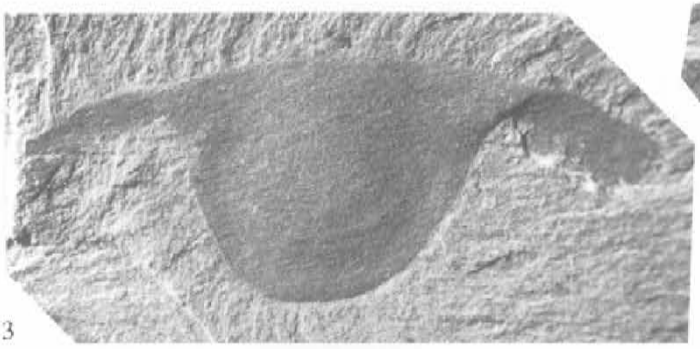

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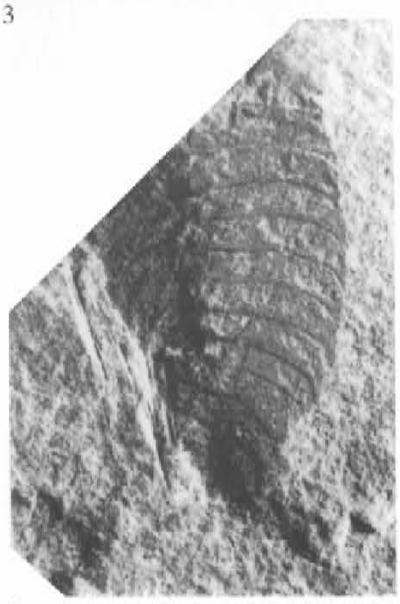

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I. Chlupáč: Lower Cambrian arthropods from the Paseky Shale (Barrandian area) (Pl. IV)

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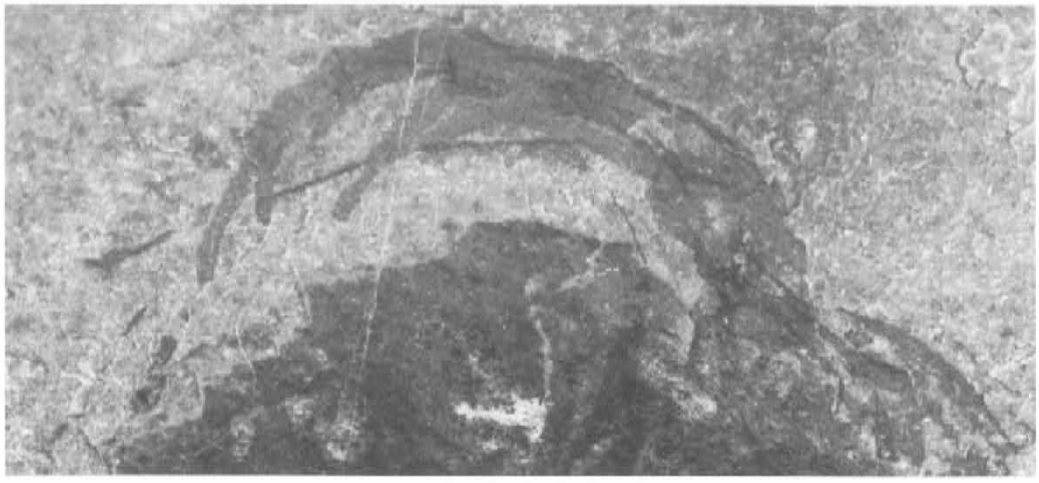

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I. Chlupáč: Lower Cambrian arthropods from the Pasecky Shale (Barrandian area) (Pl. V)

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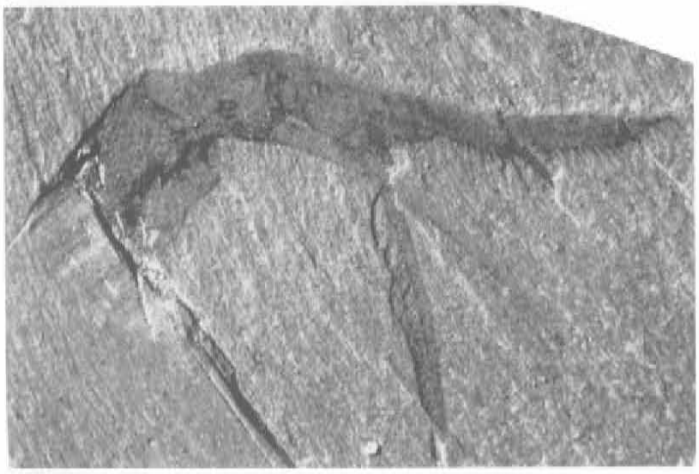

