

Isolated tubercles of some Palaeoscolecida

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Boogaard, M. van den, Isolated tubercles of some Palaeoscolecida. — Scripta Geol., 90: 1-12, 1 fig., 5 pls, Leiden, November 1989.

Tubercles of *Palaeoscolex? tenensis* Kraft & Mergl, 1989 found as isolated phosphatic microfossils in Ordovician limestones are described. The probability that the phosphatic microfossils assigned to the genera *Hadimopanella* Gedik, 1977 and *Milaculum* Müller, 1973 represent tubercles of palaeoscolecidans is discussed. A relation between Palaeoscolecida and Chordata is hinted at.

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Introduction

The fine fraction of the insoluble residue of a Lower Ordovician limestone from Killeröd (Sweden) dissolved in formic acid yielded besides abundant conodonts and phosphatic brachiopods a modest number of tiny plate-like phosphatic microfossils (max. length 226 μm) of unknown affinity. Later similar fossils were obtained from two more Ordovician limestone samples, one from Öland (Sweden) and one from Estonia (USSR). Although those from the latter sample are much better preserved they also gave no clue as to their affinity. Some months ago, however, a paper appeared about worm-like fossils from the Lower Ordovician of Bohemia (Kraft & Mergl, 1989). One of their worm-like fossils, '*Palaeoscolex? tenensis*', is adorned by transverse rows of tubercles which look identical to the platelike fossils in the Swedish and Estonian samples. Because some of my specimens show more detail than the tubercles illustrated by Kraft & Mergl, I decided to publish them as it may help in eventually establishing the affinity of '*Palaeoscolex? tenensis*' Kraft & Mergl, 1989.

Kraft & Mergl describe in the same paper a new genus – *Plasmuscolex* – of worm-like fossils which are covered with transversal rows of tubercles resembling some of the phosphatic sclerites described under the generic name *Milaculum* by Müller (1973). Some problems involved in eventually considering *Plasmuscolex* a junior synonym of *Milaculum* will be discussed in this paper.

Acknowledgements

Thanks are due to Dr Ph.J. Hoedemaeker, who has critically read an earlier draft of this paper and made suggestions that have improved the final version. I wish to thank Miss Y.A. van den Boogaard for drawing the figure, and Mr J. Timmers for combining the SEM micrographs into plates.

Palaeoscolecida Conway Morris & Robison, 1986

Palaeoscolecidae Whittard, 1953

Diagnosis (from Conway Morris & Robison, 1986) – Vermiform metazoans with a papillate epidermis, papillae typically arranged in transverse rows that may be duplicated, the annular arrangement of the papillae probably reflecting metameric segmentation. Jaws may be present, and the alimentary canal is more or less straight with a terminal anus.

Remarks – The number of segments of palaeoscolecidans is large, up to c. 400 in i.a. *Palaeoscolex ratcliffei* Robison, 1969. Each segment (or somite in Robison) is marked with double transverse rows of about 25-40 papillae across the surface. In other genera, i.a. *Plasmuscolex* Kraft & Mergl, 1989 the number of papillae (or tubercles) is even larger. In the descriptions of *Palaeoscolex piscatorum* Whittard, 1953, *P. ratcliffei* Robison, 1969, *P. antiquus* Glaessner, 1979, and *P. cf. P. ratcliffei* of Conway Morris & Robison, 1986 no information is given about the morphology of the tubercles because of poor preservation. The vermiform fossils described by Kraft & Mergl (1989) have a much better preserved cuticle because it consists of apatite or apatite-like phosphatic minerals. Kraft & Mergl supposed this to be the result of secondary phosphatization (op. cit., p. 18) but do now believe (Mergl, written communication June 1989) that the phosphatization is primary. The tubercles of their fossils show much more detail and in my opinion show that for instance the tubercles of *Plasmuscolex* Kraft & Mergl, 1989 are nothing else than the isolated phosphatic microfossils up to now described as species of the (form)genus *Milaculum* Müller, 1973. Mergl (commun., June 1989) now also is of the opinion that *Milaculum* represents the tubercles of palaeoscolecidans and

Plate 1

Phosphatic microfossils supposed to represent tubercles of *Palaeoscolex? tenensis* Kraft & Mergl, 1989. The specimens of figs. A, B and D are from sample 4750, Aru Quarry, Estonia (RGM 383 487); fig. C is a specimen from sample RGM 371 097, Killeröd, Sweden (RGM 383 473).

