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Worm-like fossils (Palaeoscolecida; ?Chaetognatha) from the Lower Ordovician of Bohemia

Vermiformní fosilie (Palaeoscolecida; ?Chaetognatha) ze spodního ordoviku Čech

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Abstract: Palaeoscolecidans (*?Annelida*) are known from the Cambrian to the Silurian; in Bohemia they occur from the Arenigian to the Dobrotivian only. The state of preservation of specimens from Bohemia enables detailed description of cuticle morphology, ultrastructure, and discussion of the systematic position of palaeoscolecidans. Their locomotion and mode of life is discussed, too. The family *Plasmuscolecidae*, and the genera *Bohemoscolex*, *Gamascolex*, and *Plasmuscolex* are erected. Five new species together with three indeterminable specimens are described in the systematic part. In addition, the description of a new genus *Titerina* (*T. rokycanensis* sp. n.) is given; this belongs probably to *Chaetognatha*.

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Introduction

The palaeoscolecidans are a characteristic group of annelid-like metazoans with uniform body plan: their bodies are composed of several hundreds of identical, usually papillate segments without distinct traces of cephalization, body appendages, chaetae, and with rigid, resistant cuticle. They range from the Early Cambrian to the Late Silurian, and judging from their rarity in fossil records, they were uncommon elements in benthic marine assemblages during the Lower Paleozoic age.

The finds of palaeoscolecidans have been reported under the generic names *Palaeoscolex* and *Protoscolex* from the Cambrian (CONWAY-MORRIS 1977, CONWAY-MORRIS - ROBISON 1986, GLAESSNER 1979, ROBISON 1969), Tremadocian (OWENS - FORTEY - COPE - RUSHTON - BASSETT 1982, WHITTARD 1953), Middle—Upper Ordovician (CONWAY-MORRIS - PICKERILL - HARLAND 1982, RUEDEMANN 1925, ULRICH 1878), and Silurian (BATHER 1920, MIKULIC - BRIGGS - KLUESSENDORF 1985). In Bohemia, palaeoscolecidans range from the Arenigian (Klabava

Formation) to the Dobrotivian (Dobrotivá Formation). Apart from "*Palaeoscolex*", three distinct new genera are present in our material. Additional material suggests further palaescolecidan species, but the material is not sufficient for determination and description of new taxons.

In the present paper we describe a minute, worm-like fossil of unclear affinity (recalling *Chaetognatha*), which occurs in Arenigian rocks, too.

Depositories: The material is deposited in the collections of the Geological Survey, Prague (GS-MM, GS-p), collections of the National Museum, Prague (NM-L) and collections of the District Museum of Dr. B. Horák, Rokycany (OMR).

Acknowledgements: We are grateful to S. Conway-Morris (University of Cambridge, England) for useful discussion and loan of information about palaeoscolecidans; J. R. Prokop (National Museum, Prague) for the privilege to examine the collections; J. Kulich (Charles University, Prague) for making SEM photos; Z. Kotrba (Geological Survey, Prague) for EMA investigation; M. Kunst (Charles University, Prague) for making the photos of *Titerina*.

Material and methods

The hitherto reported finds of palaeoscolecidans (WHITTARD 1953 a.o.) come from shales or siltstones. Palaeoscolecidan remains are mostly strongly flattened and folded, showing overall shape of bodies, fine details (papillae, pustules), and more rarely internal structures (jaws, gut). An essential part of Bohemian specimens comes from grey-green, dark-grey or reddish clayey or micaceous shales, and their remains are deformed in the same way, too. Several specimens from the Dobrotivá Formation have been obtained from siliceous nodules, and in spite of the wrinkling of their bodies, they are preserved as internal and external moulds, occasionally with cylindrical shape of the trunk preserved. These two different modes of preservation enable recognition of cuticle deformation during the compression. This is an important circumstance for investigation of the species available as flattened imprints only. All specimens of palaeoscolecidans are preserved as moulds or imprints of cuticle; the soft parts of the body are preserved very scarcely. The cuticle was undoubtedly more resistant than other parts of the body, and it is not excluded, that cuticle may be moulded as in recent priapulids (SHAPEERO 1962), or that the cuticle may be loosened from the rest of body wall by sudden contraction of body wall or decay (compare CONWAY-MORRIS 1977, p. 11).

The overall rarity of palaeoscolecidans influenced our methods. Apart from natural imprints and remains of original cuticle substance, latex casts have been used for SEM investigation.

List of specimens

"Palaeoscolex" tenensis sp. n.: Arenigian, Klabava Formation, 4 metres above base of formation.
GS-MM 199: minute fragment of trunk, preserved in wrinkled, flattened position in reddish shale; locality Těně (text-fig. 1/1).
Gamascolex herodes gen. et sp. n.: Dobrotivian, Dobrotivá Formation.
NM-L 24634: slightly deformed trunk, preserved as internal and external moulds in siliceous nodule, holotype; locality Malé Přílepy (text-fig. 1/8).
NM-L 24636: short part of slightly deformed trunk, preserved as internal and external mould in siliceous nodule; locality Malé Přílepy (text-fig. 1/8).
NM-L 24637: short part of strongly wrinkled trunk, preserved as internal and external moulds in siliceous nodule; locality Malé Přílepy (text-fig. 1/8).
NM-L 24638: short part of slightly deformed trunk, preserved as internal and external moulds in siliceous nodule; locality Šárka (text-fig. 1/9).
NM – without number: short, poorly preserved part of trunk in siderite oolitic ore; locality "Veronika" mine near Kařízek (text-fig. 1/10).
GS-MM 118: part of trunk of large, slightly flattened specimen, preserved as internal and external moulds in siliceous nodule; locality Malé Přílepy (text-fig. 1/8).
GS-p 5050: almost complete specimen, with one terminal preserved, composed of more than 250 segments. Trunk preserved as internal and external moulds, partly flattened, in siliceous nodule; locality Malé Přílepy (text-fig. 1/8).
OMR 11799: flattened part of large trunk, partly preserved as imprint in micaceous shale, partly as internal and external moulds in siliceous nodule; locality Hůrka hill near Starý Plzenec (text-fig. 1/12).
Bohemoscolex holubi gen. et sp. n.: Arenigian, Klabava Formation, Corymbograptus v-similis Biozone.
OMR 9595: flattened part of trunk with coiled terminal part in clayey shale; locality Rokycany – hospital (text-fig. 1/2).
Plasmuscolex klabavensis gen. et sp. n.: Arenigian, Klabava Formation, Tetragraptus abbreviatus Biozone.
OMR 18726: long part of trunk without terminals, preserved in flattened position in clayey shale, holotype; locality Klabava – Starý hrad (text-fig. 1/5).
OMR 18198: almost complete minute specimen, preserved in flattened position in clayey shale; locality Klabava – Starý hrad (text-fig. 1/5).
OMR 18727: fragmental decayed part of trunk, preserved in flattened position in clayey shale; locality Klabava – Starý hrad (text-fig. 1/5).
OMR 10500: almost complete specimen of minute size, preserved in flattened position in clayey shale. Trace of burrow activity preserved; locality Rokycany – Stráň (quarry) (text-fig. 1/6).
Plasmuscolex nero gen. et sp. n.: Dobrotivian, Dobrotivá Formation.
NM-L 24635: slightly deformed, contracted part of trunk, preserved as internal and external moulds in siliceous nodule; locality Šárka (text-fig. 1/9)
OMR 11679: slightly flattened part of trunk and terminal, preserved as internal and external moulds in micaceous shale, holotype; locality Sutice hill near Starý Plzenec (text-fig. 1/11).
Palaeoscolecida gen. indet. A: Arenigian, Klabava Formation, Tetragraptus abbreviatus Biozone.
OMR 18171: short fragment of very small, slightly flattened trunk in clayey shale; locality Klabava – Starý hrad (text-fig. 1/5).
Palaeoscolecida gen. indet. B: Arenigian, Klabava Formation, Hologaptus tardibrachiatus Biozone.
OMR 18751: poorly preserved, strongly flattened part of trunk in clayey shale; locality Rokycany – Valcha (text-fig. 1/3).
Palaeoscolecida gen. indet. C: Llanvirnian, Šárka Formation, Corymbograptus retroflexus Biozone.

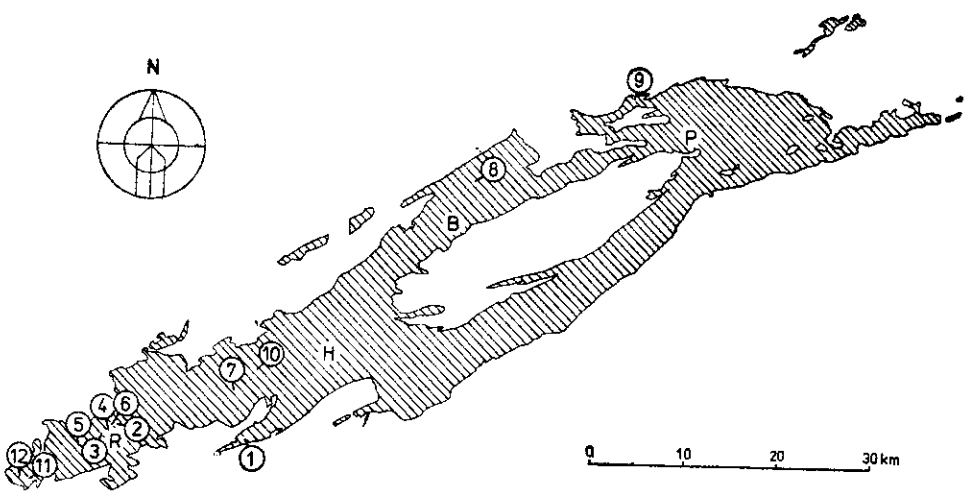
OMR 9055: poorly preserved part of trunk in siliceous nodule; locality Mýto (text-fig. 1/7). *Titerina rokycanensis* gen. et sp. n.: Arenigian, Klabava Formation, Hologratus tardibrachiatus Biozone.

OMR 15334A-C: complete (A) and fragmental (B, C) specimens, preserved in flattened position in clayey shale; locality Rokycany — Stráň (gully, section 7) (text-fig. 1/4).

Table 1

Stratigraphic occurrence of Bohemian palaeoscolecidans and *Titerina*

Series	Formation	Graptolite Biozone	Occurrence
DOBROTIV	Dobrotivá		□ Gamascolex herodes □ Plasmuscolex nero
LLANVIRN	Šárka	Didymograptus clavulus	
		Corymbograptus retroflexus	□ Palaeoscolecida C
ARENIG	Klabava	Tetragraptus abbreviatus	□ Palaeoscolecida A □ Plasmuscolex klabavensis
		Hologratus tardibrachiatus	■ Titerina rokycanensis □ Palaeoscolecida B
		Corymbograptus v-similis	□ Bohemoscolex holubi □ "Palaeoscolex" tenensis

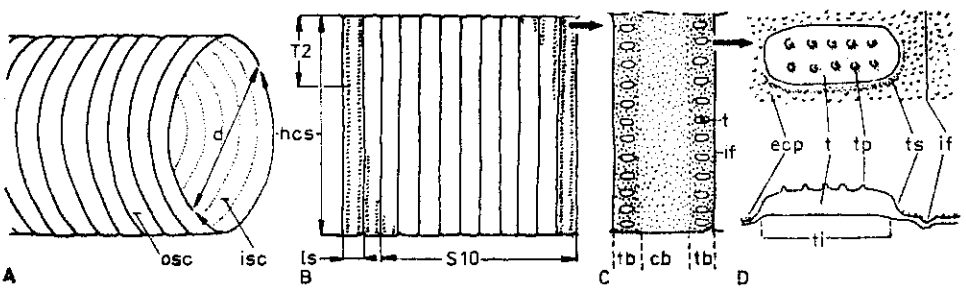


1. Distribution of Lower Ordovician rocks in the Prague basin
Localities: *1* — Těně, *2* — Rokycany (hospital), *3* — Rokycany (Valcha), *4* — Rokycany (Stráň, gully, section 7), *5* — Klabava (Starý hrad), *6* — Rokycany (Stráň, quarry), *7* — Mýto, *8* — Malé Přílepy, *9* — Šárka, *10* — Kařez (mine "Veronika"), *11* — Starý Plzenec (Sutice hill), *12* — Starý Plzenec (Hůrka hill); B — Beroun, H — Hořovice, P — Praha, R — Rokycany

Terminology

Recent annelid terminology is applied to structures of palaeoscolecidans cuticle which seem to be homologic with cuticular structures of recent annelids. The terminology is the same as in RICHARDS (1978). New terms are introduced where necessary.

Central band: Transverse band, with or without tubercles in mid-length of each segment.
Dorsal (ventral): These terms are used in description sense only, they do not indicate the original orientation of animal anatomy.
Epicuticular projections: Minute, short, mound to papillae-like outgrowths, covering densely outer cuticular surface.
Intersegmental furrow: Deep, transversal cutting between two adjacent segments.
Length of segment: Distance between bottoms of two adjacent intersegmental furrows. At coiled specimens measured at mid-width of flattened body.
Longitudinal ridge (furrow): Longitudinal, fine ridge (or suture) on dorsal and ventral outer cuticular surface.
Segment: Annulation on cuticle, anteriorly and posteriorly bordered by intersegmental furrows.
Tubercles: Circular to elongate, more or less distinctly bordered elevations, encircling in several (usually two) rows outer cuticular surface of each segment (= papillae in WHITTARD 1953).
Tubercle band: Transverse band along margin or at mid-length of each segment, bearing tubercles.
Tubercle impression: Strong to obscure impressions on inner cuticular surface, corresponding in arrangement to tubercles of outer cuticular surface.
Tubercle projections: Minute, thorn-like outgrowths extending externally from the tops of tubercles.
Tubercle slopes: Slopes connecting top of tubercle with adjacent outer cuticular surface.
hcs (cs): Half (total) circumference of segment, usually it is equal to the width of flattened specimen; diameter of body = cs/π.
T2: Number of tubercles per 2 mm at single tubercle band.
S10: Number of non-contracted segments per 10 mm.



