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Articulated palaeoscolecid sclerite arrays from the Lower Cambrian of eastern Siberia

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ABSTRACT:

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Phosphatized palaeoscolecid cuticle fragments of *Palaeoscolex lubovae* sp. nov.*, P. spinosus* sp. nov., *Palaeoscolex* sp. and *Sahascolex labyrinthus* gen. et sp. nov., as well as disarticulated sclerites, are described from the Early Cambrian Sinsk Formation (Siberian Platform) at the Achchagyy Tuoydakh fossil-Lagerstätte. These remarkably well preserved arrays of plates and platelets display ornamentation identical to widely reported isolated sclerites assigned to *Hadimopanella*, *Kaimenella*, *Milaculum,* and *Utahphospha*. The precise relationship of the Palaeoscolecida to the priapulids or alternatively with the nematomorphs remains under discussion, but suggested is their systematic position within the superphylum Ecdysozoa, comprising moulting animals. Some of the described cuticular trunks exhibit distinction between the dorsal and ventral sides: nodular sclerites occur on the dorsal and spiny sclerites on the ventral sides of the worm body. Such a pattern of ornamentation may suggest adaptation for a level-bottom, vagile benthic and probably epifaunal mode of life. The Siberian palaeoscolecids are compared with the type species of *Palaeoscolex*, *P. piscatorum* Whittard, 1953, and with palaeoscolecid worms from Australia, Bohemia and China. Sclerites recorded with microplates accreted into the basal brim may support a hypothesis that the more complex sclerite structure bearing a series of nodes was derived from simple small sclerites with a single node. The biostratigraphic utility of isolated sclerites remains low, because of the same morphology occur in different worms, and the different sclerites may occur in one scleritome.

Key words: Ecdysozoa, Nemathelminthes, Priapulida, Palaeoscolecida, worms, Cambrian, Siberia.

INTRODUCTION

Palaeoscolecids were worm-like organisms characterized by an annulated long, slender, cylindrical body covered with cuticle comprising complex ornamentation of phosphatic or phosphatized button-like sclerites arranged into arrays ("scleritome" of BENGTSON 1985). World-wide occurrence and abundance of palaoscolecid fossil remains suggest they were important components of many Cambrian to Late Silurian marine biotic communities, but their body architecture, palaeobiology and evolutionary relationships remain enigmatic and extensively disputed (e.g., KRAFT & MERGL 1989, MÜLLER & HINZ-SCHALLREUTER 1993, HOU & BERGSTRÖM 1994, ZHANG & PRATT 1996, CONWAY MORRIS 1997). They were first described as compressed body fossils from the Lower Cambrian up to the Silurian (e.g., ULRICH 1978, WHITTARD 1953, ROBISON 1969, CONWAY MORRIS & ROBISON 1986), and their disarticulated individual sclerites were subsequently found to be common and characteristic problematic fossils in Lower Cambrian to Upper Silurian rocks (e.g., BENGTSON 1977; GEDIK 1977; VAN DEN BOOGAARD 1983, 1988, 1989a, 1989b; WRONA 1982, 1987; PEEL & LARSEN 1984, BENDIX-ALMGREEN & PEEL 1988, MÄRSS 1988). These problematic isolated sclerites were recognized as palaeoscolecid plates and integrated with body fossils of these worms almost simultaneously by KRAFT & MERGL (1989), and by VAN DEN BOOGAARD (1989a, 1989b). Exceptionally preserved, almost complete cuticles with fine details of the palaeoscolecid scleritome from the Middle Cambrian of Australia and from the Arenigian (Ordovician) material of Bohemia (HINZ & *al.* 1990, MÜLLER & HINZ-SCHALLREUTER 1993), as well as from Lower Cambrian fossil-Lagerstätte of China (HOU & BERGSTRÖM 1994, ZHANG & PRATT 1996), and re-described type material of the genus *Palaeoscolex* WHITTARD, 1953 (CONWAY MORRIS 1997) allows to contribute new data to understanding their palaeobiology and taxonomy, and further to elucidate the nature of palaeoscolecid body worms and their isolated sclerites.

This paper describes and illustrates fundamental structural characters of the isolated palaeoscolecid sclerites and their articulated sclerite arrays from a new Siberian fossil-Lagerstätte, and provides interpretation of the complete scleritome of these worms, as well as elucidates the relationships of separate epidermal sclerites, widely known isolated as the microfossils *Hadimopanella, Kaimenella* and *Milaculum*.