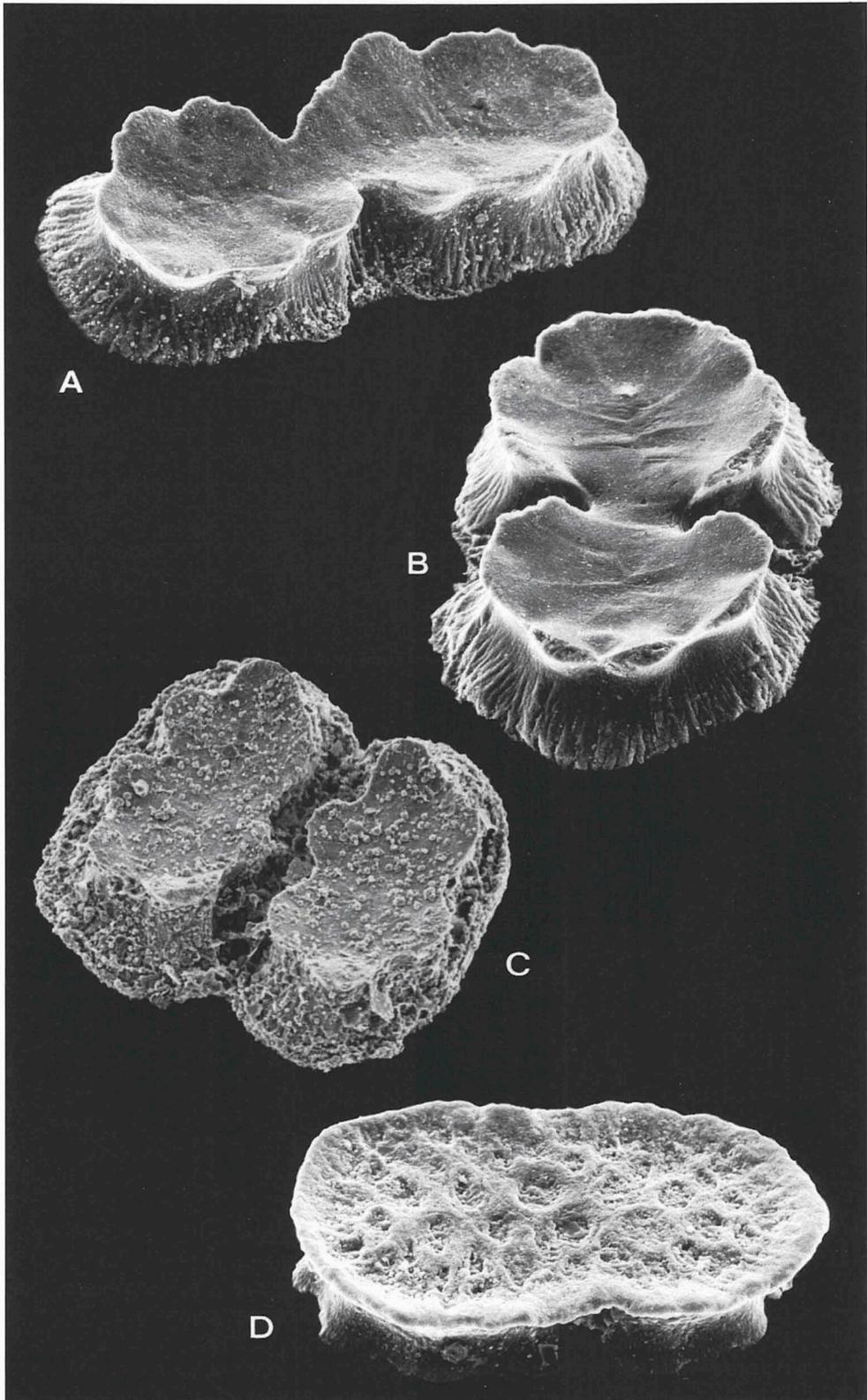
A. Oblique view of outer side (x 560).

B. Oblique view of a specimen of which the edge of the outer side is partly abraded (x 560).

C. Two adhering tubercles (x 560).

D. Oblique view of inner side (x 520).

Plate 1



that hadimopanellids too are isolated remains of that group. On the latter subject – affinity of *Hadimopanella* to the Palaeoscolecida – they (Kraft & Mergl) already submitted a paper to Lethaia. I share their opinion that the various species of the (form)genus *Hadimopanella* Gedik, 1977 may represent the sclerites of palaeoscolecidans and more in particular that *Hadimopanella oezgueli* Gedik, 1977 is the species name given to the papillae of *Palaeoscolex* cf. *P. ratcliffei* described by Conway Morris and Robison (1986) from the Middle Cambrian of northeast Spain. Their only specimen consisted of about 190 papillate bands and each papillate band contains about 70 papillae. The whole specimen thus bears more than 13 000 papillae. If these papillae (tubercles) were originally phosphatic as in several other palaeoscolecidans, disintegration of one specimen of *P. cf. P. ratcliffei* could already supply a host of phosphatic microfossils. The papillae are in this case preserved as minute (about 80 μm diameter) hemispherical structures composed of dark material. The Middle Cambrian Lancara Limestone of NW Spain contains large numbers of *Hadimopanella oezgueli* – up to 12 000 specimens per 100 g of limestone – and their diameter varies from 80-250 μm (see van den Boogaard, 1983). The shape of *H. oezgueli* is not exactly hemispherical but it has an almost flat and a convex side and a round to slightly oval outline (see van den Boogaard, 1983, fig. 4E). Although the high concentration of these fossils may but be the result of stratigraphic condensation, the thought that this multitude of microfossils represents the remains of only a small number of palaeoscolecidans is tempting.