2. Morphology of cuticle of palaeoscolecidans
A — undeformed cuticle, *B* — flattened cuticle, *C* — structures of single segment, *D* — tubercle with adjacent surface of cuticle (outer surface and lateral view)
cb — central band, *d* — diameter of body, *ecp* — epicuticular projections, *hcs* — half circumference of segment, *if* — intersegmental furrow, *isc* — inner surface of cuticle, *ls* — length of segment, *osc* — outer surface of cuticle, *t* — tubercle, *tb* — tubercle band, *ti* — tubercle impression, *tp* — tubercle projections, *ts* — tubercle slope, S10 — number of non-contracted segments per 10 mm, T2 — number of tubercles per 2 mm

Morphology of cuticle

The excellent preservation of cuticular structures of *Gamascolex* and *Plasmuscolex* enabled reconstruction of palaeoscolecidan cuticular structures, their interpretation, and comparison with cuticular structures of recent annelids. We consider, that cuticular structures, especially shape and spacing of tubercles, are significant features of palaeoscolecidans, applicable for erection of new taxons. The variability of corresponding structures within single species is very low and it is only slightly influenced by the absolute size of specimen.

External structures of cuticle

Epicuticular projections: The entire outer cuticular surfaces of *Gamascolex* and *Plasmuscolex*, apart from tubercles, are densely covered by fine outgrowths (= epicuticular projections). In *Gamascolex*, they are subequal in size (7—10 μm), circular to almost rectangular in outline. Epicuticular projections show no regular arrangement in central band, but they are arranged in irregular longitudinal rows between two adjacent tubercles at tubercle bands at dorsal side (pl. V, fig. 4). In areas adjacent to intersegmental furrow, the epicuticular projections are arranged in 12 to 16 transversal rows, they are larger and nearly rectangular in outline (pl. V, fig. 4). The bottoms of intersegmental furrows are covered by epicuticular projections of the same shape, too (pl. IV, fig. 5). The ventral side of the cuticle in *Gamascolex* shows slightly different spacing of epicuticular projections in comparison with the dorsal one, described above. The transversal rows of epicuticular projections bounding intersegmental furrows are less distinct. In tubercle bands, the areas with alternating rows of unequally large projections appear. There are large projections (15—20 μm) surrounded by smaller ones (5—7 μm; pl. VI, fig. 1). Judging from negative imprints of outer cuticular surface, the epicuticular projections are mound to papillae-like in shape, less than 10 μm high.

Epicuticular projections in *Plasmuscolex* are papillae-like in shape, less than 5 μm in diameter, uniform in size, arranged in oblique rows (pl. IX, fig. 5). This type of epicuticular projections appears at the bottoms of notches between two adjacent tubercles in tubercle bands. The second type of epicuticular projections are smaller, less regularly spaced and densely crowded outgrowths in central bands (pl. IX, fig. 6; pl. XI, figs. 1, 2). Additional Bohemian palaeoscolecidans show similar, often very complicated structures in outer cuticular surface (pl. XV).

The two size categories of epicuticular projections and their spacing (larger along segmental margins, smaller in central bands) are typical palaeoscolecidan features. The similar ornamentation patterns have been observed at palaeoscolecidans by WHITTARD (1953), ROBISON (1969), and CONWAY-MORRIS - ROBISON (1986), too. In a shape and arrangement, the epicuticular projections of palaeoscolecidans recall epicuticular projections or microvilli of recent annelids (RICHARDS 1978).

Tubercles: Tubercles are variably developed large outgrowths or elevations, forming two, exceptionally one transversal bands on each segment. Stage of tubercle complexity differs in each genus.

Plasmuscolex possesses simple tubercles. Its tubercles are strong, longitudinally elliptical to pear-shaped steep elevations, with indistinct boundaries with the rest of the cuticular surface (pl. IX, figs. 4—6; pl. XI). Tubercle projections are very similar in the shape and spacing to epicuticular projections, differing only in having larger size, and they cover entire tubercle surface.

Gamascolex has two types of tubercles. The dorsal type tubercles are formed by moderately elevated platforms, longitudinally elliptical to nearly circular, 70—250 μm long (pl. V, figs. 3, 4; pl. VI, fig. 2; pl. IV, fig. 4). Their width is nearly uniform. The length of tubercles depends on their position on the body; the longest tubercles are located on dorsal side, whereas lateral and ventrolateral ones are shorter, attaining nearly circular outline. Tubercles in central band on ventral side of *Gamascolex* are conical in shape, with circular outlines, and are uniform in size (pl. IV, figs. 1, 2). Tops of all tubercles (dorsal and ventral) are smooth, without epicuticular projections, but bear two longitudinal rows of tubercle projections. The total number of tubercle projections depends on the size of the tubercle and ranges from 4 to 14.

Tubercles of *Palaeoscolex* were described by WHITTARD (1953). On the whole they are similar to tubercles of *Gamascolex*. "*Palaeoscolex*" *tenensis*, although poorly known, shows another type of tubercles. They are concave externally, with scallop-shaped or spinned margins and with undercut margins; their outline is longitudinally elliptical. Indeterminable palaeoscolecidans and *Bohemoscolex* indicate that tubercles are prominent, highly differentiated, but probably unnecessary structure of palaeoscolecidans.

Tubercle projections have been interpreted as bases of minute chaetae (WHITTARD 1953); this assumption has been discussed by CONWAY-MORRIS - ROBISON (1986). In recent annelids, the chaetae originate in epidermal follicles and penetrate the cuticle (STEPHENSON 1930). We suppose that tubercle projections did not house the chaetae due to their compact structure built of cuticular material, and their spacing. Tubercle projections are in contracted segments in opposite position; therefore, the suggestion that they bear the chaetae is hardly acceptable. Tubercles were more probably some sense organs. They externally recall wart-like structures serving as secretory cells openings in some priapulids (HAMMOND 1970).

Longitudinal ridge: Longitudinal ridge or furrow shows a very fine structure on outer cuticular surface. The ridge is developed both on dorsal and ventral sides, and the body along the ridge is bilaterally symmetrical. In *Bohemoscolex* the ridge is substitued by a furrow. Longitudinal ridge was observed in *Gamascolex* and *Plasmuscolex*, but undoubtedly it was present in other palaeoscolecidans, too (pl. IV, figs. 1, 2; pl. XIV, fig. 3).

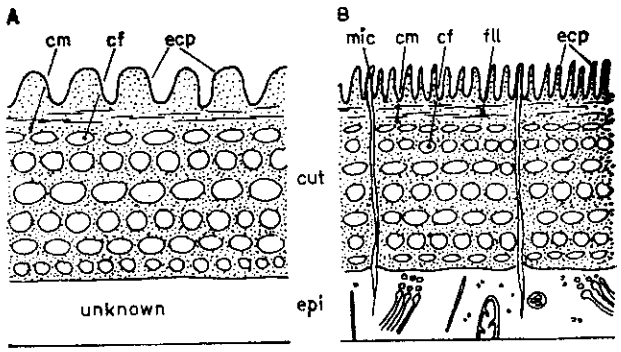
Table 2

Comparative data of Bohemian (A) and foreign (B) palaeoscolecidans

species	length of fragment (in mm)	maximum of hcs (in mm)	S10	T2	tubercles at single segment	shape of tubercles
A						
"Palaeoscolex" tenensis specimen GS-MM 199	5	0.7	50	50—70	40—50 × 2	elongate
Gamascolex herodes specimen GS-p 5050	80	8	23—25	15—16	100—120 × 2	dorsal elongate ventral circular
GS-MM 118	about 30	13.0	16—18	15—17	100—115 × 2	ditto
NM-L 24634	22	9.5	19—22	14—17	90—120 × 2	ditto
OMR 11799	28	14.5	9—10	11—15	undeterminable	ditto
Plasmuscolex klabavensis specimen OMR 18198	9.4	0.5	275	130—140	72 × 2	elongate pear-shaped
OMR 10500	28.7	1.9	76	33—40	62 × 2	ditto
OMR 18726	58.0	3.5	22—25	15—18	58 × 2	ditto
OMR 18727	28.5	3 3	27—30	15—17	58 × 2	ditto
Plasmuscolex nero specimen OMR 11679	35.0	4.0	22—23	13—15	55—60 × 2	elongate elliptial
Bohemoscolex holubi specimen OMR 9595	about 6.0	11.0	16—18	absent	absent	absent
B						
Palaeoscolex antiquus (GLAESSNER 1979)	—	about 13	6—20	9—12	60 × 1?	circular
Palaeoscolex ratcliffei (ROBISON 1969)	125	2—5	30—40	30—50	50—80 × 2	circular
Palaeoscolex cf. *ratcliffei* (CONWAY-MORRIS – ROBISON 1986)	81	7	24	10	70 × 2	circular
Palaeoscolex piscatorum (WHITTARD 1953)	49	1.5	80—100	50—60	60—80 × 2	circular to slightly elongate

Internal structures of cuticle

The cross-lamellar structure is preserved in original cuticular substance of *Gamascolex*. The lamellae lie at an angle of 60° to one another and at 60° to the body axis (pl. VI, figs. 3, 4). Lamellae are subequal in size, 2—3 μm wide, several times repeating throughout the thickness of the cuticle, overlapping one another. The



3. Sections through cuticle of palaeoscolecidans (*Gamascolex*), and recent annelids (*Branchiobdella*)
A — *Gamascolex herodes*, ×1800, *B* — *Branchiobdella pentodonta*, ×18 000
cut — cuticle, *epi* — epidermis, *cf* — collagen fibres, *cm* — cuticle matrix, *ecp* — epicuticular projections, *fll* — felt-like layer (epicuticle), *mic* — microvilli; *B* — according to FARNESI (1973)

cross-lamellar structure is developed in the whole cuticle except for tubercles. Tubercles are built of amorphous material with no structure visible. Cross-lamellar structure recalls cross-lamellar arrangement of collagen fibres in the cuticle of recent annelids (RICHARDS 1977). The angles contained by collagen fibres range from 45° (FARNESI 1975) to 90° (STEPHENSON 1930). In recent annelids, however, the fibres are much slender than those in palaeoscolecidans, they reach 0.3—0.5 μm in diameter only.

The size difference between the palaeoscolecidan and recent annelid fibres is difficult to explain, since the thickness variability of collagen fibres in recent groups is very restricted. In spite of this difference we believe that both structures are identical.

Segmentation

The question of segmental units is widely discussed by CONWAY-MORRIS - ROBISON (1986). They suggest that boundaries between segments lie between papillate bands, in the unarmed (= central) bands. However, the unarmed bands are covered by finer ornamentation only in comparison to the remaining segmental surface. The overall uniformity of palaeoscolecidan body plan suggests that segmental boundaries lie in mid-length between two tubercle bands, and they are marked by deeply cut grooves (intersegmental furrows). The segmental deformations on the inner side of coiled specimens (pl. II, fig. 2) and the formation of transversal ridges in contracted segments are better explainable by presumed seg-

ment boundaries than by the opinion of CONWAY-MORRIS - ROBISON (1986). It should be emphasized, however, that outer segmentation (and/or annulation) of a cuticle does not necessarily reflect the internal metameric segmentation.

Chemical composition of cuticle

The cuticle is fossilized by dark brown-grey material, which changes into light grey-blue due to the effects of weathering. The EMA investigation of unweathered *Gamascolex* and *Bohemoscolex* cuticles enables to estimate the chemical composition. The cuticle is composed of Ca, P, and traces of Fe, S, and Si (C omitted). P: Ca ratio ranges about 4:5, and is almost constant in all the measured sites. It is evident that the cuticle is fossilized by apatite or other phosphatic minerals (Ca:P ratio is as in apatite standard).

Systematic position of palaeoscolecidans

The discussions about relationships of palaeoscolecidans have been given in papers of BATHER (1920), WHITTARD (1953), and more recently of CONWAY-MORRIS - ROBISON (1986).

Our recent knowledge of palaeoscolecidans is based almost entirely on their cuticle shape; other features (shape of the gut, jaws) possess only limited taxonomic value. Lack of information about soft parts of the animal (e.g. reproductive system) and about structures of body terminals makes our assumptions about palaeoscolecidans affinity tentative. The main palaeoscolecidan features are as follows:

1) Firm, rigid, against decay rather resistant cuticle. The cuticle of recent annelids, although thick in some groups (RICHARDS 1979), is probably less resistant in comparison with the cuticle of palaeoscolecidans. Palaeoscolecidans occur in the rocks with rich assemblage of skeletal animals. Although the cuticle of palaeoscolecidans is undoubtedly secondarily phosphatized, no soft-bodied or lightly skeletized animals are preserved in the same rocks, in spite of common bioturbation and presence of scolecodonts.

2) Internal cross-lamellar structure of the cuticle. Cross-lamellar structure of the cuticle observed at *Gamascolex* strongly resembles similar structures in the cuticle of recent annelids (RICHARDS 1977; RUTSCHKE 1970; STORCH - WELSCH 1970).

3) Absence of cephalization and parapodia, both common in polychaetes. Palaeoscolecidans share with oligochaetes poorly differentiated body terminals, but the latter exhibit some structures (e.g. clitellum) unknown in palaeoscolecidans.