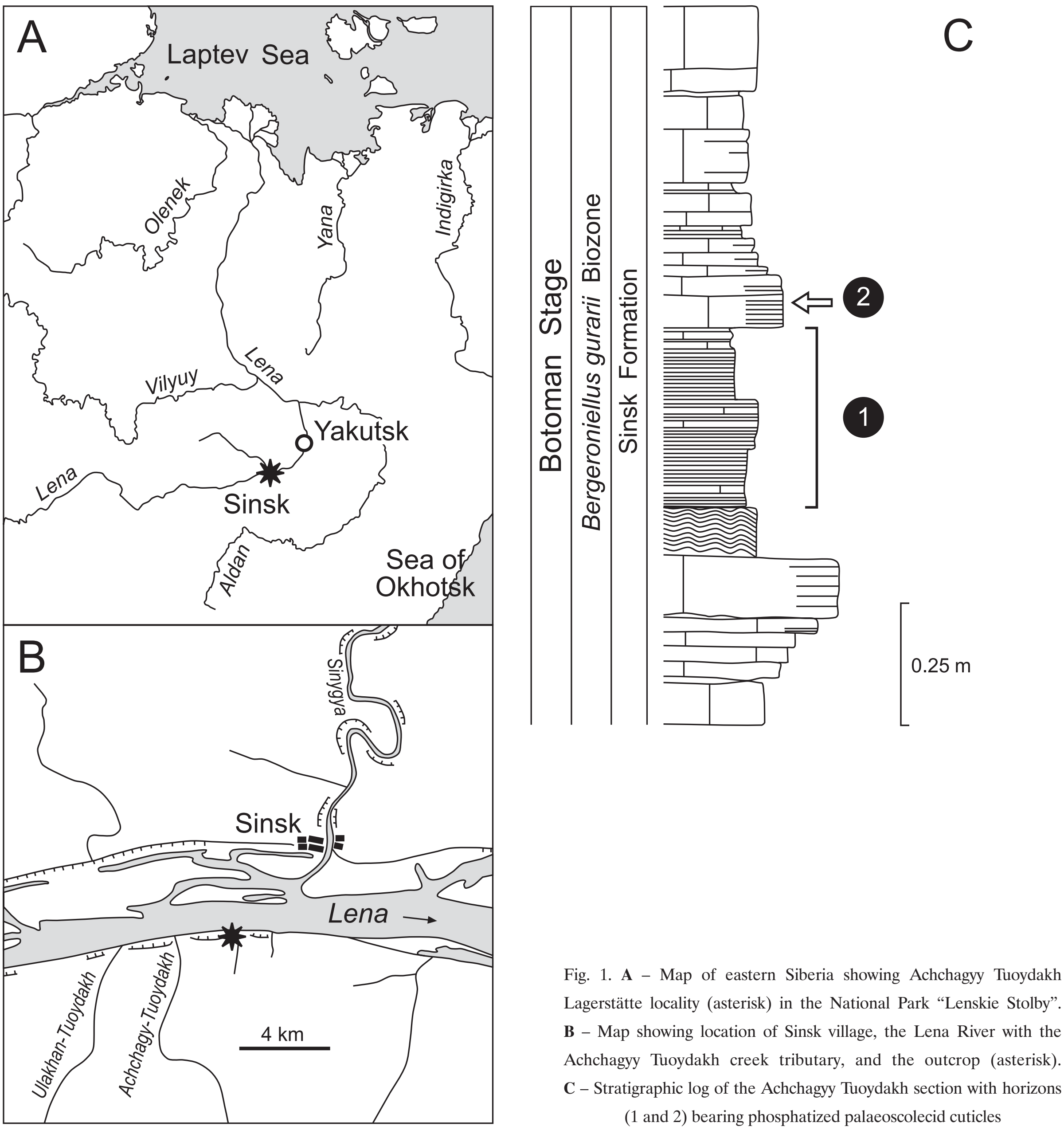


Fig. 1. **A** – Map of eastern Siberia showing Achchagyy Tuoydakh Lagerstätte locality (asterisk) in the National Park "Lenskie Stolby". **B** – Map showing location of Sinsk village, the Lena River with the Achchagyy Tuoydakh creek tributary, and the outcrop (asterisk). **C** – Stratigraphic log of the Achchagyy Tuoydakh section with horizons (1 and 2) bearing phosphatized palaeoscolecid cuticles

Geographical and geological setting

A new Early Cambrian fossil-Lagerstätte (cf. SEILACHER & *al.* 1985) with extraordinary fossil algae and animals was discovered in the National Park "Lenskie Stolby" (IVANTSOV 1996, 1997), in the Saha Republic (Yakutia), eastern Siberia. This termed the Achchagy-Tuoydakh locality is situated on the right bank of the Lena River, opposite Sinsk village, 2.5 km below the mouth of Achchagy-Tuoydakh creek (Text-fig. 1). The beds of bituminous limestone, chert, and laminated argillaceous, siliceous and calcareous, sapropelic and pyriferous black shales represent the Sinsk Formation (BAKHTUROV & *al.* 1988). These beds are traditionally assigned to the Botoman Stage and according to ASTASHKIN & *al.* (1990) lie probably within the *Bergeroniellus gurarii* Biozone (see ZHURAVLEV 1998).

The palaeoscolecid worms are preserved as body fossils with folded annuli and articulated sclerite arrays. They come from a layer, informally named "algal lens", which is characterized by the mass occurrence of non-calcified algae. Besides paleoscolecids, the "algal lens" contains a diverese biota including abundant remains of the coiled cyanobacterium *Obruchevella*, the caulerpacean chlorophyte *Margaretia antiquissima* and also specimens of the trilobite-like arthropod *Phytophilaspis pergamena* IVANTSOV, 1999, as well as the polymeran trilobites *Pagetiellus lenaicus*, *Neopagetina primaeva* and *Bergeroniellus spinosus* among others (ASTASHKIN & *al.* 1990), the bradoriids *Sinskolutella ordinata*, *Duibianella* sp., *Tubuterium ivantsovi* and *T. seletiensis* (MELNIKOVA 1998, 2000), the lobopod *Microdictyon*, undetermined arthropod-like and worm-like remains, the lingulate brachiopod *Eoobolus rotundus* (USHATINSKAYA 2001), the sponge *Choia unica*, chancelloriids, eldoniids, probable pterobranchs and acritarchs (IVANTSOV & *al.* 1997; IVANTSOV 1998, 1999). It is worth noting that the well-defined fleshy alga *Margaretia* has also widespread distribution in Burgess Shale-type fossil deposits (see RESSER & HOWELL 1938, CONWAY MORRIS & ROBISON 1988, ROBISON 1991, GARCIA-BELLIDO CAPDEVILA & CONWAY MORRIS 1999). The fossil assemblage in the algal lens was transported before burial. Algal thalli are often broken and crumpled, disarticulated valves of large lingulate brachiopods are oriented perpendicular to the bedding plane, and elongated carapaces of *Phytophilaspis* and polymeran trilobites display a similar orientation oblique to bedding. Most specimens, in particular the larger ones, are overturned.

The sediments of the Sinsk Formation were deposited in relatively deep-water conditions, in the slope/basin environment characterized by a trilobite fauna dominated by Protolenidae and Pagetiidae (PEGEL 2000). The whole fossil community, including entire planispirally coiled or recurved worms and fragile exoskeletons of *Phytophilaspis,* was transported from a relatively shallow-water, photic environment, near reef shoals (BAKTHUROV & *al.* 1988) into a deep-water, probably anoxic setting, and rapidly buried.

Botoman anoxic conditions appear to be correlated worldwide, and most probably were related to the extinction event pronounced and widespread on the Siberian Platform, referred to as the early Botoman Sinsk event (ZHURAVLEV & WOOD 1996). This probably global event was responsible for a major reduction of the "Tommotian fauna" and indirectly responsible for the extraordinary preservation of the "Sinsk fauna" in the Achchagy-Tuoydakh fossil-Lagerstätte.

To date all previous body fossils of palaeoscolecid worms from the Siberian Platform have been reported only from one other locality. These are much less well preserved seemingly without discernible microstructural details of the sclerites. They are carbonized remains of probably just one species, ?*Protoscolex tchopkoensis* BARSKOV & ZHURAVLEV, 1988 from the Upper Cambrian of the Sakski Stage, Tchopkinsk Formation, in the section along the Tchopko River, a tributary of the lower Jenisey River in the northern Krasnoyarsk area (BARSKOV & ZHURAVLEV 1988). Isolated palaeoscolecid sclerites of *Hadimopanella knappologica* (BENGTSON, 1977) have also been recorded from the early Atdabanian (Lower Cambrian) informal "Transitional Formation" of the Achchagyj-Kyyry-Taas section, near the Lena River, Yakutia (BENGTSON 1977; DZIK 1994).