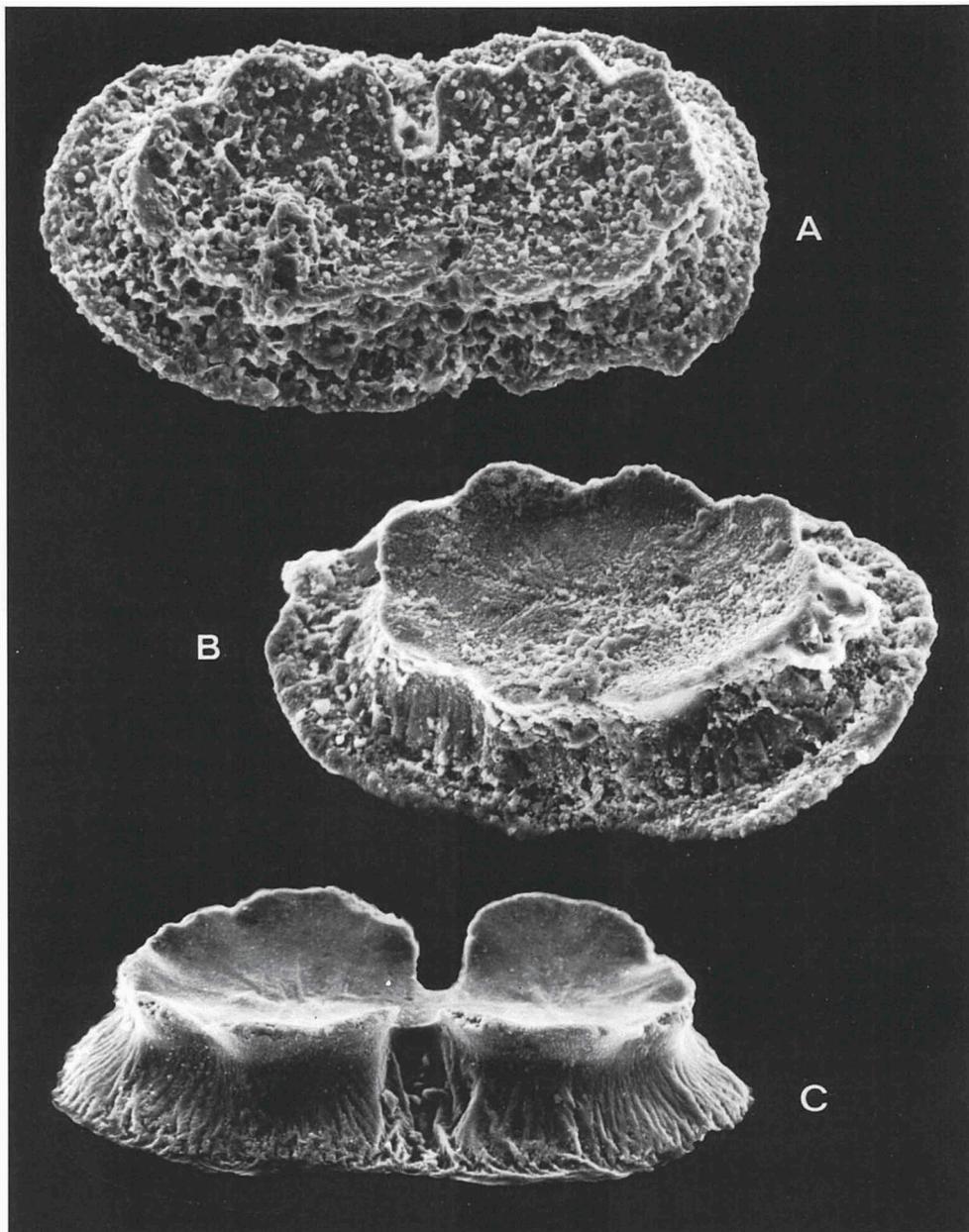
Palaeoscolex? tenensis Kraft & Mergl, 1989
Plates 1-3.

The assignment of the species *tenensis* to *Palaeoscolex* by Kraft & Mergl is tentative because only one fragment is known showing four parallel rows of parallel-orientated tubercles which differ from those of the type species *Palaeoscolex piscatorum* Whittard, 1953. The tubercles of this fragment are morphologically very similar to isolated phosphatic microfossils found by the author in Ordovician limestone samples from Killeröd and Öland in Sweden and the Aru Quarry in Estonia.

Description – The tubercles (the nomenclature of Kraft & Mergl is adopted) are longitudinally oval, generally about twice as long as wide. The length of the studied specimens varies between 108 μm and 226 μm , the width between 81 and 108 μm . Some of the tubercles are less elongate, almost round oval. The length/width ratio varies from 1.16 to 2.56. The edge of the outer (upper) surface is scalloped and often strongly constricted near the middle of the unit. This constriction proceeds to the inner (lower) surface of the tubercles but is there less pronounced (see Pl. 1, figs. A and D). The outer surface is concave and consists of dense material. In some specimens parts of the edge are abraded and the porous material underneath the thin dense layer is exposed (Pl. 1, fig. B; Pl. 3, fig. A). The sides of the tubercles slope steeply down to the rim of the inner surface, often undercutting the edge of the outer surface (Pl. 2, fig. C). The sides are strongly grooved and are composed of ridges which become thinner and seem to furcate towards the outer surface (Pl. 3, fig. A). The inner surface (Pl. 1, fig. D) is also concave and consists of shallow circular pits – with a rather porous surface – separated by denser ridges.