4) Presence of jaws. Two specimen of *Palaeoscolex piscatorum* possess structures interpreted as the jaws (WHITTARD 1953). In our material no similar structure was

observed, but that was due to the limited number of body terminals. Presence of jaws may be a significant feature distinguishing palaeoscolecidans from oligochaetes (WHITTARD 1953; CONWAY-MORRIS - ROBISON 1986).

5) Absence of chaetae. No signs of chaetae are preserved on the material available. Tubercle projections, interpreted as chaetae bases (WHITTARD 1953), are probably of other origin. In the remaining cuticular surface, uneven structures interpreted as chaetae or chaetae epidermal follicles (pores, penetrations through the cuticle) are absent. It is evident that palaeoscolecidans are without large chaetae; tiny, hair-like chaetae and cilia lack potential for preservation and their traces in the cuticle may be very delicate. Thus, the question of tiny chaetae presence/absence remains open for future investigation.

6) Double bands of tubercles (or papillae) encircling each segment in majority of palaeoscolecidans are of arrangement unknown in any recent annelid groups. However, some taxons (*Bohemoscolex*) indicate that the body plan significantly deviates from the definition of palaeoscolecidans given by CONWAY-MORRIS - ROBISON (1986).

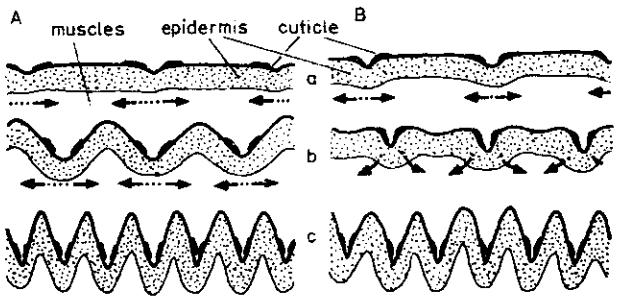
In external shape, the leeches (*Hirudinea*) are the closest of annelids to the palaeoscolecidans. Both groups share some features (presumed absence of chaetae, probably duplicated external annulation), but there are significant differences (absence of a sucker and higher number of segments in the latter). Similar external shape of the cuticle as that in palaeoscolecidans is developed in some nematodes (BOSTRÖM - GYDEMO 1983; WIDER - BARUŠ - TENORA 1978), and priapulids (CONWAY-MORRIS 1977; HAMMOND 1970; POR 1983).

Locomotion

Recent annelids commonly used propagate waves for crawling or burrowing (TRUEMAN 1978). Each locomotion wave results in shortening — lengthening cycle, forming retrograde or direct waves. The limit to the changes of dimension and on that depending dimension of wave is met by the elastic limit of muscles and of the body wall (GRAY 1968).

Palaeoscolecidans have rigid, flexible but only slightly elastic cuticle covering the entire body surface. In a single segment, the thickness of the cuticle, and on this depending elasticity, varies. The central bands and areas flanking intersegmental furrows are built by a thinner cuticle in comparison with the cuticle thickness in tubercle bands. Accordingly, the former were more elastic than the latter. In *Gamascolex*, the dorsal and lateral parts of segments were able to form a fold along the central band and a deep groove along intersegmental furrow. Tubercle bands remain without change, becoming only steeply inclined (text-fig. 3; pl. IV, fig. 4). Ventral side of *Gamascolex*, bearing tubercle rows in central band of each segment, formed a set of extremely convex segments during contraction;

it exhibited no sharp transversal ridges in central bands of the segment (pl. IV, figs. 1, 2). In *Plasmuscolex*, non-contracted segments show gently elevated central bands with tubercle bands moderately inclined toward intersegmental furrows. At the beginning of contraction, tubercle bands are recurved, becoming steeply sloping towards the intersegmental furrows; central bands are without change or form a slightly concave transversal depression (text-fig. 4). Further contraction



4. Schema of contraction of segments at *Gamascolex* (*A*) and *Plasmuscolex* (*B*)
a — non-contracted segments, *b* — segments at beginning of contraction, *c* — maximum contraction. Arrows indicate muscle contraction. Note origin of folds (*A-b*) and depressions (*B-b*) at the beginning of contraction

formed in central bands sharp, prominent ridges similar to the fold of *Gamascolex*. Tubercles in the tubercle bands of adjacent segments are nearly touching each other, forming tooth-like clinching in maximally contracted segments (pl. XI, fig. 2; pl. XII, fig. 5). In *Bohemoscolex* contracted segments have developed sharp ridges in the central bands.

The contraction of palaeoscolecidan segments is significant, reaching almost 1/3—1/4 of the non-contracted length (pl. IX, figs. 1, 2). Due to this strong contraction we suppose that intersegmental septa allowed migration of coelomic fluids, or that the external segmentation does not reflect underlying metameric one.

The function of tubercles as a penetration anchor (CONWAY-MORRIS - ROBISON 1986) is questionable. During body contraction the tubercles are not in contact with the sediment (except for the ventral side of *Gamascolex*) because of their location along segmental margins. The transversal sharp ridges originating during contraction in the central bands have more probably function as the penetration anchor.

The elastic lengthening and shortening developed in recent annelids have been partly substituted in palaeoscolecidans by folding and straightening of each segment. Locomotive propagate waves originating by the repeated folding – straightening cycles allowed crowling and burrowing of the palaeoscolecidans.

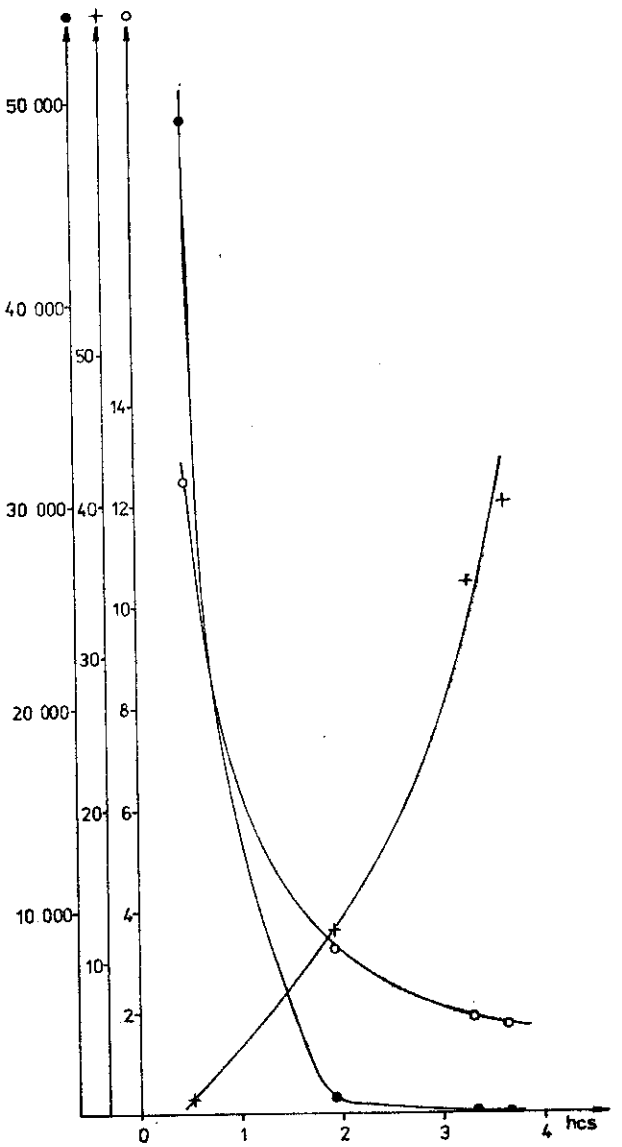
Mode of life

Palaeoscolecidans were supposed deposit feeders (WHITTARD 1953). Their cylindrical body, absence of body appendages, and poorly or no differentiated dorsal and ventral sides indicate infaunal mode of life (ROBISON 1969; CONWAY-

MORRIS - ROBISON 1986). Trace od burrowing activity is preserved in *Plasmuscolex klabavensis* (specimen OMR 10 500). The short, cylindrical (secondarily flattened) coiled burrow is preserved close to the body terminal. This trace (*Planolites*-like) indicates infaunal mode of life of palaeoscolecidans, too.

Growth

Four specimens of different size enable estimation of the growth changes during ontogeny in *Plasmuscolex klabavensis* (text-fig. 5).



5. Graphs indicating growth changes of *Plasmuscolex klabavensis*
Graphs showing dependence of *hcs* (in mm) on the:
a — number of tubercles equal to 1 mm³ of body mass (*dot*), *b* — bulk of 10 mm long sequence of cylindrical body (in mm³; *cross*), *c* — surface of body equal to 1 mm³ of the body mass (in mm²; *circle*). It is evident that palaeoscolecidans show quick relative growth during early adult stage. During evenly increasing bulk of body number of body outgrowths (= tubercles) and corresponding surface of body quickly decrease. This decrease was very quick originally but became more slow later

Pathology

Pathologic malformations are rather common in *Gamascolex*. Imperfect or irregular course of a segment is the most common malformation; it is marked by bifurcation or fusing of intersegmental furrows. Segments are discontinuous (pl. III, fig. 5) or fused (pl. III, fig. 4). Fine details of cuticle (tubercles a.o.) are often fused or show irregular course. Different malformations are represented by much shorter segments laying between longer ones (pl. IV, fig. 1). This pathologic malformation differs in ornamentation and tubercle shape, too. These pathologic malformations did not originate due to injury, they are more probably results of growth deffects of the animal.

?*Annelida* LAMARCK, 1809

Palaeoscolecida CONWAY-MORRIS et ROBISON, 1986

Palaeoscolecidae WHITTARD, 1953

Genera assigned: *Palaeoscolex* WHITTARD, 1953; Middle Cambrian — Lower Ordovician.
Gamascolex gen. n.; Lower Ordovician.
?*Protoscolex* ULRICH, 1878; Upper Ordovician—Upper Silurian.

Species probably belongs to the family: *Palaeoscolex antiquus* GLAESSNER, 1979; Lower Cambrian.

Palaeoscolex WHITTARD, 1953

"*Palaeoscolex*" *tenensis* sp. n.
Pl. I

Holotype: Specimen GS-MM 199, figured on pl. I.
Type horizon and locality: Arenigian, Klabava Formation, 4 metres above base; Těně.

Description: The fragment of flattened trunk less than 0.7mm wide, with prominent transversal rows of tubercles. Boundaries between segments indistinct. Tubercles densely arranged in transversal tubercle bands, probably two in each segment. All tubercles equal in shape and size. They are about twice longer than wide (maximum length is nearly 90 μm), elliptical, with strongly scalloped to spined margins of outer tubercle surface. The outer surface of tubercle concave, tubercle slopes vertical to nearly undercut. Inner tubercle surface (= corresponds to tubercle impression) is concave, too, and bears shallow circular pits in two longitudinal rows. Pits in spacing and number correspond to spines of outer tu-

bercle surface. If the width of preserved trunk is equal to the whole cuticle, there are 40—50 tubercles in one tubercle band; T2 = 50—70.

Gamascolex gen. n.

Type species: *Gamascolex herodes* gen. et sp. n.

Diagnosis: Large palaeoscolecidan with probably cylindrical body composed of more than 250 equal segments. Body with differentiated dorsal and ventral sides of the cuticle. Each segment with two transversal rows of tubercles; elongate dorsal flanking intersegmental furrows and circular ventral in central band. Outer surface of tubercles with prominent, paired tubercle projections. Microornamentation of fine epicuticular projections, papillae-like to mound-like in shape. Inner cuticle surface nearly smooth, with obscure tubercle impressions. Intersegmental furrow simple, narrow, sharply cut but rather shallow. Longitudinal ridge developed both on dorsal and ventral sides.

Discussion: *Gamascolex* differs by its tubercle shape and differentiated dorsal and ventral sides from *Palaeoscolex*. Moreover, the new genus attains much larger size than other palaeoscolecidans.

Species: *Gamascolex herodes* gen. et sp. n.; Ordovician, Dobrotivian, Dobrotivá Formation; Bohemia.

Gamascolex herodes gen. et sp. n.

Pls. II—VI; pl. VIII, fig. 3

1978 *Paleoscolex* sp.; MERGL, p. 28

Holotype: Specimen NM-L 24634, figured on pl. III, figs. 1, 2 and pl. IV, figs. 1, 2, 4.
Type horizon and locality: Dobrotivian, Dobrotivá Formation; Malé Přílepy.

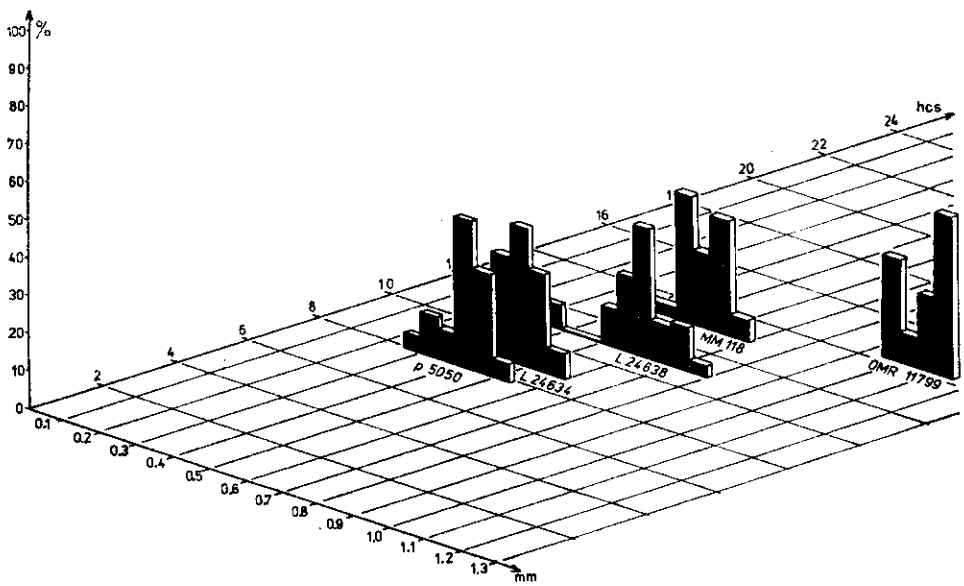
Shape of the body: The largest flattened specimen 20 mm wide (= 12 mm in diameter at originally cylindrical body), the smallest 7.5 mm wide (= 5 mm in diameter). Body slightly tapering at terminal parts, with terminals suddenly ended. Maximum of segments preserved is 248, the entire animal possesses 300 to 400 segments. Segments 0.4—1.2 mm long, their length depends on absolute size of the specimen, but within one specimen varies only a little (text-fig. 5). Intersegmental furrows narrow, sharply cut, shallow, simple. Judging from the fragments, the absolute length of non-contracted specimen may reach 20 to 40 cm. S10 = 9—25. T2 = 13—25.