Material, Methods and Preservation

Sclerites with intersclerite tissues were replaced by amorphous apatite. Large and more or less complete worm cuticles, compressed due to compaction of the sediment, were found as parts and counterparts on bedding surfaces in calcareous black shales and limestones. Isolated sclerites, sclerite aggregates and trunk cuticle fragments were extracted chemically from the limestone bedrock using 10% acetic acid. Some specimens were photographed dry (Text-fig. 2A), while others were immersed in distilled water or alcohol and photographed under ordinary white light (Text-figs 2C; 5A). This procedure reveals some details, such as carbonized gut or hooks, which are obscure or invisible when dry. One specimen (PIN 4349/851), split longitudinally down the centre, therefore did not show the surface ornament of the sclerites (Text-fig. 5). This speci-

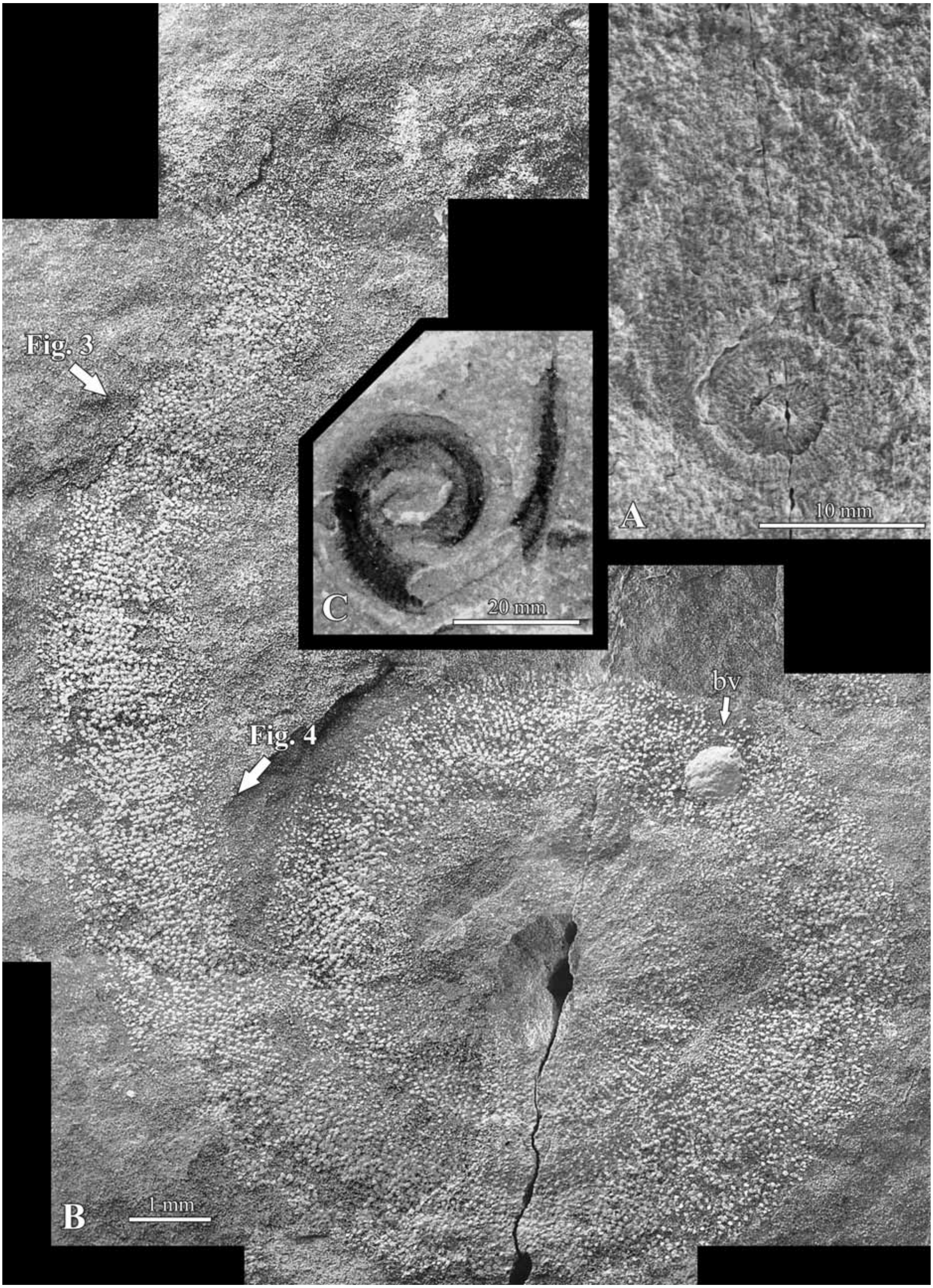


Fig. 3
A
10 mm
C
20 mm
bv
Fig. 4
B
1 mm

men was coated with epoxy resin (Araldite 2020 CIBA Polymers) and then immersed in weak 5-10% acetic acid to remove the rock. The resulting epoxy resin cast, with phosphatized sclerites partly embedded within, was then gently washed in distilled water and dried. These dry casts with embedded or adhering sclerites were transferred onto aluminium SEM stubs and, together with extracted cuticle fragments and disarticulated single sclerites examined using the scanning electron microscope Philips LX-20 at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw.

Specimens are deposited in the paleontological collections at the Paleontological Institute, Russian Academy of Sciences, Moscow (abbreviated PIN and numbered 4349/850 to 870). Numbers within square brackets [S1/1...9] refer to the number of specimen on a scanning electron microscope stubs; [S1] means the stub no. 1 and /1, 2...9 means number of the specimens respectively on the stub surface. The terminology used here for descriptions follows mainly that of MÜLLER & HINZ-SCHALLREUTER (1993).

SYSTEMATIC PALAEONTOLOGY

Superphylum Ecdysozoa AGUINALDO & *al*., 1997

REMARKS: A clade comprising moulting animals, such as arthropods, tardigrades, onychophorans, nemathelminthes, nematodes, nematomorphs, kinorynchs and priapulids (see AGUINALDO & *al*. 1997; AGUINALDO & LAKE 1998; GAREY & SCHMIDT-RHAESA 1998).

Phylum Nemathelminthes VOGT, 1851

REMARKS: A phylum comprising the nemathodes with horse hair worms, and acanthocephalans, rotifers, gastrotrichs, and kinorynchs. They are all more or less worm-like animals with an elongated cylindrical unsegmented body covered by an ectoderm that can secrete an external cuticle.