The above description is based on tubercles found in a limestone sample from the Aru Quarry (Estonia). The tubercles extracted from the Swedish samples are less well preserved. Those from the Öland sample show grooved sides which, however, do not reach the rim of the inner surface (Pl. 2, fig. B; Pl. 3, fig. C). The tubercles from the

Plate 2



Phosphatic microfossils supposed to represent tubercles of *Palaeoscolex? tenensis* Kraft & Mergl, 1989.

A. View of outer side of a specimen from sample RGM 371 097 from Killeröd, Sweden; RGM 383 473 (x 600).

B. Oblique view of outer side of a specimen from sample 6596 from Öland, Sweden; RGM 383 495 (x 780).

C. Same specimen as Pl. 1, fig. B, lateral view (x 560).

Killeröd sample are rather strongly recrystallized and no microstructure could be observed (Pl. 2, fig. A). This sample yielded one specimen of two adhering tubercles (Pl. 1, fig. C; Pl. 3, fig. D) with their long axis parallel, in the same manner as they occur in the Bohemian fossils. This specimen shows that where the edge of the outer surface of one tubercle bulges outward the edge of the outer surface of the other shows an inward bend, as if they tend to interlock. As a result the longer axis of the tubercles is not an axis of symmetry. The same phenomenon can be observed in some parts of the Bohemian specimen of *P. ? tenensis* (Kraft & Mergl, 1989, pl. I, figs. 1, 3, 4).

The maximum length of the tubercles of the Bohemian specimen is c. 90 μm (Kraft & Mergl, 1989, p. 22). But this specimen, which probably represents only a relatively small fragment of the cuticle of the whole animal, gives no information on the variation in size of the tubercles of a complete animal. The isolated tubercles described here are larger, up to 226 μm long, but in other aspects so very similar to those of the Bohemian fossil that I assume that they derive from vermiforms conspecific with *P. ? tenensis* or, because they are somewhat younger, direct descendants.

Material – Twenty-eight tubercles from sample 4750 collected in 1912 from the Aru Quarry near Port Kunda (Estonia). The sample consists of grey limestone with ferruginous oörites of the 'Upper Linsenschicht' (Schmidt, 1858) = the Dubowiki Formation of Raymond (1916) = Horizon d'Azeri (Likharev, 1958), and is of Early Llanvirnian age. It furthermore contains remains of the trilobite *Asaphus cornutus* Pander and a rich microfauna: acritarchs, abundant chitinozoa, many specimens of *Milaculum* sp. a van den Boogaard, 1988, some scolecodonts, some specimens of the enigmatic microfossil *Phosphannulus* sp., a few phosphatic brachiopods and abundant conodonts, i.a. *Baltoniodus prevariabilis* (Fahraeus, 1966), *Eoplacognathus suecicus* Bergström, 1971 and *Amorphognathus* cf. *A. variabilis* Sergeeva, 1963 confirming an Early Llanvirnian age (storage numbers RGM 383 474-383 487).

Sample RGM 371 097 contains 55 tubercles from a micritic limestone collected by students of Leiden University during an excursion in 1971 in an abandoned quarry at Killeröd near Flagabro in Skåne (Sweden) from the Upper Arenigian (*Asaphus* series) *Orthoceras* Limestone. The sample furthermore contains small phosphatic brachiopods (very abundant), some *Milaculum scandinavicum* Müller, 1973, some *Phosphannulus* sp. and a modest amount of conodonts, i.a. *Amorphognathus variabilis* Sergeeva, 1963 and *Baltoniodus prevariabilis* (Fahraeus, 1966). Some other, more clayey limestones from the same outcrop did not yield any tubercle of *P. ? tenensis* (RGM 383 462-383 473).

Sample 6596 consists of 12 tubercles from a sample taken in 1935 in Öland from an *Orthoceras* Limestone with *Endoceras* sp. No other data are available. The microfauna consists of phosphatic brachiopods (very abundant), *Milaculum scandinavicum* (abundant), *Phosphannulus* sp. and conodonts, i.a. many *Baltoniodus prevariabilis* (RGM 296 222-296 229; 383 488-383 496).

Plate 3

Phosphatic microfossils supposed to represent tubercles of *Palaeoscolex? tenensis* Kraft & Mergl, 1989 (scale bar is 10 μm).