Outer surface of the cuticle: The dorsal side of each segment (about 2/3 of body circumference) has two transverse bands of regularly spaced low tubercles along segment margins. The central band smooth apart from microornamentation. Dorsal tubercles 70—80 μm wide and 180—250 μm long, with slopes gently

decreasing to the adjacent surface. Size and shape of tubercles correspond to location on the body (dorsally they are longer). Tubercle projections arranged in two longitudinal rows, arising from the outer surface of tubercles, numbered 12—14 on the dorsal side, laterally and ventrally their number decreases to 4 (2 pairs). Ventral third of the segment bears conus-shaped tubercles of circular outline, 90—110 μm in diameter and comparatively high, arranged in two irregular rows in the central band. Margins of segments on the ventral side are without tubercles or with minute, irregularly spaced tubercles of dorsal type. Ventral tubercles have 4 tubercle projections at their tops, identical in shape with those on the dorsal side. The contact of both tubercle types is rather sharp. The dorsal tubercles suddenly become much smaller, and are arranged closer to the intersegmental furrows. Ventral tubercles suddenly appear in the central band between dorsal ones. In one transverse row, there are 60 to 120 tubercles of dorsal type and 28 to 40 ones of ventral type. Their number is nearly identical at adjacent segments but decreases toward body terminals. On dorsal and ventral sides the fine longitudinal ridge, slightly elevated above segmental surface, is developed.

Microornamentation: The outer cuticular surface is densely covered, apart from tubercles, by very fine epicuticular projections, mound to papillae-like in shape. They cover the bottoms of intersegmental furrows, too. For details on their shape, size and spacing see chapter Morphology of cuticle.

Inner surface of the cuticle: The inner surface of the cuticle is smooth,



6. Histogram of segment length-variability of *Gamascolex herodes*
hcs — half circumference of segments (in mm), *mm* — length of segments (in mm), % — percentage presence; $n = 25-40$ segments

with prominent transversal ridges corresponding to the intersegmental furrows. Tubercle impressions poorly preserved, elongate in outline. Other internal structures not preserved.

Plasmuscolecidae fam. n.

Diagnosis: Palaeoscolecidans with two transverse bands of indistinctly bordered tubercles on each segment, with tubercle tops and slopes covered by poorly differentiated tubercle projections. Dorsal and ventral sides not differentiated.

Discussion: *Plasmuscolecidae* differs from *Palaeoscolecidae* WHITTARD, 1953 in having a simpler external morphology of the cuticle, and especially poorly differentiated tubercles and tubercle projections.

Genus assigned: *Plasmuscolex* gen. n.; Lower Ordovician.

Plasmuscolex gen. n.

Type species: *Plasmuscolex nero* gen. et sp. n.

Diagnosis: Medium-sized palaeoscolecidan with probably cylindrical body composed of more than 200 segments, with undifferentiated dorsal and ventral sides of the body. Segments equal in size, bordered by very deep intersegmental furrows. Each segment with nearly smooth central band, and two tubercle bands. Tubercles ridge-like, strong, elliptical to pear-shaped in outline, with indistinct boundaries, entirely covered by tubercle projections. Outer cuticular surface densely covered by epicuticular projections, more coarse at tubercle bands. Inner surface of cuticle with prominent ellipsoidal tubercle impressions. Number of tubercles at one tubercle band is nearly constant, and ranges from 50 to 70.

Discussion: *Plasmuscolex* differs from other palaeoscolecidans in having a different shape of tubercles and in poorly differentiated tubercle projections.

Species: *Plasmuscolex nero* gen. et sp. n.; Ordovician, Dobrotivian, Dobrotivá Formation; Bohemia.
Plasmuscolex klabavensis gen. et sp. n.; Ordovician, Arenigian, Klabava Formation; Bohemia.

Plasmuscolex nero gen. et sp. n.
Pl. VII; pl. VIII, figs. 1, 2; pl. IX

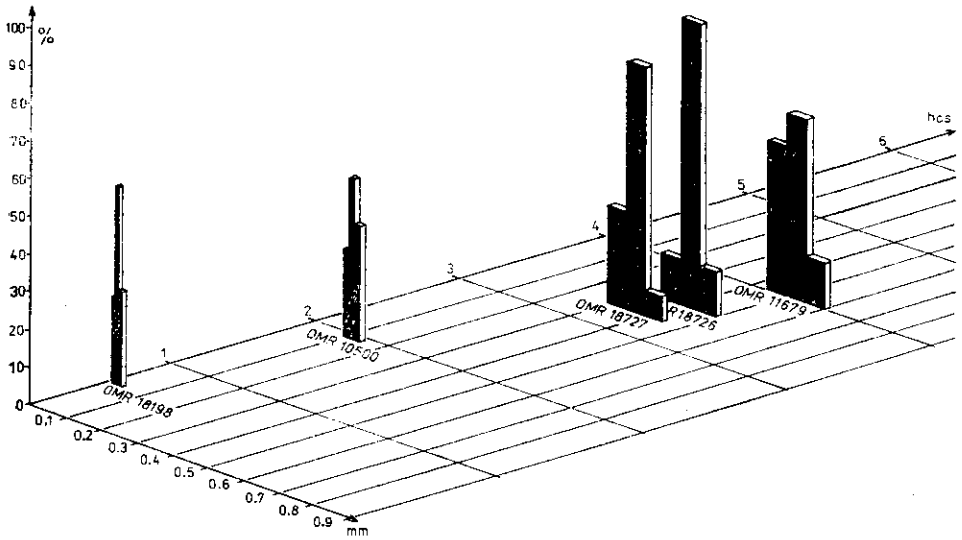
1978 *Paleoscolex* sp. (sp. n.); MERGL, p. 44

Holotype: Specimen OMR 11 679, figured on pl. VII, pl. VIII, figs. 1, 2 and pl. IX, figs. 4–6.
Type horizon and locality: Dobrotivian, Dobrotivá Formation; Sutice hill near Starý Plzenec.

Shape of the body: Flattened body 4.5 mm wide (= 4 mm in diameter in originally cylindrical body). Segments 0.45—0.55 mm long in non-contracted position, equal in size, separated by narrow, deep intersegmental furrows. The single known terminal of the body composed of identical segments, slightly tapering to the terminal. The maximum of segments preserved is 90, but entire animal possesses probably 200—300 segments. Absolute length of non-contracted specimen may reach 70—150 mm. S10 = 18—22.

Outer surface of the cuticle: Each segment possesses strongly elevated central band, 70—80 % as long as the segment, with both marginal tubercle bands steeply sloping toward intersegmental furrows. Both these slopes are deeply notched in regular intervals, forming zig-zag course of the central band. The strong, elliptical ridge, originating between two adjacent notches has an identical function as the tubercle in other palaeoscolecidans. Tubercle surfaces are covered with very fine tubercle projections, arranged in several (6—8) longitudinal rows. The tubercle projections are the largest at the tubercle tops and moderately decrease in size toward tubercle margins, near the bottom of notches they pass into epicuticular projections without clear boundaries. Dorsal and ventral longitudinal ridges very fine, preserved only at bottoms of notches. One tubercle row exhibits 55—60 tubercles.

Microornamentation: The bottoms of notches in tubercle bands are covered with regularly spaced (in oblique rows), papillae-like epicuticular projections. They are less than 5 μm in diameter being slightly higher than wide. The surface



7. Histogram of segment length-variability of *Plasmuscolex klabavensis* and *P. nero* species
Explanation as in text-fig. 6

of central bands is covered with low, pustule-like, densely crowded epicuticular projections, less than 3 μm in diameter.

Inner surface of the cuticle: Inner surface of the cuticle bears on each side of segment a lot of short, sharp ridges corresponding with the notches of the outer surface of the cuticle. Elliptical, deeply cut tubercle impressions are developed between ridges; their surface is convex internally.

Internal structures of the body: Specimen NM-L 24635 has preserved 0.6 mm wide and 2 mm long cylindrical structure, which may be sedimentary infilling of the intestine.

Plasmuscolex klabavensis gen. et sp. n.

Pls. X–XIII

Holotype: Specimen OMR 18726 figured on pl. X as fig. 1, 2 and pl. XI.

Type horizon and locality: Arenigian, Klabava Formation, Tetragraptus abbreviatus Biozone; Klabava, Starý hrad.

Shape of the body: The largest flattened specimen is 3.5 mm wide (= 2.3 mm in diameter), the smallest only 0.5 mm wide (= 0.3 mm in diameter). Overall shape of the body is the same as that in *P. nero*. Maximum of segments preserved is 250. Segments are 0.04–0.4 mm long, their length depends on specimen size. Absolute size of non-contracted specimens ranges from 10 mm to more than 100–150 mm. S10 = nearly 275 in minute specimen; in adults 20–30.

Outer surface of the cuticle: In arrangement of tubercles, tubercle projections and shape, size, and spacing of epicuticular projections this species is the same as *P. nero*, differs only in having pear-shaped outline of tubercles.

Family uncertain

Bohemoscolex gen. n.

Type species: *Bohemoscolex holubi* gen. et sp. n.

Diagnosis: Large palaeoscolecidan-like worm with body composed of more than 150 (probably several hundreds) identical segments. Dorsal and ventral sides probably undifferentiated; intersegmental furrows sharp and deep. Central band with gently wrinkled, shallow groove. Surface of segments smooth, with no signs of tubercles or papillae except for very minute (less than 30 μm in diameter) circular structure irregularly spaced. Narrow, sharply cut longitudinal furrow is developed on the ventral (?) side.

Discussion: *Bohemoscolex* is assigned to the palaeoscolecidans on the basis of 1) very long body composed of several hundreds identical segments with distinct boundaries, 2) rather rigid cuticle, and 3) by thinner cuticle along central bands

allowing folding of contracted segments. However, the new genus lacks tubercles and the outer surface of the cuticle does not bear epicuticular projections. Moreover, palaeoscolecidans have developed longitudinal ridge; this is substituted by a deep furrow in *Bohemoscolex*. Polygonal structure of cuticle is unknown in other palaeoscolecidans, too.

Species assigned: *Bohemoscolex holubi* gen. et sp. n.; Ordovician Arenigian, Klabava Formation; Bohemia.

Bohemoscolex holubi gen. et sp. n.

Pl. XIV

Holotype: Specimen OMR 9595 figured on pl. XIV.

Type horizon and locality: Arenigian, Klabava Formation, Corymbograptus v-similis Biozone; Rokycany – hospital.

Name: After Karel Holub, outstanding collector in Rokycany.

Shape of body: Flattened body 11 mm wide (= 7 mm in diameter at originally cylindrical body). Body terminals unknown. Maximum of segments preserved is nearly 90. Segments 0.6—0.7 mm long, all subequal in length. Intersegmental furrows narrow, deep, simple. Judging from a single coiled specimen, the absolute length may reach minimally 8—12 cm in uncontracted specimen. S10 = 16—18.

Outer surface of the cuticle: Tubercle bands smooth, without tubercles or similar structures. Central band with wrinkled shallow groove. Remaining surface of the cuticle with minute circular structures, irregularly spaced, at some places forming indistinct, longitudinal rows. These structures represent shallow pits or hollow secondarily broken outgrowths infilled with clayey substance. Narrow sharp and deep longitudinal furrow is developed on the ventral (?) side. SEM investigation shows small areas with polygonal structures, irregularly spaced on the outer surface of cuticle. Polygons are about 8 μm in diameter, bordered by less than 1 μm wide interspaces. This structure of cuticle may be interpreted as imprints of epithelian supporting cells (compare epithelian moulds of some fossil inarticulate brachiopods; CURRY - WILLIAMS 1983). The structure and arrangement of fine circular structures irregularly spaced on the surface of the cuticle recall papillae in intrapapillate zone of *Palaeoscolex antiquus* GLAESSNER, 1979.

Palaeoscolecida gen. indet. A

Pl. XV

Description: Body finely segmented. Cuticle composed of several layers, with some structures dissimilar and/or showing reverse spatial orientation of the structures in comparison with other palaeoscolecidans. Single fragment (pl. XV) is probably a positive imprint, showing outer surface of the cuticle. Specimen shares

with palaeoscolecidans deep intersegmental furrows, rigid cuticle, and slightly contracted segments forming folds. Tubercle projections form outgrowths more or less regularly spaced in shallow depressions.

However, tubercles are substituted by shallow depressions of semiglobular shape; they are arranged along intersegmental furrows and their number is unclear. Epicuticular projections are substituted by shallow pits, covering whole surface of the segment. Close to segmental margins they are longitudinally elongate, become nearly circular to hexagonal in outline at central bands. The bottoms of the pits are smooth, but their walls are vertically striated.