Class Palaeoscolecida CONWAY MORRIS & ROBISON, 1986

FAMILIES ASSIGNED: Palaeoscolecidae WHITTARD, 1953 and Plasmuscolecidae KRAFT & MERGL, 1989 (see KRAFT & MERGL (1989).

REMARKS: These nemathelminthan worms possessed an elongated, cylindrical unsegmented body covered by papillate epidermis with cuticle. The papillae (tubercles) are arranged in transverse rows (often duplicated) separated by an intercalation (CONWAY MORRIS 1997) or furrow (KRAFT & MERGL 1989) which gives rise to their annular surface pattern, although this arrangement did not reflect an internal metameric segmentation (see e.g., CONWAY MORRIS 1997). The epidermis may have contained amorphous apatite forming sclerotized cuticular structures, resulting in sclerites covering the entire body. The complete array of sclerites formed an armour or scleritome (BENGTSON 1985) which perhaps could have been periodically exuviated (KRAFT & MERGL 1989; MÜLLER & HINZ-SCHALLREUTER 1993, fig. 14C), suggesting a systematic position within the newly proposed superphylum Ecdysozoa (see AGUINALDO & *al.* 1997; AGUINALDO & LAKE 1998; GAREY & SCHMIDT-RHAESA 1998). The anterior part of the trunk is rarely observed due to its incomplete preservation, but the posterior portion is quite common in coiled fossils. The enteric canal is more-or-less linear connecting to the terminal anus.

The articulated sclerites in the holotype of *Palaeoscolex piscatorum* WHITTARD, 1953 (see CONWAY MORRIS 1997), and in a recently collected compressed specimens (KRAFT & MERGL 1989; HOU & BERGSTRÖM 1994), as well as in cylindrical cuticles of unflattened trunks (MÜLLER & HINZ-SCHALLREUTER 1993), show distinctive features which place palaeoscolecids in close relationship to the priapulids (CONWAY MORRIS 1993, 1997; MÜLLER & HINZ-SCHALLREUTER 1993; HOU & BERGSTRÖM 1994; ZHANG & PRATT 1996) or alternatively with the nematomorphs (HOU & BERGSTRÖM 1994). Nevertheless, the precise relationship of the Palaeoscolecida to these taxa is incompletely resolved and their exact systematic position within the Metazoa remains under discussion (HOU & BERGSTRÖM 1994, 2003; CONWAY MORRIS 1997). This difficulty is mainly due to the differential preservation represented by compressed and carbonized specimens on bedding planes versus phosphatized cuticular structures recovered using acid-etching techniques.

Fig. 2. Phosphatized bedding plane specimens from the Lower Cambrian Sinsk Formation, Achchagyy Tuoydakh section. **A** – Holotype of *Palaeoscolex lubovae* sp. nov. (PIN 4349/850), photographed dry in ordinary light. **B** – Same specimen in a scanning electron photomicrograph, showing sclerites grouped in double-row belts giving an annular pattern; large arrows point to approximate positions of scanning electron photomicrographs pictured in Figs 3 and 4, and small arrow indicates phosphatic lingulate brachiopod valve (bv). **C** – Carbonized specimen of *Palaeoscolex* cf. *P. lubovae* sp. nov. (PIN 4349/866) immersed in alcohol and photographed under ordinary white light

Family Palaeoscolecidae WHITTARD, 1953

GENERA INCLUDED: WRONA & HAMDI (2001) listed genera that are mainly based on specimens laterally flattened on the bedding plane (WHITTARD 1953; KRAFT & MERGL 1989) or as exceptionally well-preserved three-dimensional cuticles with articulated sclerites (MÜLLER & HINZ-SCHALLREUTER, 1993). Three genera only are known as isolated microfossils – phosphatic epidermal sclerites *Hadimopanella* GEDIK, 1977, *Kaimenella* MARS, 1988, and *Milaculum* MÜLLER, 1973b. Detailed studies by KRAFT & MERGL (1989) as well as these of VAN DEN BOOGAARD (1989), HINZ & *al*. (1990), MÜLLER & HINZ-SCHALLREUTER (1993) and CONWAY MORRIS (1997) have documented and discussed palaeoscolecid affinities of these disarticulated single sclerites. The problematic phosphatic microfossils described by REPETSKI (1981) as *Utahphospha cassiniana* are in fact not hollow cone-shaped fossils and therefore can be regarded as cuticle fragments of palaeoscolecid worms, probably belonging to *Hadimopanella*.

Genus *Palaeoscolex* WHITTARD, 1953

TYPE SPECIES: *Palaeoscolex piscatorum* WHITTARD, 1953

SPECIES INCLUDED: *Palaeoscolex piscatorum* WHITTARD, 1953 (for re-description see CONWAY MORRIS 1997); *P. ratcliffei* ROBISON, 1969; *P. sinensis* HOU & SUN, 1988 (also HOU & BERGSTRÖM 2003, p. 64, fig. 9, 1); *P. huainanensis* LIN, 1995. *P*. cf. *P. ratcliffei* ROBISON (CONWAY MORRIS & ROBISON 1986; GÁMEZ VINTANED 1995).

DIAGNOSIS: Long, slender, cylindrical annulated worm without parapodia, covered by paplilate epidermis with cuticle. The papillae (tubercles) are arranged in transverse double rows separated by an intercalation or furrow accentuating their annular surface pattern. The epidermis may form sclerotized cuticular structures, button-like phosphatic sclerites covering the entire body as an armour. Sclerites may be differentiated in size and ornamentation; the largest are plates, equal in size, circular or sub-circular with prominent nodes on the upper surface, and similar to but smaller than plates are platelets, which can be accompanied by much smaller microplates of simple morphology.

REMARKS: The diagnosis is a compilation of the original definition of the genus introduced by WHITTARD (1953), with the SEM-based re-examination and re-description of the type specimen of *Palaeoscolex piscatorum* by CONWAY MORRIS (1997). All species of this genus are known as entire body fossils with wrinkled annuli and regularly arranged sclerite arrays. There are other taxa seemingly closely related to *Palaeoscolex* that show similar plate ornamentation, but dissimilar plate arrangements (see CONWAY MORRIS 1997). Due to the above-mentioned differences, inclusion of *P. antiquus* GLAESSNER, 1979 within the genus has also been questioned (e.g., CONWAY MORRIS & ROBISON 1985; HUO & SUN 1988; HOU & CHEN 1989).

Palaeoscolex lubovae sp. nov.
(Text-figs 2-4, 11A)

HOLOTYPE: Nearly complete trunk with in situ sclerite array, PIN 4349/850, illustrated in Text-figs 2-4.