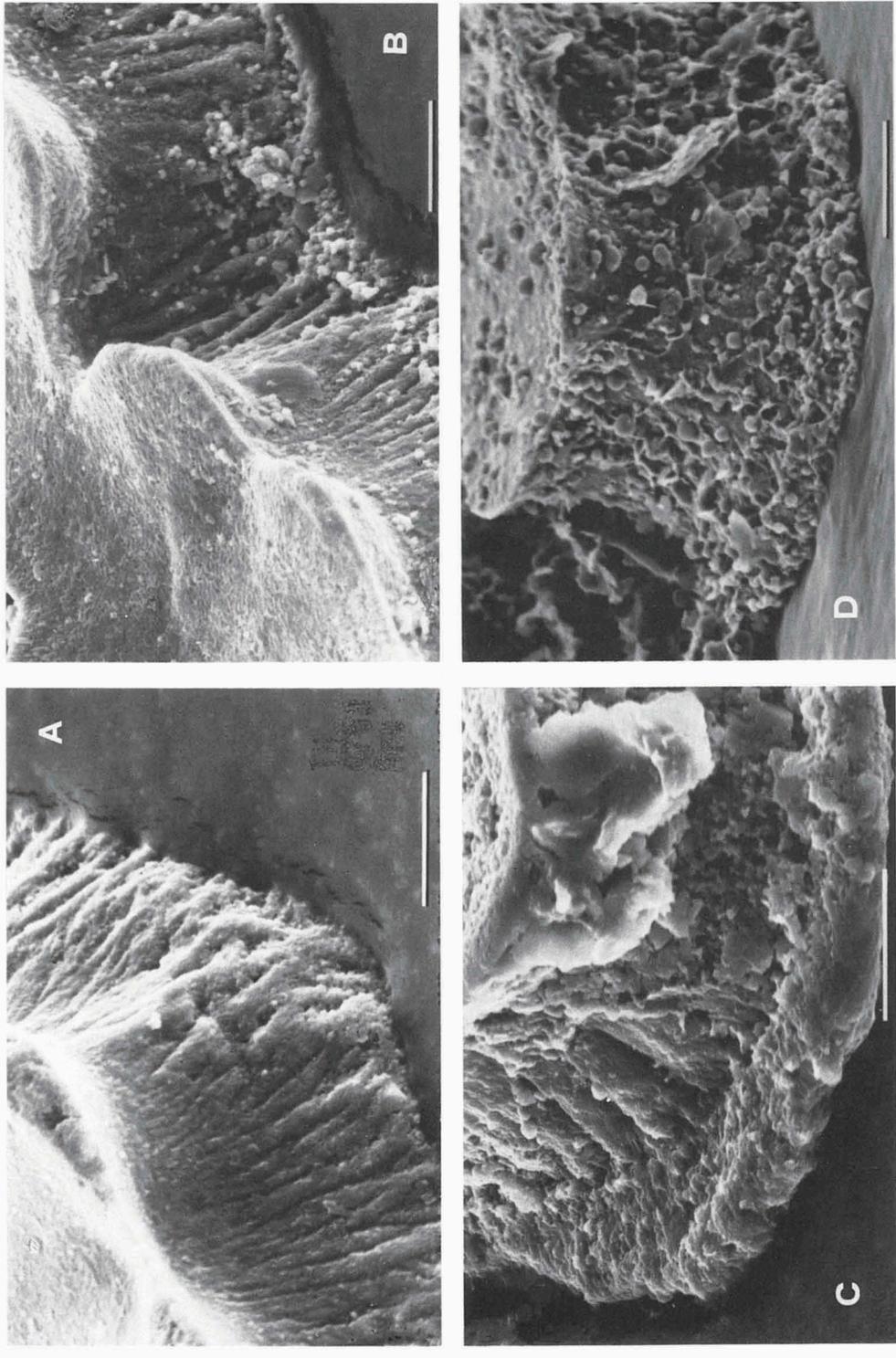
A. Detail of Pl. 1, fig. B, showing abraded edge of outer side and grooved lateral side.

B. Detail of Pl. 1, fig. A, constriction of the tubercle.

C. Detail of Pl. 2, fig. B, showing grooved lateral sides.

D. Detail of Pl. 1, fig. C, recrystallization obscuring eventual microstructure.

Plate 3



Milaculum Müller, 1973

As mentioned in the introduction, the phosphatic microfossils described as various species of *Milaculum* may represent tubercles of the palaeoscolecidan genus *Plasmuscolex* Kraft & Mergl, 1989. This vermiform fossil consists of a large number of segments (more than 200). The segments are equal in size and bordered by deep intersegmental furrows. Each segment has a nearly smooth central band and two tubercle bands at the rim of the intersegmental furrows (see Fig. 1).