If available imprint represents an external mould, then segments are bordered by strong ridges, structures of cuticle are reverse compared to aforementioned ones, and contractions of segments originate by concave bending.

Occurrence: Arenigian, Klabava Formation, Tetragraptus abbreviatus Biozone; Klabava — Starý hrad locality.

Palaeoscolecida gen. indet. B

Description: Distinctly segmented, 14.3 mm long fragment of a trunk, due to poor preservation with only segmentation preserved. Maximum width = 6.7 mm, length of segment 0.25—0.3 mm. S10 = 38—42.

Occurrence: Arenigian, Klabava Formation, Hologratus tardibrachiatus Biozone; Rokycany — Valcha locality.

Palaeoscolecida gen. indet. C

Description: Short part of distinctly segmented trunk with no other structures visible. Length of trunk = 25 mm, maximum of width = 8 mm, length of segment 0.3—0.4 mm. S10 = 26—27.

Occurrence: Llanvirnian, Šárka Formation, Corymbograptus retroflexus Biozone; Mýto locality.

?Chaetognatha Leuckart, 1854

Class, Order and Family uncertain

Titerina gen. n.

Type species: *Titerina rokycanensis* gen. et sp. n.

Description: Worm-like body minute, elongate, at mid-length gently widened. Anterior part distinctly differentiated. Jaw apparatus composed of a single pair of large, hollow, slightly incurved spines, with anterior ends narrowly

pointed (= grasping spines). The anterior part of the body exhibited preserved intestine. Both sides of intestine are bordered by narrow, axially strongly elongate structures, which have the same location as ovaria at recent chaetognaths. In posterior terminal of a single specimen the remains of fibrillar structure are preserved (= fin?). The posterior third of the body (behind the intestine) contains globular, tiny (less than 70 μm in diameter) bodies, with shallow concave depression on their surfaces (pl. XVI, fig. 5).

Preservation: All specimens are preserved in dark brown organic substance, forming thin film on the bedding plane. Grasping spines, some parts of intestine and globular bodies show three-dimensional preservation. Ovaria and remaining parts of the intestine are flattened and are distinguishable by their darker colour only. Minute globular bodies are fossilized by transparent, brown-red substance.

Remarks: *Titerina* recalls *Chaetognatha* by its anatomy, but this assignment is only provisional. *Spadella* (according HYMAN 1959) is morphologically the closest to the new genus. *Titerina* shares with *Chaetognatha*: 1) elongate, worm-like body of minute size; 2) jaw apparatus with paired, slightly incurved grasping spines. *Titerina* has one pair, but recent chaetognaths have four pairs minimally. Complex, multipaired grasping spine apparatus is known from the Cambrian (SZAMAWSKI 1982), but grasping spines may be absent in poorly developed specimens (SCHRAM 1973); 3) The intestine of *Titerina* ends at 3/5 of the body length and determines location of the trunk-tail septum and anus. The space in the posterior part of the body may correspond to tail coelom of recent chaetognaths; 4) remains of fibres at the posterior terminal of the body recall by location and shape supporting rays in the fin of recent chaetognaths; 5) elongate, narrow spots running parallel with the body axis and rimming the intestine recall by location and shape the ovaria of recent chaetognaths.

Species assigned: Type species only.

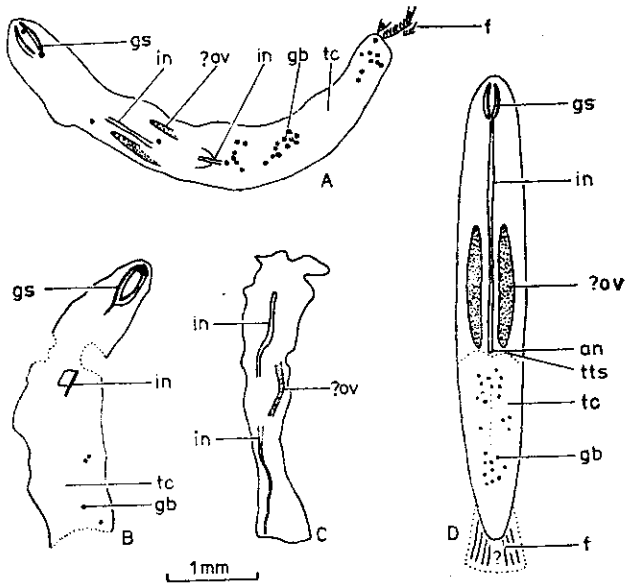
Titerina rokycanensis gen. et sp. n.

Pl. XVI, text-fig. 8

Holotype: Specimen OMR 15334A figured on pl. XVI as figs. 1, 4; text-fig. 8A.

Type horizon and locality: Arenigian, Klabava Formation, Hologratus tardibrachiatus Biozone; Rokycany – Stráň (gully, section 7).

Description: see description of the genus. The width of the intestine depends on mode of preservation, non-deformed has 40 μm in diameter, width of the flattened one ranges from 10 to 250 μm. Posterior end of the intestine reaches 3/5 of the body length. The paired elongate structures bounding the intestine (ovaria) have anterior ends at half-length the intestine, and nearly reach trunk-tail septum. The globular tiny bodies with concave depression at their surfaces have been observed mainly at posterior part of the body. They have been found at specimens OMR 15334A (35 bodies) and OMR 15334B (3 bodies). The diameter of these



8. *Titerina rokycanensis* gen. et sp. n.
Specimens OMR 15334A (*A*), 15334B (*B*), 15334C (*C*), and reconstruction of anatomy (*D*)
an — anus, *gb* — globular bodies, *gs* — grasping spines, *f* — fin, *in* — intestine, *?ov* — ovaria, *tc* — tail coelom, *tts* — trunk-tail septum

Table 3

Dimensions of *Titerina rokycanensis* gen. et sp. n.

specimen	length of body (in mm)	maximum of body width (in mm)	length of grasping-spines (in mm)	width of grasping spines (in mm)
OMR 15334A	4.9	0.7	0.41	0.06
OMR 15334B	3.1	0.9	0.48	0.06
OMR 15334C	3.4	0.6?	—	—

bodies ranges from 20 to 70 μm, and apart from 4 bodies, all have been found at posterior third of the body. Close to specimen 15334B and 15334C a lot of minute, cylindrical, 50—70 μm long and 35—55 μm wide dark bodies have been found. They are distributed near the posterior third of specimens and may be interpreted as coprolites. Specimen 15334C shows squeezing of these bodies from broken part of the intestine.

K tisku doporučil M. Plička

Přeložil M. Mergl

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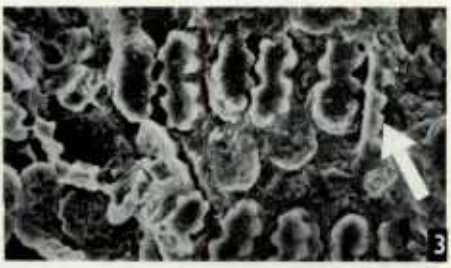
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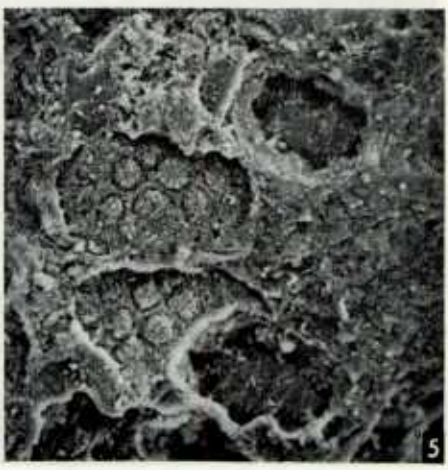
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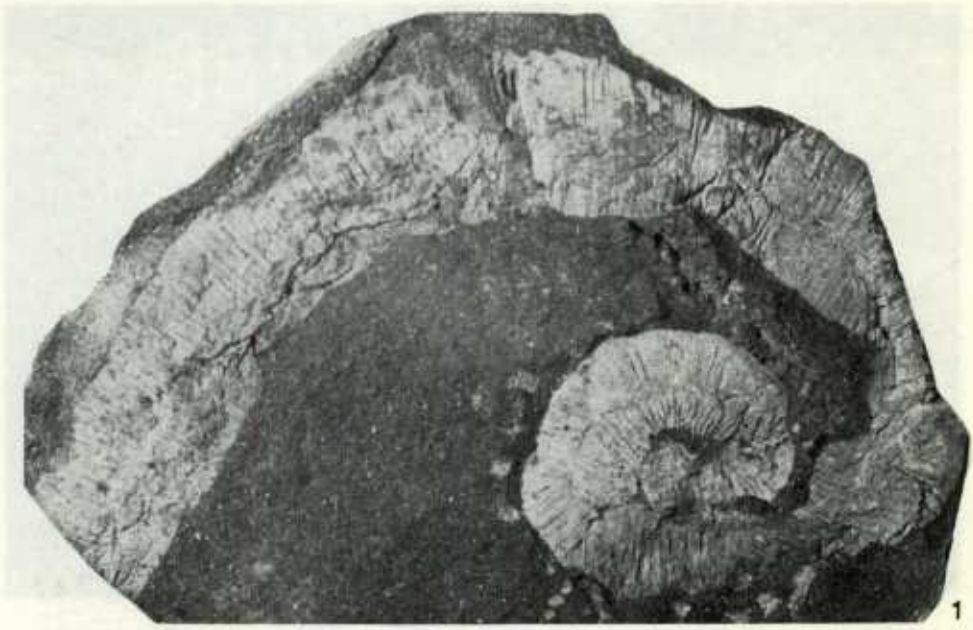

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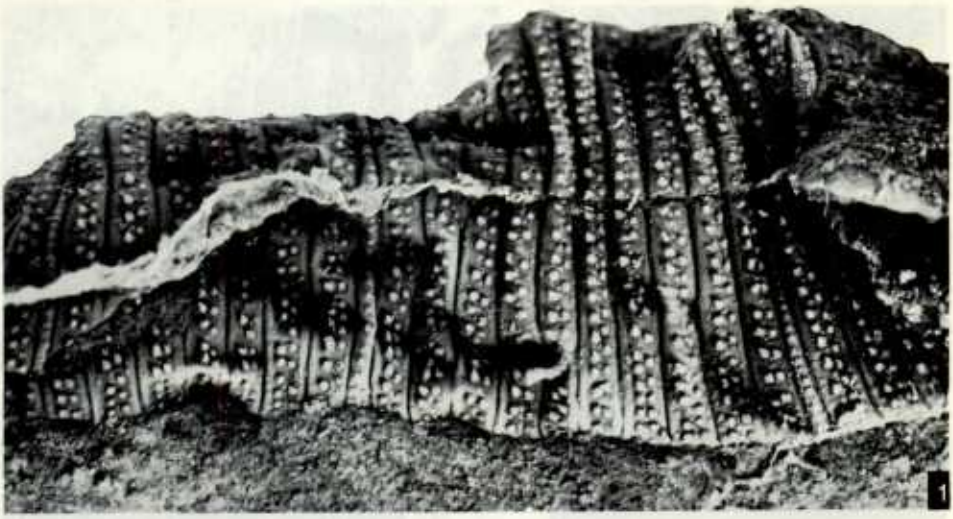
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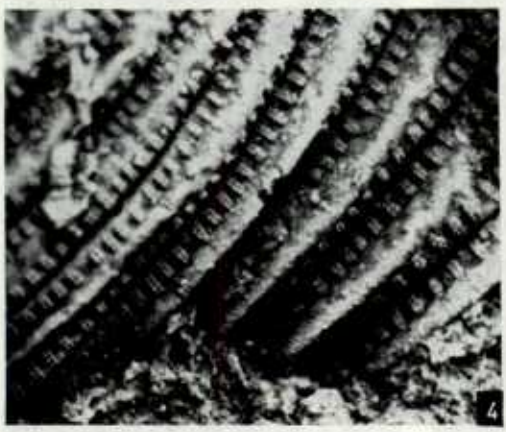
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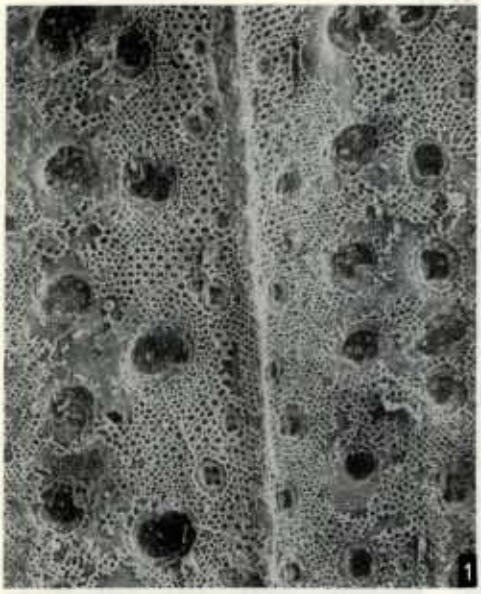