TYPE HORIZON: Early Cambrian, Botoman Stage, *Bergeroniellus gurarii* Biozone, Sinsk Formation.

TYPE LOCALITY: Achchagy-Tuoydakh section, on the right bank of the Lena River, opposite the Sinsk village, 2.5 km below the mouth of the Achchagy-Tuoydakh creek, eastern Siberia, Russia.

DERIVATION OF NAME: In honour of Mrs. Lubov Danilovna Konstantinova (Yakutsk), the director of the National Park "Lenskie Stolby" who kindly supported the field team and encouraged this study.

DIAGNOSIS: Cylindrical cuticle with dense annulation. Intercalations not recognizable or lacking. Annuli with two rows of plates and platelets. Plates sub-equal in size, circular, with strongly convex upper surface covered by usually 6-8 nodes arranged in a circlet, sometimes also with a central node. Nodes sharp, and on the ventral side of the trunk, sometimes lengthening into spines. Platelets as miniaturized versions of plates, arranged alternately with the plates.

MATERIAL: Three incomplete enrolled specimens flattened on the bedding plane (PIN 4349/850, 866), several cuticle fragments, and numerous aggregated and isolated plates.

DESCRIPTION: Phosphatized cylindrical cuticle fragments of large worms, compressed laterally and partially more or less carbonized (Text-fig. 2C), were found as part and counterpart on bedding surfaces. A single specimen with the uncoiled anterior part possesses a poorly visible, dark ?proboscis (Text-fig. 2A-B), and has the pos-

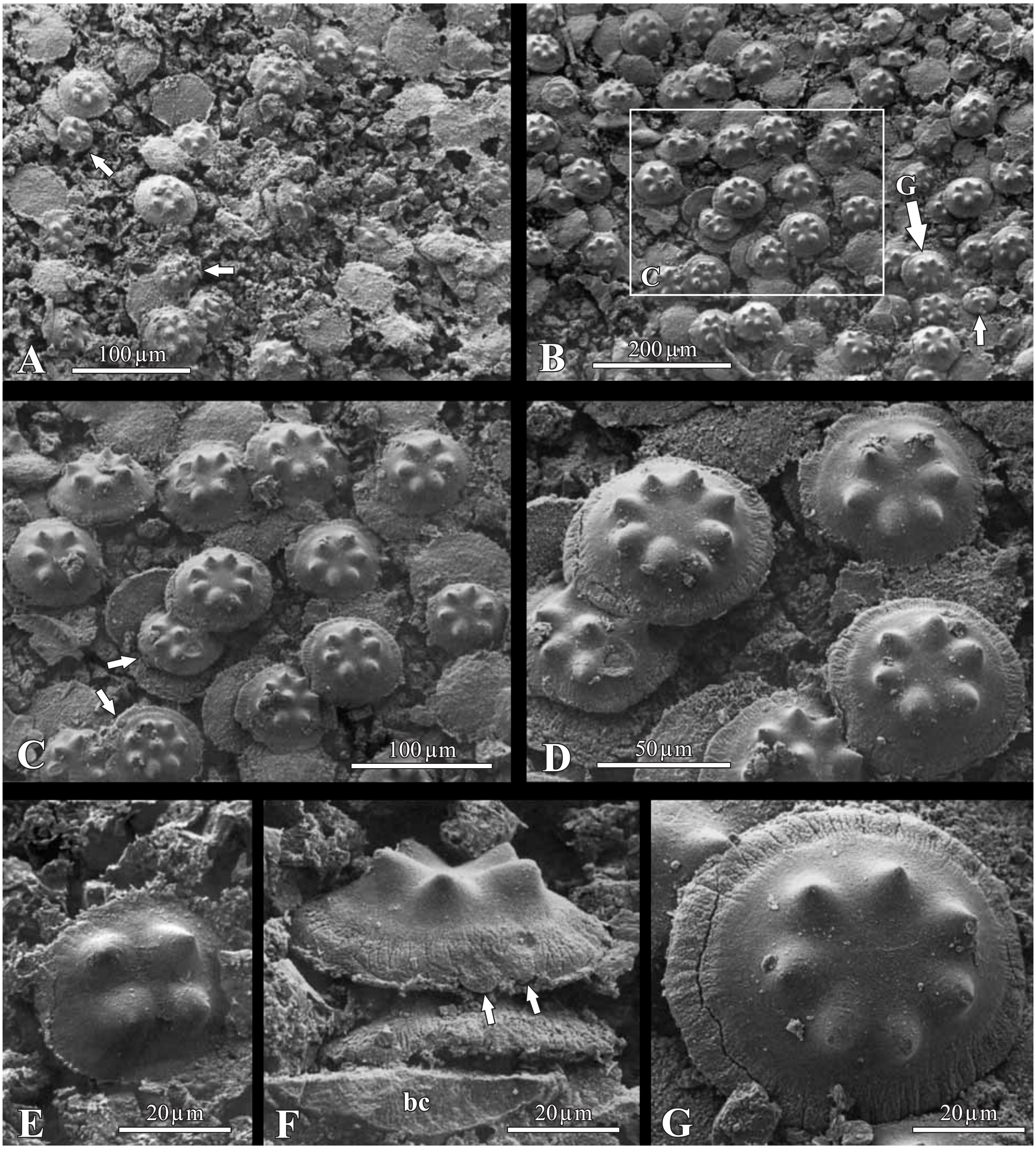


Fig. 3. General view of phosphatized cuticle surface of holotype of *Palaeoscolex lubovae* sp. nov. (PIN 4349/850); **A** – Sclerite arrangement on the flattened trunk, showing dimorphism in the sclerite size: “large” sclerites are plates and “small” sclerites are platelets (some arrowed); **B** – Another part of the same specimen, showing upper cuticle layer with nodular (outer) sclerite surface facing upwards and lower cuticle layer with nodular surface facing downwards such that, smooth, basal (inner) sclerite surface are visible. Small arrow points to a platelet and large arrow points to the single plate shown in Fig. G; frame indicates position of enlargement in Fig. C; **C** – Juxtaposed back-to-back sclerites in two layers of the compressed trunk, showing co-occurrence of sclerites with different nodular ornamentation: - with nodes surrounding in a circle and central node (arrowed) or with nodes arranged in circle only; **D** – Enlargement of C; **E** – Platelet from the same trunk surface, showing that it is a miniaturized and in ornamentation simplified equivalent of the larger plates; **F** – One of the sclerites in lateral-oblique view, with circular ?microplates (arrowed) incorporated into the basal sclerite margin; broken sclerite margin (upside-down) shows basal core (bc) section; **G** – Details of the plate ornamentation arrowed in Fig. B