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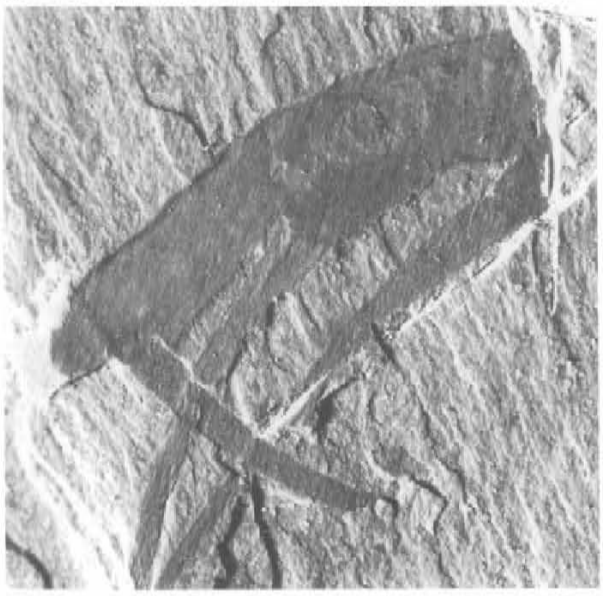

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I. Chlupáč: Lower Cambrian arthropods from the Paseky Shale (Barrandian area) (Pl. VI)

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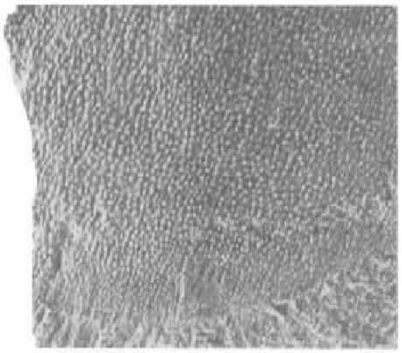

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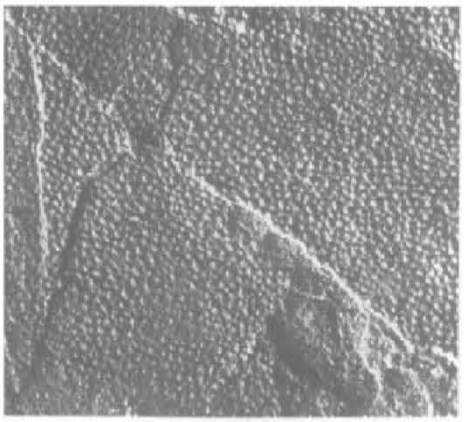

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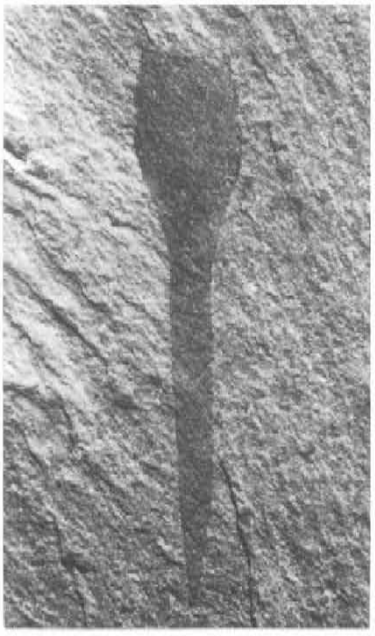

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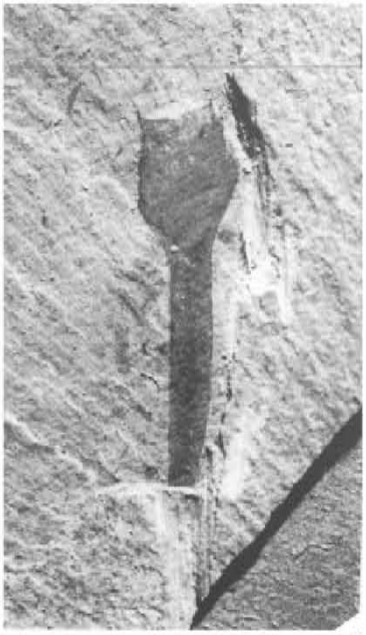

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I. Chlupáč: Lower Cambrian arthropods from the Paseky Shale (Barrandian area) (Pl. VII)

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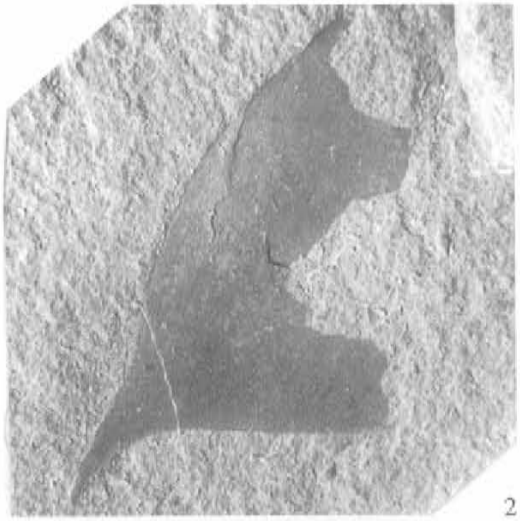