In a study on several species of *Milaculum*, I concluded (van den Boogaard, 1988) that the *Milaculum*-bearing animal had a scleritome composed of different types of sclerites, the common or oval form (Cm type), the 'crocodile head' to pear-shaped form (Cr type), the cone form (Co type), the bald plates, and the flat plates, because comparable forms occurred in several faunas of different localities and ages and in most cases at the same ratio (about 60-70% of the Cm type and 17-25% of the Cr type and smaller percentages of the other types). If this conclusion is correct the *Milaculum*-bearing palaeoscolecidan would have had more than one type of tubercle at different parts of its body. *Plasmuscolex* tubercles seem to be rather uniform although in studying the illustrations of *P. klabavensis* Kraft & Mergl, 1989 one notes that one specimen (op. cit., pl. XI, figs. 1-2) has pear-shaped tubercles comparable to the Cr type of *Milaculum scandicum* Müller 1973 (see van den Boogaard, 1988, fig. 7D) and another specimen (Kraft & Mergl, pl. XIII, figs. 2-3) has oval tubercles comparable to the Cm type of *M. scandicum* (see van den Boogaard, 1988, fig. 7B). Closer inspection of the vermiform fossils will be necessary to ascertain whether they really show the same differentiation in tubercles as found in the faunas of isolated tubercles and whether or not the different types were restricted to different areas of the animal's cuticle. What, for instance, was the position of the hollow cone-like tubercles which are found occasionally (generally less than 2 %) (Pl. 4 fig. B; Pl. 4, fig. C; van den Boogaard 1988, figs. 2D, 7C and 8C)?

Kraft & Mergl (1989, p. 15) suppose that the tubercles probably are an unnecessary structure of the palaeoscolecidans. Van den Boogaard (1988, p. 6) observed that some *Milaculum* specimens show features suggesting that they originated by coalescence of smaller platelets. The forming of such relatively robust tubercles should in my opinion have served some purpose. Did the basal side function as an attachment-plane for muscles? Are the pits on the inner surface of the other palaeoscolecidan, *Palaeoscolex? tenensis* (Pl. 1, fig. D), muscle scars? The inner (basal) side of *Milaculum* does not show rounded pits but a rhombic pattern (see Pl. 4, fig. E; Pl. 5, fig. B).

Kraft & Mergl (op. cit.) observed that during contraction of *Gamascolex* as well as *Plasmuscolex* (their fig. 4) the tubercle bands become steeply inclined in the interseg-

Plate 4

Milaculum, a phosphatic microfossil supposed to represent tubercles of *Plasmuscolex* Kraft & Mergl, 1989.

A. *Milaculum* sp., Cr type showing some abrasion of the nodes of the widest part (left side photograph); sample 4750 from the Aru Quarry; RGM 383 487 (x 400).

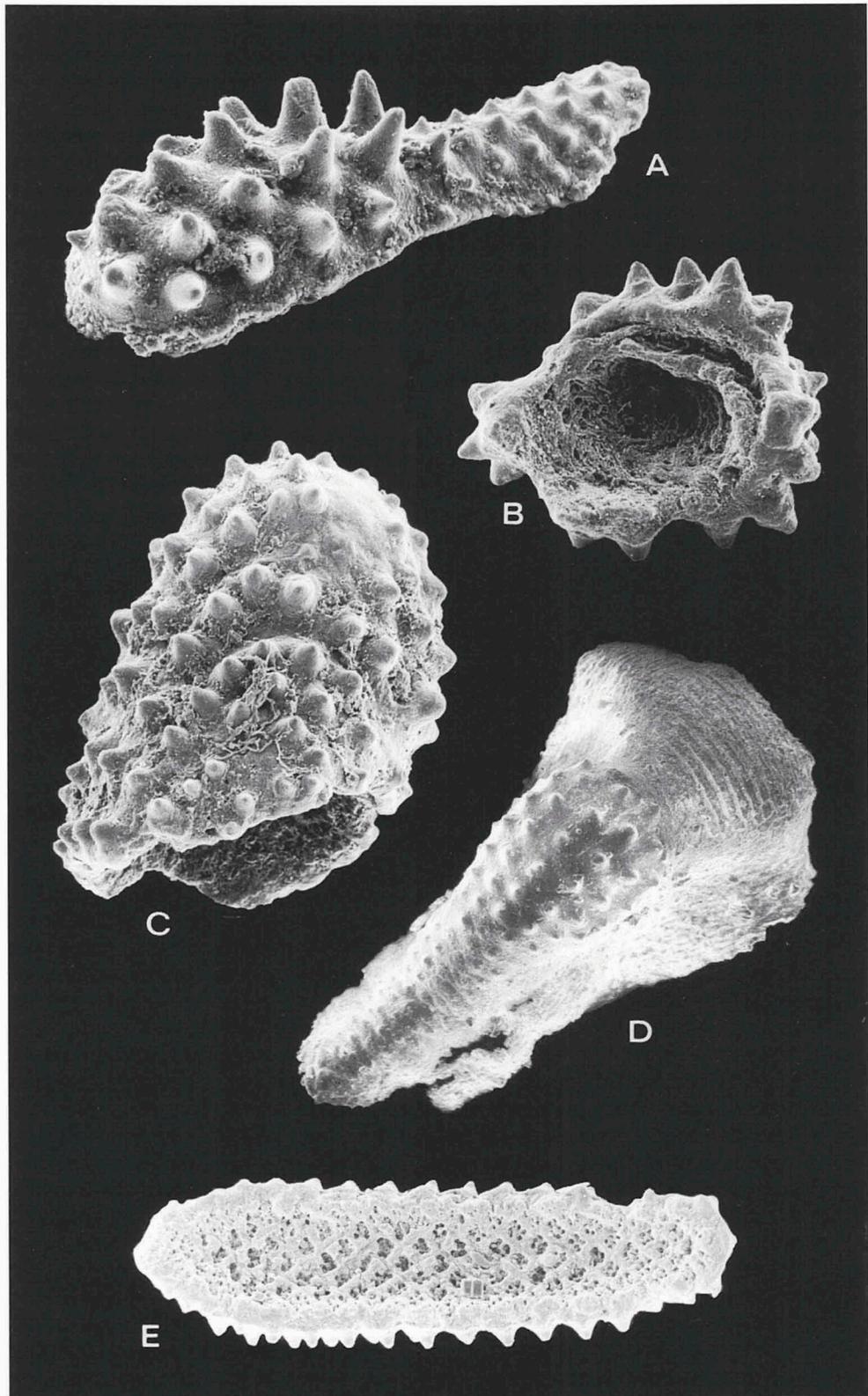
B. *Milaculum* sp., cone type showing hollow inner side. Malla Quarry near Port Kunda, Estonia (see van den Boogaard, 1989 for details on locality); RGM 383 517 (x 280).