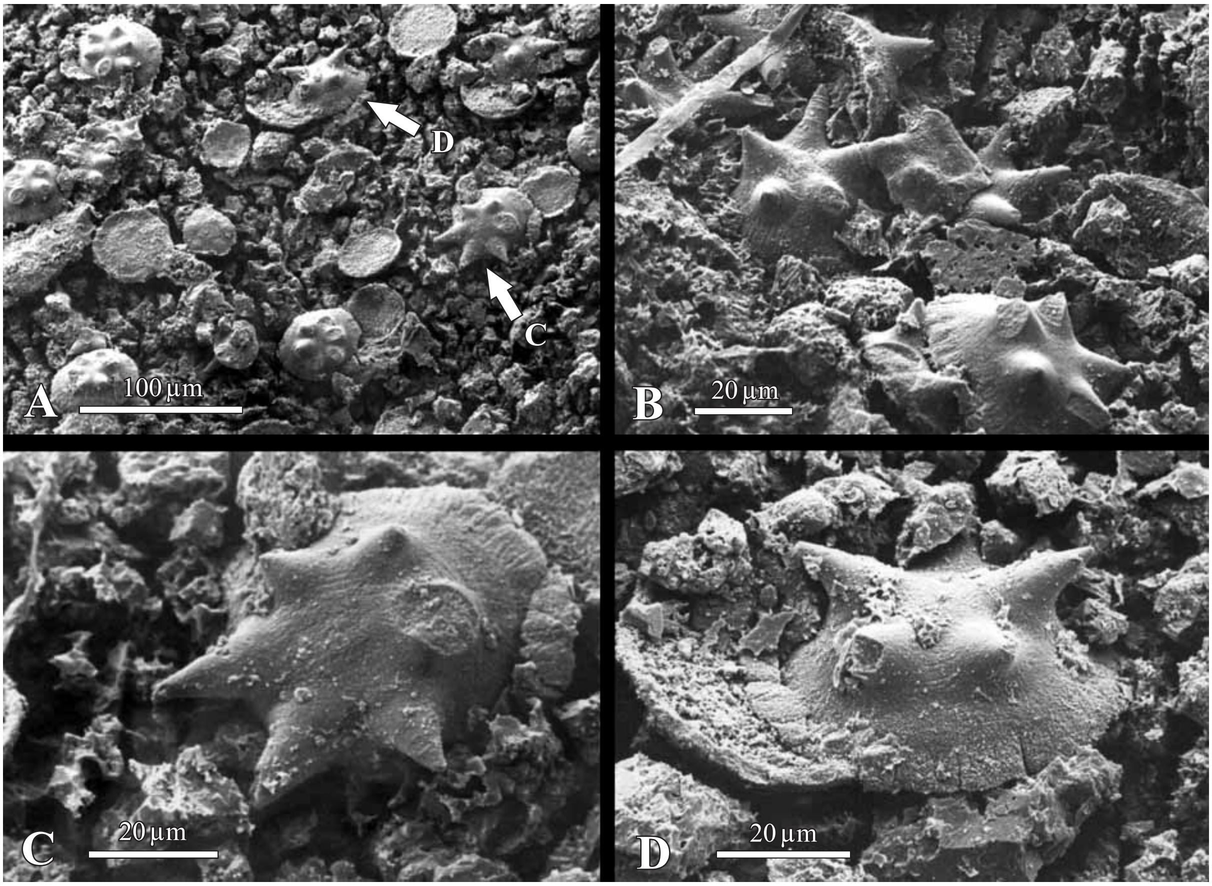
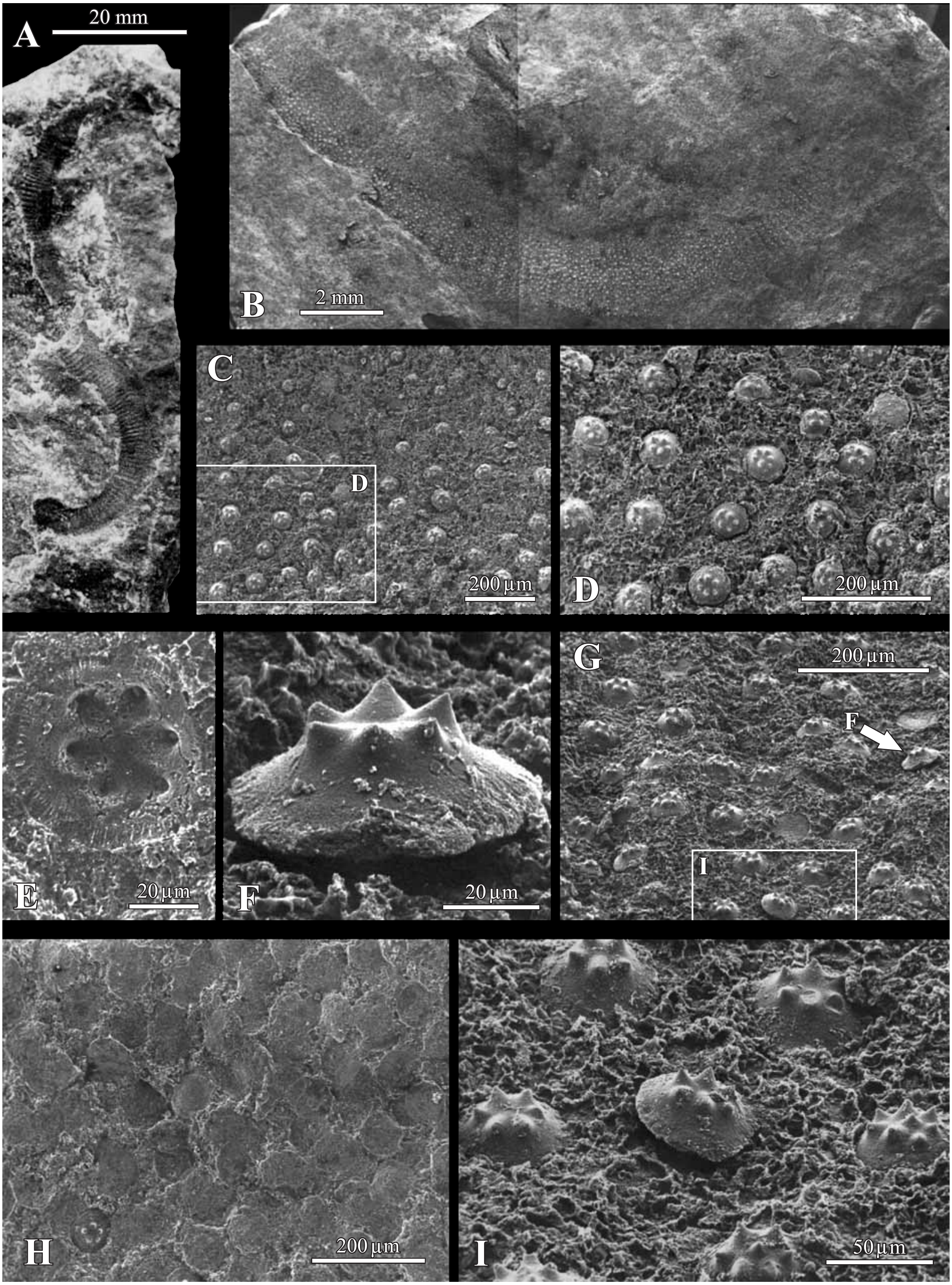