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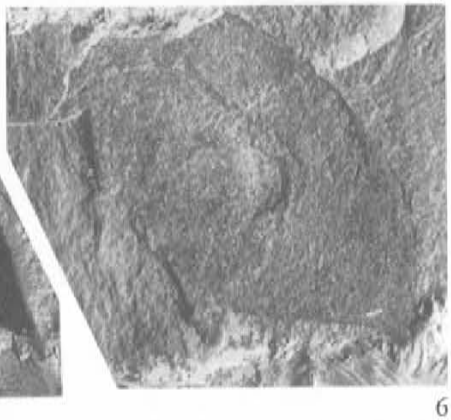

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I. Chlupáč: Lower Cambrian arthropods from the Paseky Shale (Barrandian area) (Pl. VIII)

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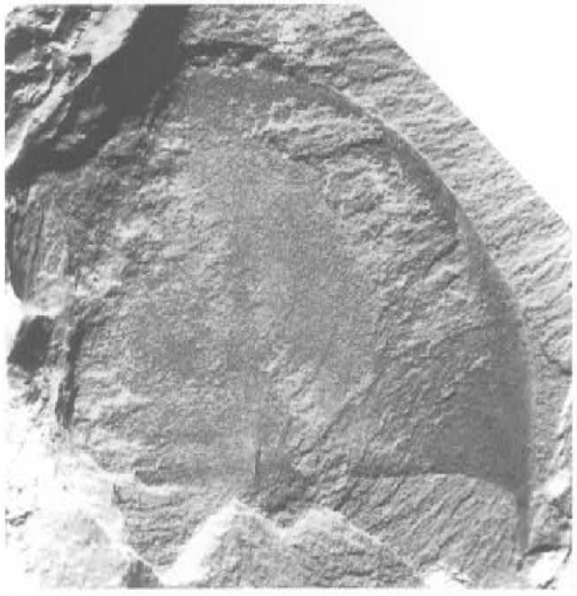

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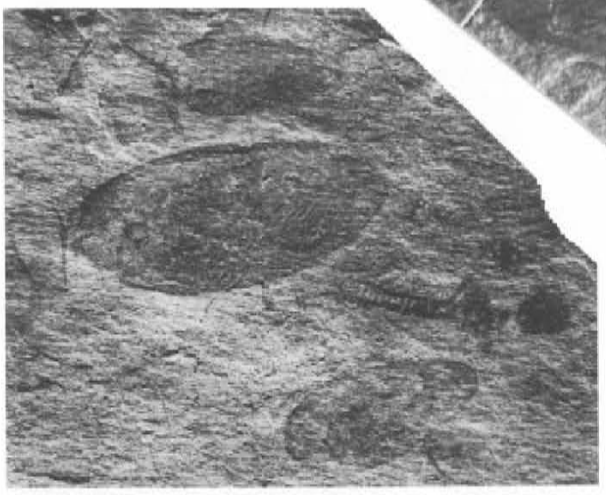

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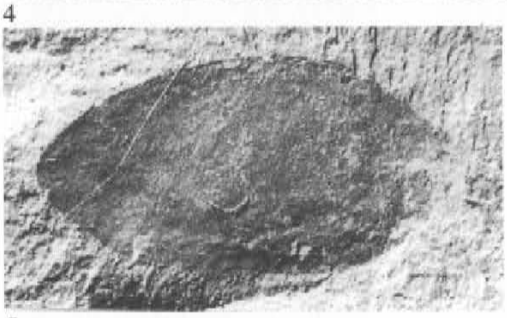

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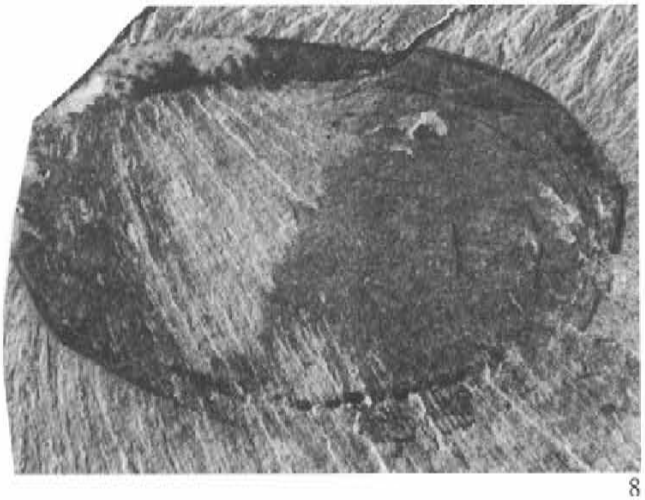

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