C. *Milaculum* sp., cone type, lateral view. Same sample as Pl. 4, fig. B (x 220).

D. *Milaculum balticum* van den Boogaard, 1988, Cr type from sample RGM 173 756 from Kukruse, Estonia (see van den Boogaard, 1988 for details on locality); RGM 383 382. Note alignment of the smooth platelets around the wider part of the nodose tubercle (x 170).

E. *Milaculum* sp., inner side showing rhombic pattern. Same sample as Pl. 4, fig. B (x 190).

Plate 4



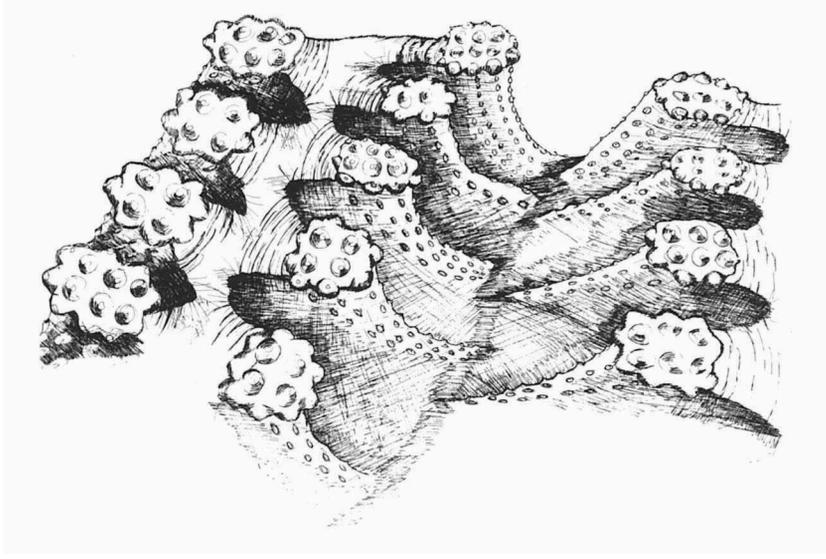


Fig. 1. Artist's impression of part of the epidermis of a palaeoscolecidan, bearing tubercles assigned to the form-species *Milaculum balticum* van den Boogaard, 1988. It is based on the specimen of *M. balticum* illustrated by van den Boogaard (1988, fig. 3B) and the specimen of *Plasmuscolex klabaensis* illustrated by Kraft & Mergl (1989, pl. XI, fig. 6).

From left to right: a tubercle band, the smooth central band, a tubercle band, the deep intersegmental furrow, and the tubercle band of the next segment.