Fig. 4. Details of sclerite arrangement in the approximately ventral portion of the flattened body of the holotype of *Palaeoscolex lubovae* sp. nov. (PIN 4349/ 850); **A** – Sclerites of upper and lower cuticle layers compressed into the same plane in the sediment matrix, also showing coexistence of different sized plates and platelets and different sclerite ornamentation with both typical conical and spine-shaped nodes; arrows indicate position of C and D; **B** – Approximately the same area on the worm trunk possessing spiny sclerites embedded in the matrix; **C** – Detail of sclerite with broken spine; **D** – juxtaposed back-to-back sclerites of the two cuticle layers of the compressed trunk, showing sclerites with spine-shaped nodes

terior end enrolled. All cuticles show regular annulation through the entire length. Each annulus is covered with plates arranged in densely spaced duplicate rows (Text-fig. 2B), accompanied by small platelets (Text-fig. 3A; Text-fig. 4A). The plates are circular (diameter 58-81 μm), with strongly convex upper surface ornamented by 5-8 (usually 6-7) coarse nodes (maximum diameter 10 μm) arranged in circle (Text-fig. 3D), sometimes also with a central node (Text-fig. 3C). The plates have flat or gently concave ventral surface, and vary in upper surface ornamentation. Plates located on the ventral side of the trunk are ornamented with a circlet of outwardly directed sharp cones, sometimes extending into spines (Text-fig. 4). Outer margins of plates form a fairly broad marginal brim, which is flatter than the nodular central crown, and exhibits radial ribbing or striae. Some sclerites show circular microplates (diameter ca. 6 μm) accreted into this brim (Text-fig. 3F). Fractured sclerites (Text-fig. 3D, F) show their two layered internal structure: the thick lower unit forming basal core, with a

Fig. 5. Holotype of *Palaeoscolex spinosus* sp. nov. (PIN 4349/ 851) on a bedding plane from the Lower Cambrian Sinsk Formation, Achchagyy Tuoydakh section. **A** – Specimen immersed in alcohol and photographed in ordinary white light. **B** – Scanning electron photomicrograph of the epoxy resin cast from the surface of the same specimen (PIN 4349/ 851), with sclerites embedded in or adhering to the cast surface; **C** - Portion of cast surface with embedded sclerites; frame indicates position of enlargement in Fig. D; **D** – Enlarged portion of cast surface showing disturbed positions of some sclerites; **E** – Same portion of cast surface with sclerite mould; **F** – Magnified details of individual plate (arrowed in Fig. G); **G** – Portion of cast surface with sclerites embedded and peeled off (arrowed as F) from their places; frame indicates position of enlargement in Fig. I; **H** – Portion of cast surface showing basal sides of sclerites peeled off, with disordered and densely packed arrangement of sclerites caused by post-mortem shrinkage in the worm cuticle; **I** – Enlargement of G, showing co-occurrence of sclerites with different ornamentation: - with nodes arranged in a circle as well as with nodes arranged in circle with a central node (lower right corner)


A
20 mm
B
2 mm
C
D
200 µm
D
200 µm
E
20 µm
F
20 µm
G
200 µm
F
I
H
200 µm
I
50 µm

smooth upper contact, covered by a thin hyaline central crown ornamented with a nodes. Platelets are smaller versions of plates and simplified in ornamentation (Text-fig. 3A-B, E). Plates : platelets ratio about 1:2 (Text-fig. 3A). Platelets were probably arranged alternately with the plates in the central zone of annulus (Text-fig. 11A). All types of sclerites (plates, platelets and microplates, if present) were comparatively loosely spaced; thus they are circular, not polygonal in outline (Text-fig. 3F).

REMARKS: The new species differs from the other species of this genus in the presence of two rows of identically ornamented but differently sized sclerites (plates and platelets), arranged in an alternating pattern, and in the spiny sclerites on the ventral side of the trunk. Flattened cuticles found as part and counterpart on bedding surfaces show juxtaposed back-to-back sclerites in two layers of the compressed worms (Text-fig. 3A-D). The lower cuticle layer has its nodular surface facing downwards, thus showing the smooth basal surface, and the upper cuticle layer with the ornamented surface of the sclerites pointing upwards. Sclerites similar in ornamentation and structure to *Hadimopanella oezgueli* GEDIK, 1977 have been discovered in many different configurations (MÜLLER & HINZ-SCHALLREUTER 1993; CONWAY MORRIS 1997; WRONA & HAMDI 2001) likely because they may occur in the cuticles of a variety of different palaeoscolecid species and even genera. Sclerites ornamented with upwardly directed sharp spines seems to be restricted to the ventral side of the worm body. Sclerites with circular microplates accreted into the basal brim (Text-fig. 3F) resemble fused microplates observed in *H. antarctica* (WRONA 2004, fig. 18B) and in *Milaculum* (e.g., *M. balticum* VAN DEN BOOGAARD, 1988, figs 1A, 2D). This accretion may support a hypothesis that during the evolutionary process, the more complex sclerite structure bearing a series of nodes was derived from simple small sclerites with a single node (DZIK 1986, p. 249).

Palaeoscolex spinosus sp. nov.
(Text-figs 5-6, 11B)

HOLOTYPE: Nearly complete trunk with in situ sclerite array, PIN 4349/851, illustrated in Figs. 5-6.

TYPE HORIZON: Early Cambrian, Botoman Stage, *Bergeroniellus gurarii* Biozone, Sinsk Formation.

TYPE LOCALITY: Achchagy-Tuoydakh section, on the right bank of the Lena River, opposite the Sinsk village, 2.5 km below the mouth of the Achchagy-Tuoydakh creek, eastern Siberia, Russia.