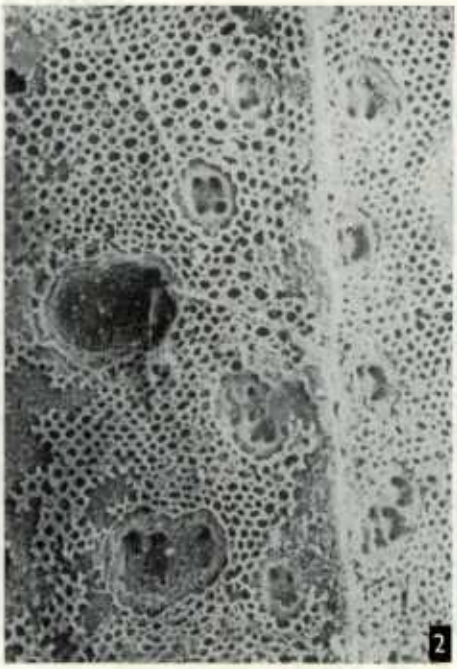

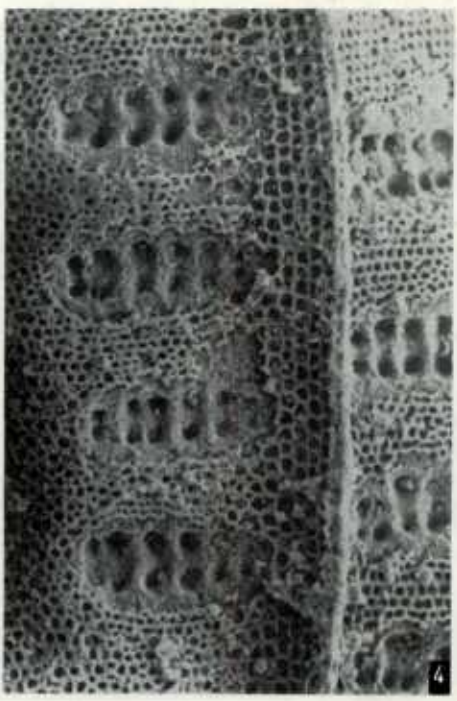

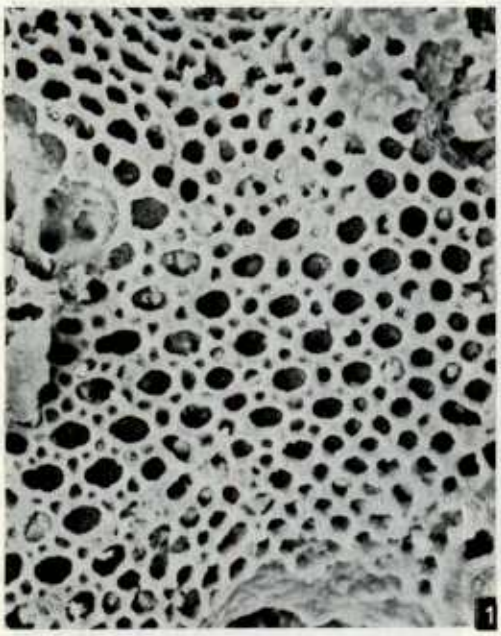
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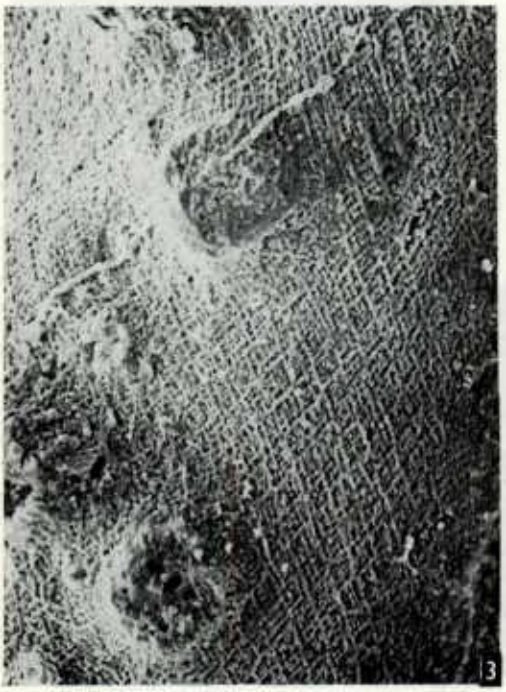
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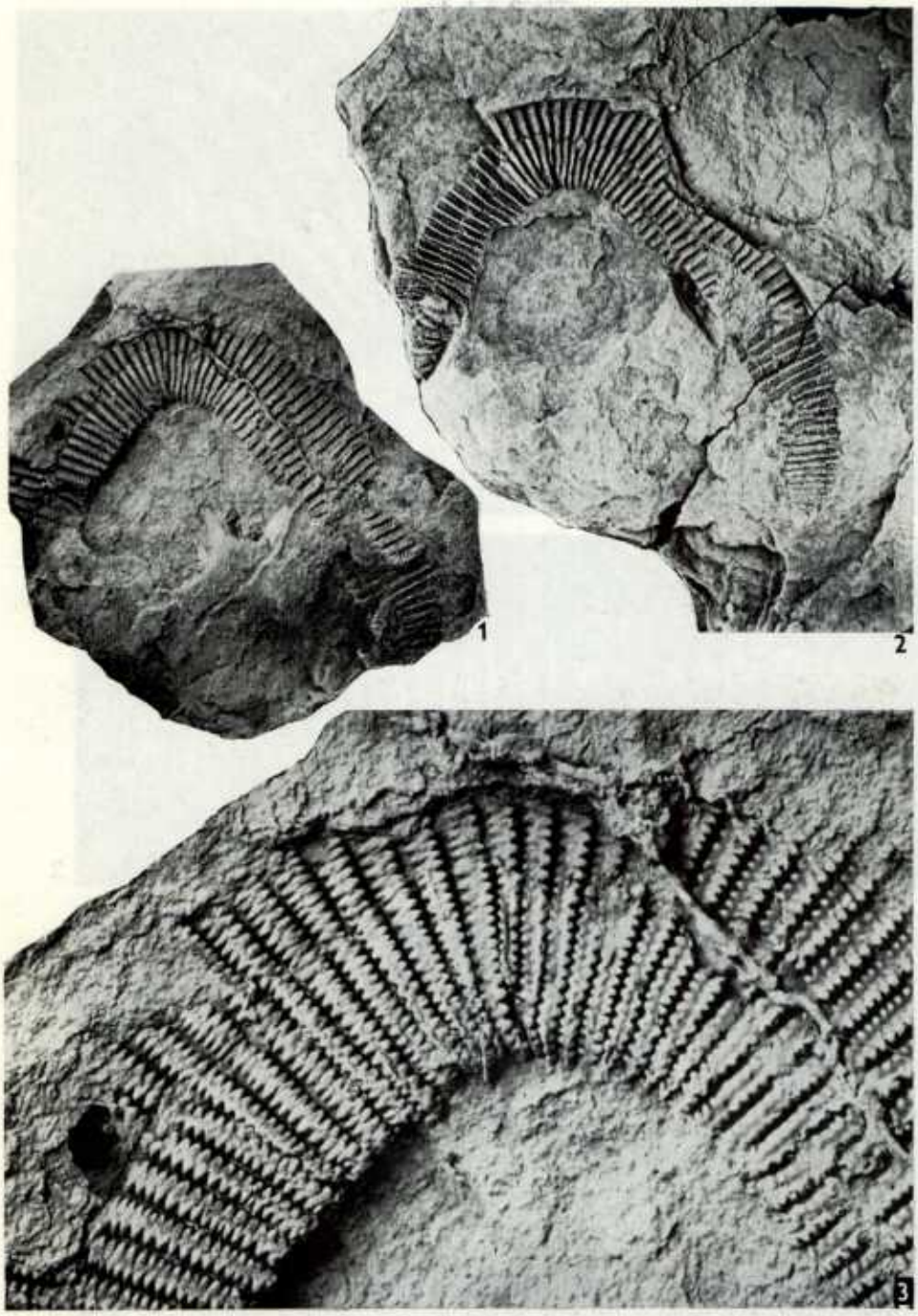
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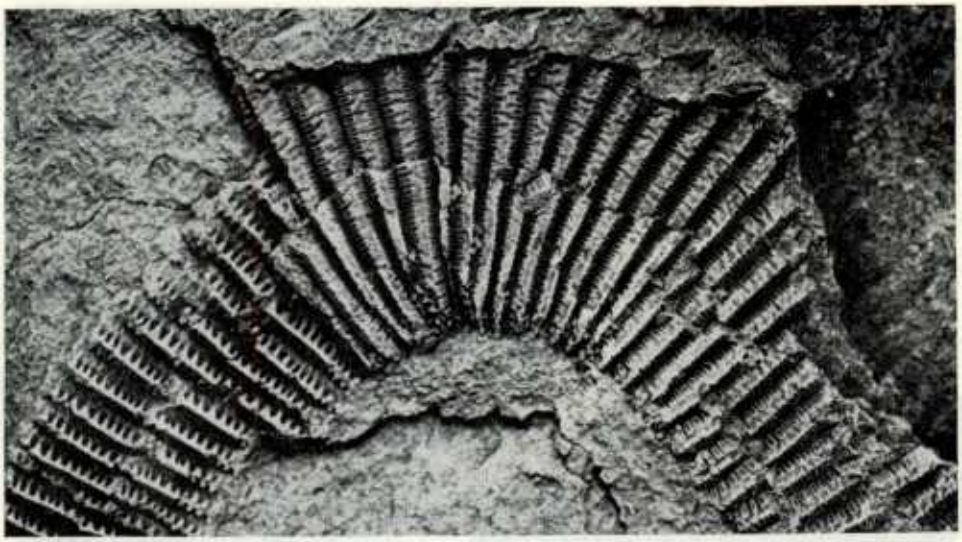

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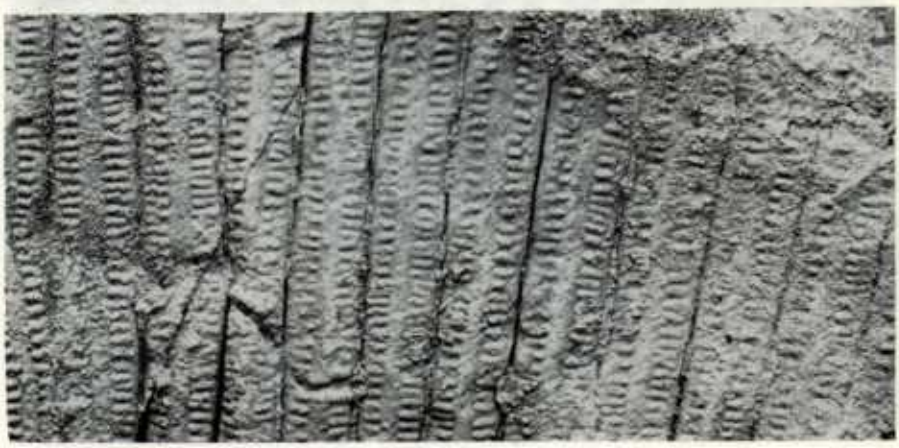