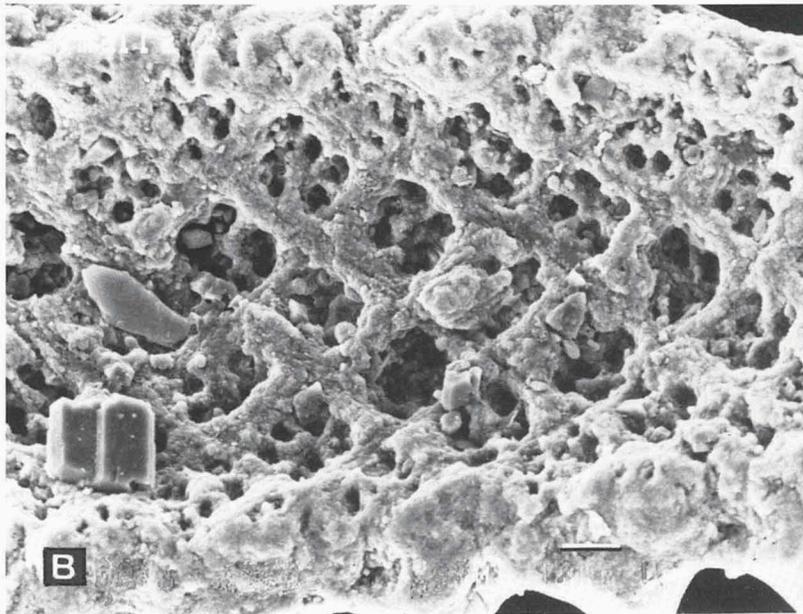
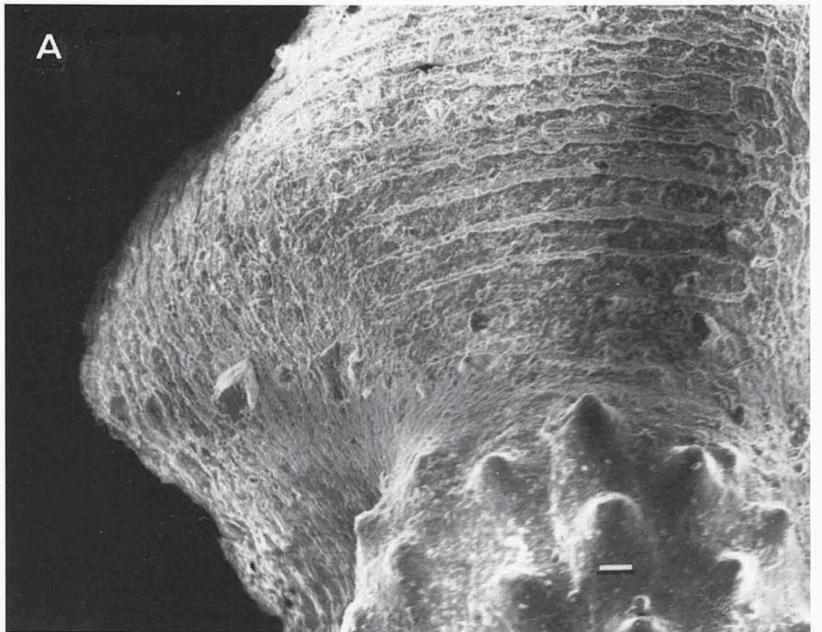
mental furrows nearly touching those of the next segment, thus not providing a protective cover. Only in non-contracted state the spines or nodes of the tubercles did protrude and touch the surrounding substrate. From the Cr type of *Milaculum* – the type supposed to have been bordering the intersegmental furrows – generally the nodes or spines of the widest part (Pl. 4, fig. A; van den Boogaard, 1988, figs. 7E-F, 10C) are somewhat abraded, indicating that indeed only that part of the tubercle bordering the central band did protrude during stages of the animal's activity. May be a stretched part of the animal held on to the sediment while another part was contracting.

Prove that the Cr type of *Milaculum* could somewhat move with regard to its surroundings can be deduced from the alignment of the neighbouring platelets (Pl. 4, fig. D; Pl. 5, fig. A; van den Boogaard 1988, fig. 3B), which more or less show the same alignment as the tiny wrinkles of the skin around your knuckles.

Affinity

The systematic position of palaeoscolecidans is discussed by Kraft & Mergl (1989, see also references therein) and their opinion is that at present nothing definite is known to place those animals in any annelid group. They emphasize that the outer segmentation of the cuticle not necessarily reflects the internal metameric segmentation. We indeed do have too little information to assign the palaeoscolecidans to any established phylum, but it must be remarked that several students of the phosphatic microfossils *Milaculum* and *Hadimopanella* (see van den Boogaard 1988, 1989 and references

Plate 5



Scale bar is 10 μm .

A. *Milaculum balticum* van den Boogaard, 1988. Detail of Pl. 4, fig. D.

B. *Milaculum* sp. Detail of Pl. 4, fig. E.

therein) consider an affinity to the Chordata because the construction plan of these microfossils resembles that of the dermal plates of some primitive chordates. The Palaeoscolecida, which range from the Early Cambrian into the Silurian, will not be ancestral to the chordates but perhaps have derived from the same stock.

Concluding remarks

Although it seems very likely that the fossils described as species of *Milaculum* are nothing else than isolated tubercles of *Plasmuscolex* Kraft & Mergl, 1989, I am inclined to delay considering *Plasmuscolex* a junior synonym of *Milaculum* Müller, 1973 until it is ascertained that Müller's type species *Milaculum ruttneri* also is found as tubercles of a species of *Plasmuscolex*, for it is imaginable that several – be it closely related – genera were adorned by tubercles assigned to the form genus *Milaculum*.

Concerning the taxonomy of all other Palaeoscolecida the shape of the tubercles has also to be investigated, because tubercle morphology may be a character to distinguish palaeoscolecidan genera.

Because more or less completely fossilized Palaeoscolecida are rare, they were assumed to be uncommon elements in the Early Palaeozoic marine environment. The numerous occurrences of the isolated tubercles, however, show that they were not that uncommon, but often even rather common constituents of marine faunas.

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