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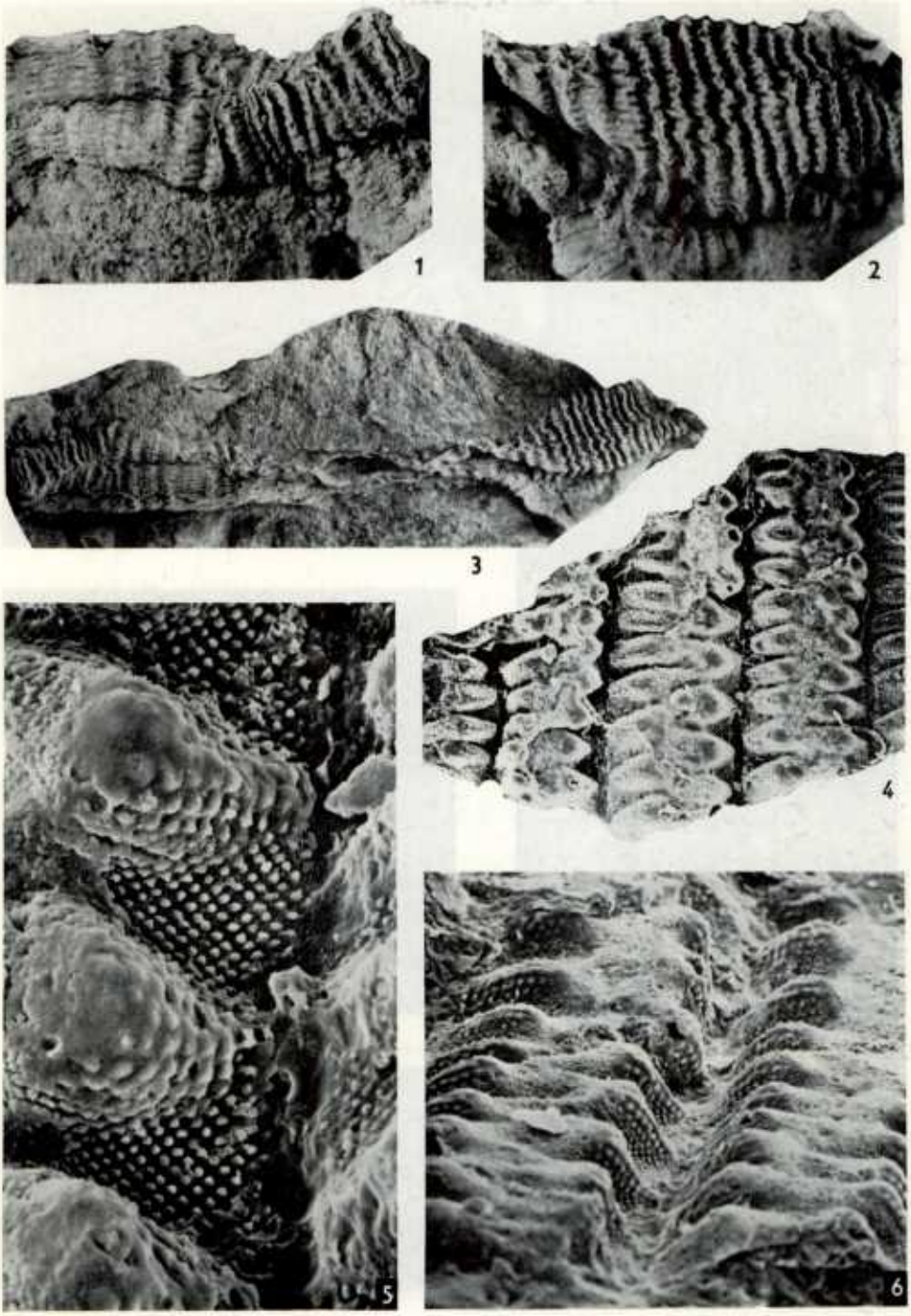
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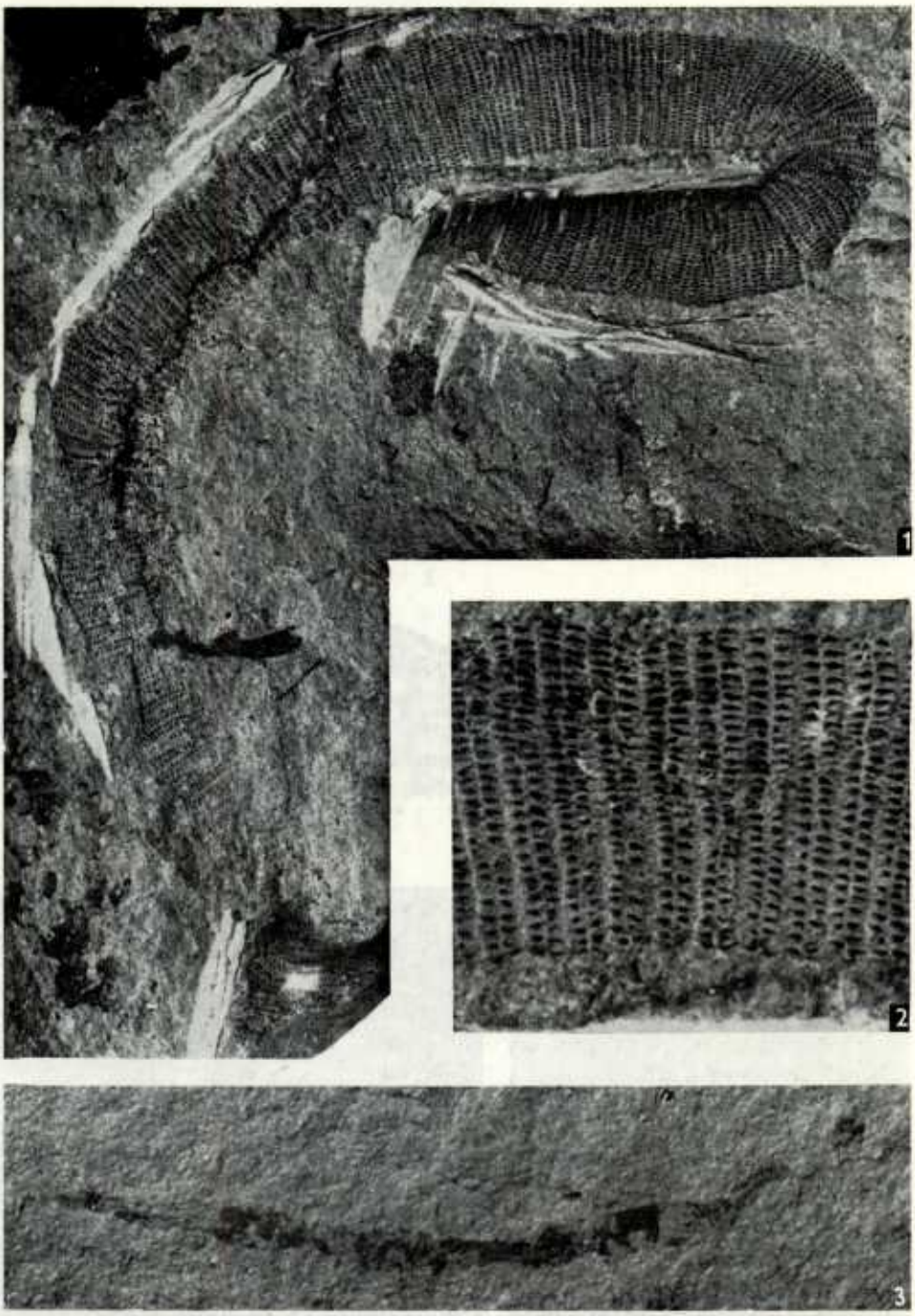
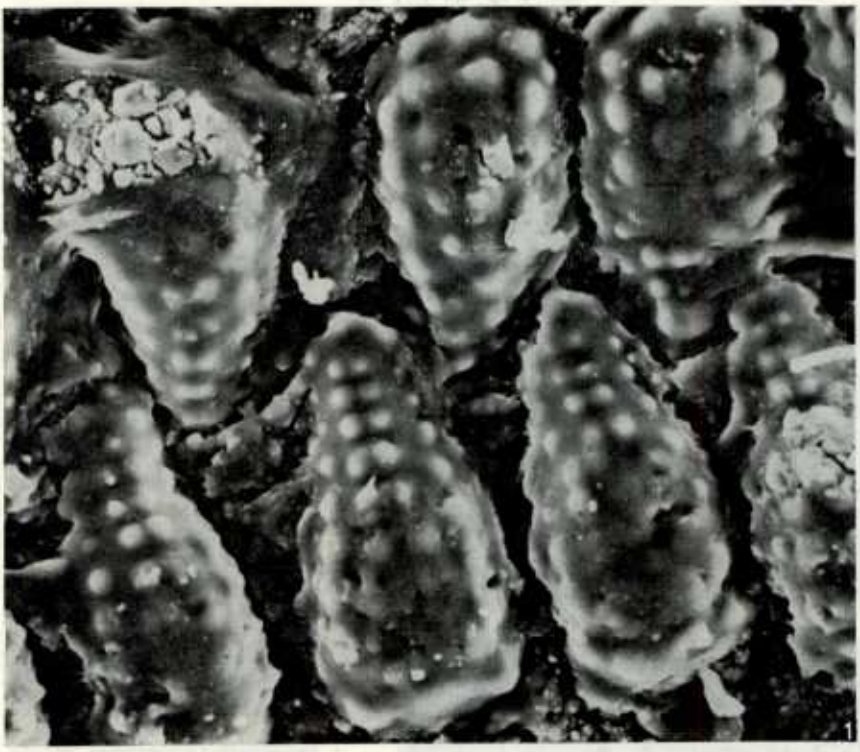
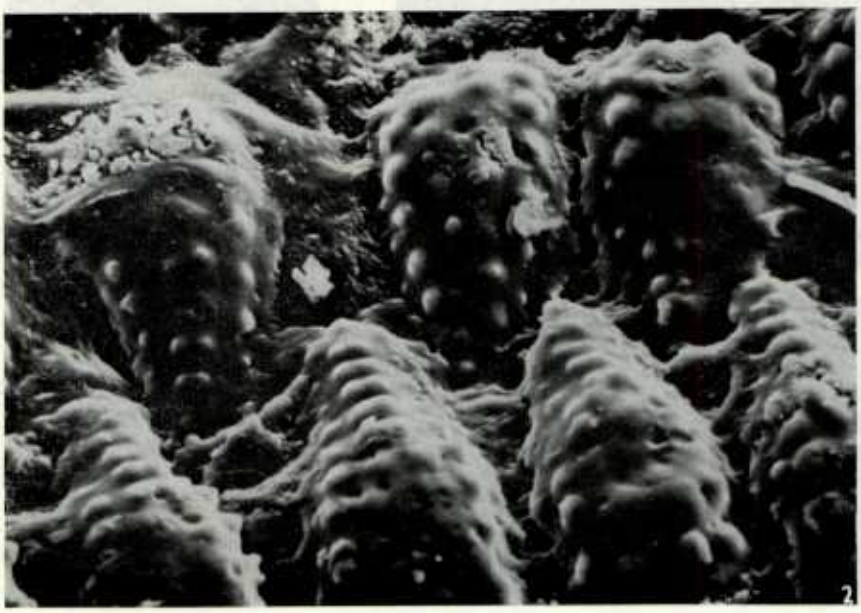
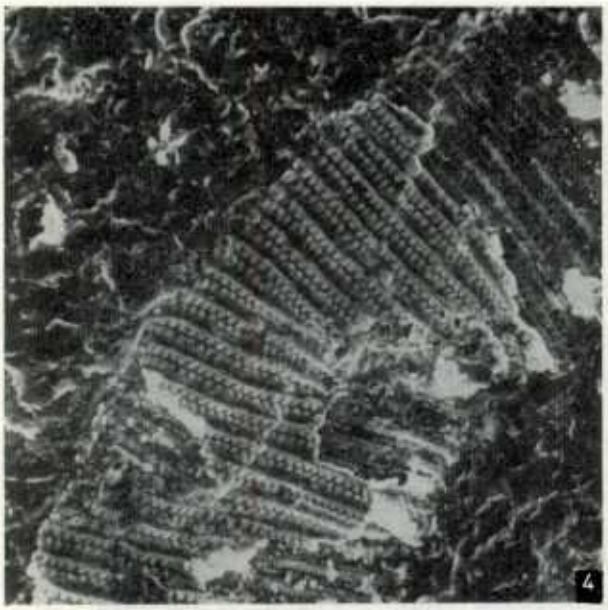
Pl. X





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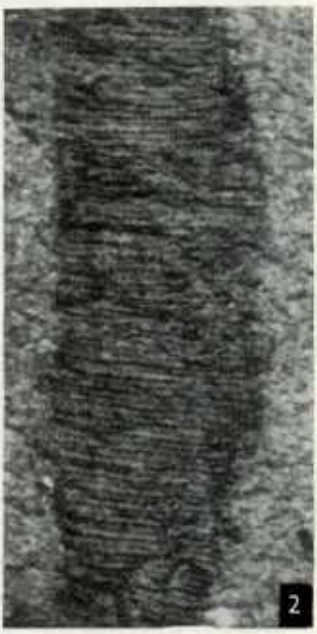
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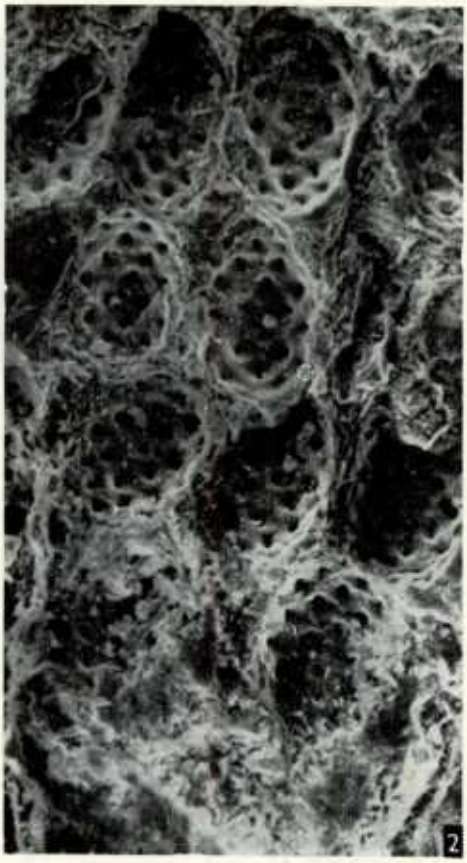
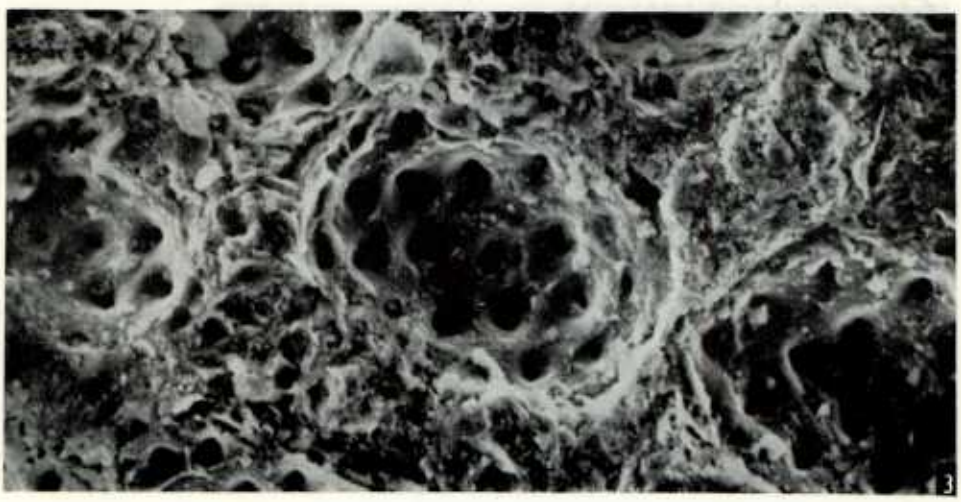
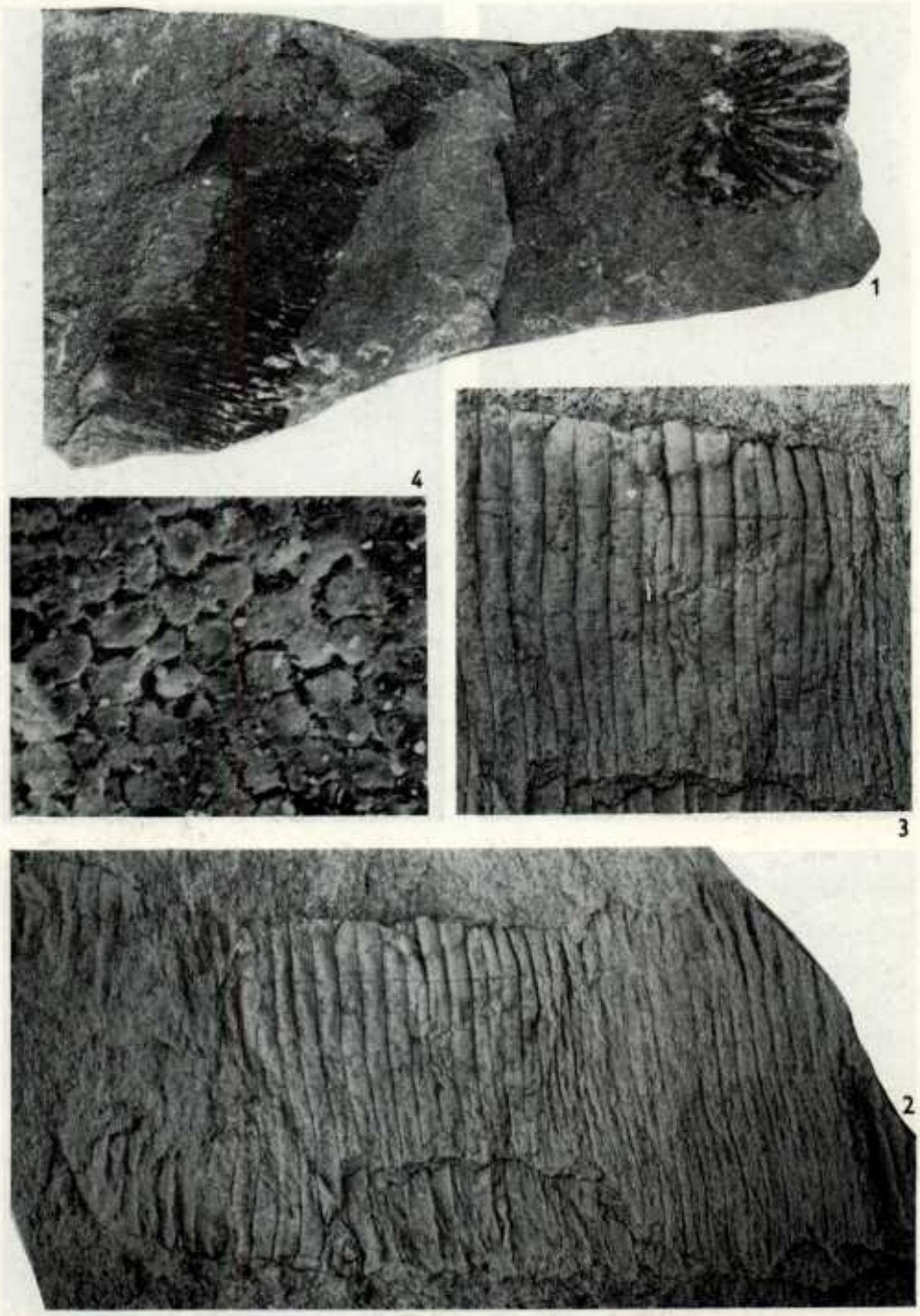




Pl. XIV

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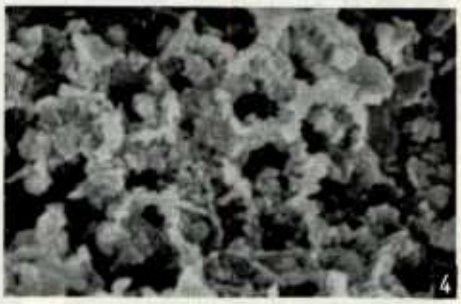
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Pl. XVI

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Explanation of plates

Pl. I

"Palaeoscolex" tenensis gen. et sp. n.
Specimen GS-MM 199, Klabava Formation, Těně locality; latex casts (1—3), external moulds (4,5); SEM photo (1—5).
1,3 — transversal rows of tubercles, showing spined outer and pitted inner surfaces of tubercles, arrow indicates vertically oriented tubercle, ×150, ×150; 2 — inner surface of tubercle, ×490; 4,5 — inner and outer surfaces of tubercles, ×370, ×250.

Pl. II

Gamascolex herodes gen. et sp. n.
Specimen GS-p 5050, Dobrotivá Formation, Malé Přílepy locality; uncoated external mould (1), latex casts coated with ammonium chloride (2,3).
1 — almost complete specimen, composed of more than 250 segments, ×2.8; 2 — coiled trunk showing folded segments at ventral side, ×9.0; 3 — trunk showing ventral (left) and dorsal (right) tubercles, ×9.0.

Pl. III

Gamascolex herodes gen. et sp. n.
Specimens NM-L 24634 (1, 2) and GS-MM 118 (3—5), Dobrotivá Formation, Malé Přílepy locality; latex casts coated with ammonium chloride (1—5).
1, 2 — outer and inner surfaces of cuticle, the same part of trunk, ×20, ×20; 3 — outer dorsal surface of cuticle, ×10; 4, 5 — pathologic segments, arrow indicates discontinuous intersegmental furrow, ×10, ×25.

Pl. IV

Gamascolex herodes gen. et sp. n.
Specimens NM-L 24634 (1, 2, 4), GS-NM 118 (3, 5), Dobrotivá Formation, Malé Přílepy locality; latex casts coated with ammonium chloride (1, 2, 4) and SEM photos (3, 5).
1 — outer surface of cuticle, ventral side near body axis, ×18; 2 — longitudinal ridge on ventral side, ×25; 3 — outer surface of cuticle with original substance preserved, note mound-like epicuticular projections surrounded by ventral type tubercles, ×140; 4 — outer surface of cuticle, dorsal side, showing tubercles, and folds at central bands originating during contraction, ×25. 5 — bottom of intersegmental furrow with epicuticular projections, ×140.

Pl. V

Gamascolex herodes gen. et sp. n.
Specimen GS-MM 118, Dobrotivá Formation, Malé Přílepy locality; external moulds (1—4), SEM photos (1—4).
1, 2 — external moulds of outer surface of cuticle, ventral sides showing large circular pits (= tubercles) and minute pitting (= epicuticular projections), ×70, ×140; 3, 4 — external moulds of outer surface of cuticle, dorsal sides showing elliptical areas with two rows of pits (= tubercles with tubercle projections) and fine pitting (= epicuticular projections) ×45, ×140.

Pl. VI

Gamascolex herodes gen. et sp. n.
Specimen GS-MM 118, Dobrotivá Formation, Malé Přílepy locality; external moulds (1, 2) and original cuticle substance (3, 4); SEM photos (1—4).
1 — external mould of outer surface of cuticle, ventral side showing alternating of two size categories of epicuticular projections, ×350; 2 — external mould of dorsal type tubercle on ventral side, ×700; 3, 4 — cross-lamellar structure of original cuticular substance, ×180, ×700.

Pl. VII

Plasmuscolex nero gen. et sp. n.
Specimen OMR 11679, Dobrotivá Formation, Sutice hill near Starý Plzenec locality; internal mould (2), and latex casts (1,3); coated with ammonium chloride (1—3).
1—3 — trunk with terminal, holotype, ×3, ×3, ×10.

Pl. VIII

Plasmuscolex nero gen. et sp. n.
Specimen OMR 11679, Dobrotivá Formation, Sutice hill near Starý Plzenec locality; internal (1) and external (2) moulds; coated with ammonium chloride (1, 2).
1, 2 — part of trunk showing negative imprint of inner surface of cuticle and tapering body terminal, ×10, ×10.
Gamascolex herodes gen. et sp. n.
Specimen OMR 11799, Dobrotivá Formation, Hůrka hill near Starý Plzenec locality; imprint in shale; coated with ammonium chloride.
3 — dorsal side of large specimen, ×10.

Pl. IX

Plasmuscolex nero gen. et sp. n.
Specimens NM-L 24635 (1—3) and OMR 11679 (4—6), Dobrotivá Formation, Šárka (1—3) and Sutice hill near Starý Plzenec (4—6) localities; latex casts (1—6); coated with ammonium chloride (1—3), SEM photos (4—6).
1—3 — trunk with contracted terminal parts, ×10, ×10, ×4; 4, 5 — five incomplete segments showing outer surface of cuticle with tubercles, tubercle projections and epicuticular projections, ×35, ×150; 6 — the same part, oblique view, ×80.

Pl. X

Plasmuscolex klabavensis gen. et sp. n.
Specimens OMR 18726 (1,2), and OMR 18198 (3), Klabava Formation, Klabava — Starý hrad locality; uncoated imprints (1—3).
1, 2 — almost complete specimens flattened in shale and detail of segments, ×5, ×15; 3 — minute complete specimen with partly preserved substance of cuticle, ×12.

Pl. XI

Plasmuscolex klabavensis gen. et sp. n.
Specimen OMR 18726, Klabava Formation, Klabava — Starý hrad locality; latex casts; SEM photos.
1, 2 — detail of several tubercles in vertical and oblique views, ×280, ×280.

Pl. XII

Plasmuscolex klabavensis gen. et sp. n.
Specimens OMR 18198 (4,5) and OMR 10500 (1—3), Klabava Formation, Rokycany — Stráň

(quarry) (1—3), and Klabava — Starý hrad (4, 5) localities; imprints (1—3) and latex casts (4, 5); uncoated specimens (1, 2), and SEM photos (3—5).
1, 2 — almost complete specimen flattened in shale and detail of segmentation, ×5, ×15; 3 — negative imprint of epicuticular projection (on the left), ×350; 4, 5 — part of trunk with partly contracted segments, and detail of segments, ×100, ×450.

Pl. XIII

Plasmuscolex klabavensis gen. et sp. n.
Specimen OMR 18727, Klabava Formation, Klabava — Starý hrad locality; imprint (1), external moulds (2, 3); uncoated specimen (1), SEM photos (2, 3).
1 — fragmental flattened trunk in shale, ×5; 2, 3 — detail of tubercles with tubercle projections ×200, ×500.

Pl. XIV

Bohemoscolex holubi gen. et sp. n.
Specimen OMR 9595, Klabava Formation, Rokycany — hospital locality; imprint with cuticle substance preserved; uncoated (1), coated with ammonium chloride (2, 3), and SEM photo (4).
1 — incomplete flattened specimen in shale, ×2.5; 2, 3 — details of trunk with segments, central bands and longitudinal furrow preserved, ×5, ×7; 4 — polygonal structure of cuticle, ×800.

Pl. XV

Palaeoscolecida gen. indet. A
Specimen OMR 18171, Klabava Formation, Klabava — Starý hrad locality; imprints (1—4) and latex cast (5); SEM photos (1—5).
1 — several segments showing segment boundaries and pitting of cuticle, ×350; 2 — the same part, showing tubercle pits and details of cuticular surface, ×1600; 3 — several segments, ×265; 4 — epicuticular pits at central band with scalloped outline, ×3600; 5 — part of segment with large tubercles (?) and epicuticular projections (?), ×370.

Pl. XVI

Titerina rokycanensis gen. et sp. n.
Specimens OMR 15334A (1, 4), OMR 15334B (2,5), and OMR 15334C (3), Klabava Formation, Rokycany — Stráň (gully, section 7) locality; imprints (1—5); uncoated specimens (1—4) SEM photo (5).
1, 4 — complete specimen with grasping spines and ovaria, and enlarged anterior end of body, ×15, ×60; 2 — incomplete specimen with anterior end and grasping spines preserved, ×15; 3 — incomplete specimen with intestine preserved, ×15; 5 — globular body with concave depression on the right, ×950.

Photographs on pl. XVI, fig. 4 made by M. Kunst, all SEM made by J. Kulich, remaining by authors.

Vermiformní fosilie (Palaeoscolecida; ?Chaetognatha) ze spodního ordoviku Čech

(*Résumé anglického textu*)

PETR KRAFT – MICHAL MERGL

Předloženo 6. října 1986

Paleoskolecidi (?*Annelida*) představují charakteristickou skupinu vermiformních metazoí. V zahraničí se vyskytují v marinních sedimentech kambrického až silurského stáří; z Čech jsou známi pouze ze spodního ordoviku (arenig—dobrotiv). Jejich kutikula, dokonale zachovalá díky fosfatizaci, má poměrně složitou morfologii. Její povrch je typicky členěn (tuberkule, epikutikulární výrůstky aj.); kutikula je laminována a připomíná podobné struktury v kutikule recentních annelidů. Svou vnější morfologií paleoskolecidi připomínají kromě annelidů i nematody a priapulidy, avšak vzhledem k nedostatku údajů o vnitřní anatomii a morfologii tělních zakončení je jejich pozice v systému nevyjasněná. V systematické části je popsána 1 nová čeleď, 3 nové rody a 5 nových druhů.

Kromě toho je popsán drobný organismus, který svou velikostí, vnější morfologií, přítomností čelistního aparátu a vnitřní anatomií připomíná ploutvenky (*Chaetognatha*). Tento organismus je přiřazen k novému rodu *Titerina*.

Ископаемые червеобразные (*Palaeoscolecida*; ? *Chaetognatha*) **из нижнего ордовика Чехии**

Palaeoscolecida (? *Annelida*) известны с кембрия по силур; в Чехии они встречаются лишь с аренига по добротив. Степень сохраненности индивидов из Чехии позволяет детально описать морфологию кутикулы, ультраструктур и обсудить систематическую позицию палеосколецидов. Обсуждаются также их способ движения и образ жизни. Определяются семейство *Plasmuscolecidae* и роды *Bohemoscolex*, *Gamascolex* и *Plasmuscolex*. В систематической части описано пять новых видов и три неопределимых индивида. В качестве дополнения описан новый род *Titerina* (*T. rokycanensis* sp. n.), относящийся, вероятно, к *Chaetognatha*.

Přeložil A. Kříž