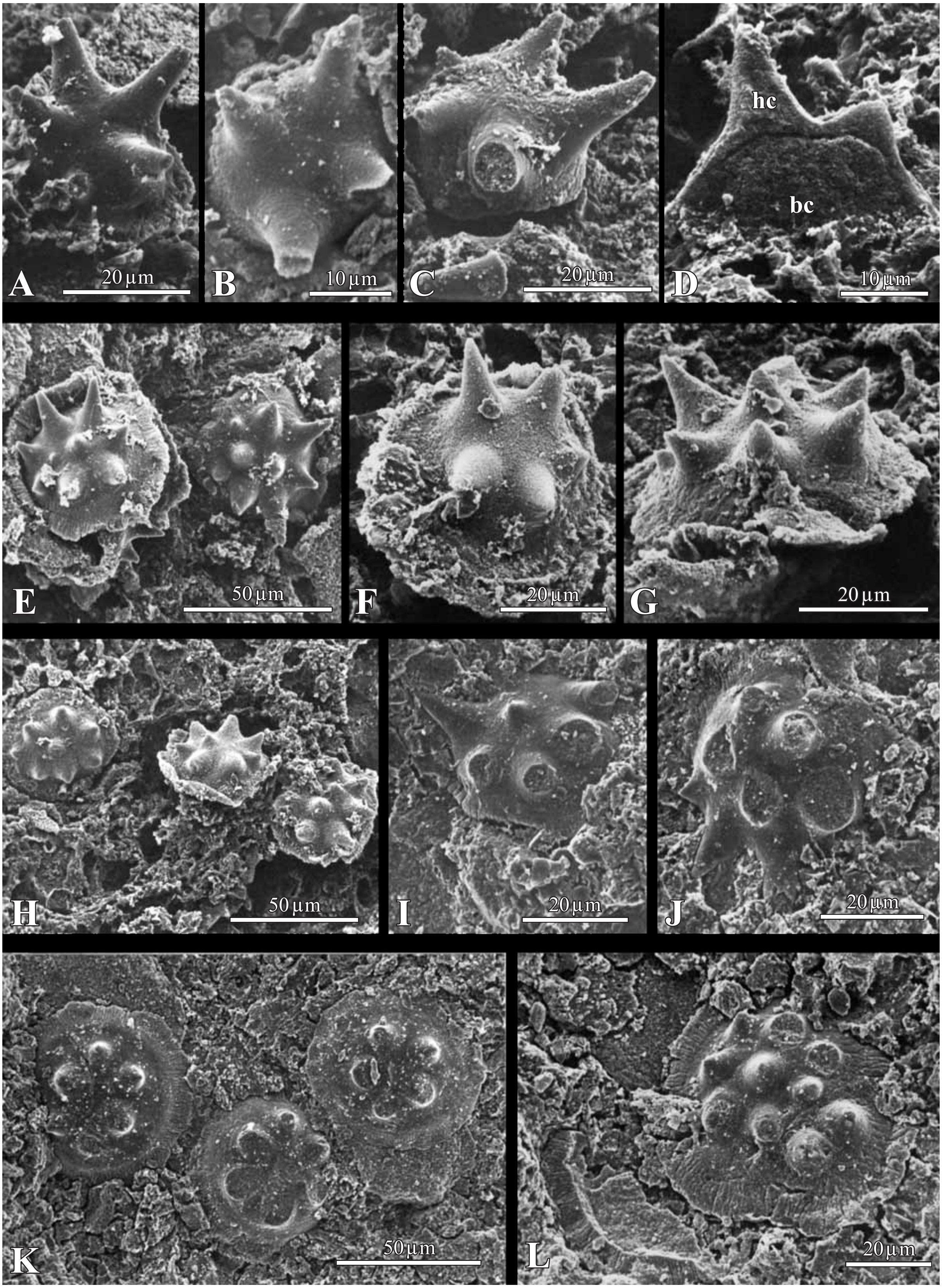
DERIVATION OF NAME: From the Latin *spinosus* – spiny, referring to the spiny upper surface ornamentation of the sclerites.

DIAGNOSIS: Cylindrical cuticle of worm with closely spaced annulation. Intercalations lacking. Annuli with one or two rows of plates widely arranged, and no platelets nor microplates. Plates vary in size and ornamentation, circular to oval-shaped, with strongly convex upper surface covered by 4-10 (usually 6) sharp cones, often protruding as spines arranged in circle or rows, sometimes also with a central node. Plates with spiny ornament are grouped on the ventral side of the trunk.

MATERIAL: Single sinuous specimen flattened on the bedding plane (PIN 4349/851), several cuticle fragments, and a numerous aggregated and isolated plates.

DESCRIPTION: An incomplete large specimen of the flattened, sinuously curved, cylindrical trunk has the anterior and posterior ends partly preserved. This cuticular fragment was found on a bedding surface and was a split longitudinally down the centre. Thus the surface ornament of the sclerites was obscured. The specimen was covered with epoxy resin and than extracted with acetic acid for SEM investigations (see Methods). The cuticular structure shows regular annulations along the entire trunk. Each annulus is covered with plates arranged in densely spaced duplicate rows (Text-fig. 5A-B), and no intercalations were observed. Plates are

Fig. 6. Details of individual sclerite ornamentation from approximately ventral portion of the flattened body of holotype specimen of *Palaeoscolex spinosus* sp. nov. (PIN 4349/ 851); **A** – Sclerite ("coronata-type") crowned with five spines; **B** – Sclerite ("coronata-type") crowned with four spines; **C** – Sclerite crowned with five spines of different length and one low node looking like an initial spine; **D** – Lateral view of broken sclerite section showing conical shape of the sclerite ("coronata-type"), the dense (hyaline cap) outer layer (hc) covers porous basal core (bc), with spines entirely formed by the capping layer; **E** – Sclerites crowned with eight and nine spines of different length, with one or two in the centre as low nodes, and radially striated marginal sclerite rim; **F** – single spiny sclerite with mineralised inter-sclerite tissue adhering to the basal margin; **G** - Single sclerite with seven spines of different length arranged in a circle, with one node in the centre; **H** – Sclerites with seven nodes arranged in a circle around a central node; **I**, **J** – Selected sclerites with broken-off spines of different length and arrangement; **K** – Sclerites showing ornamentation characteristic of *Hadimopanella oezgueli* GEDIK; **L** – Similar sclerite but considerably more elongated, with nodes forming well-defined rows and closely similar to those of *H. knappologica* (BENGTSON)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loosely spaced, and thus rounded, not polygonal (Text-fig. 5D-I), primarily embedded in a cuticular tissue. The plates are circular (diameter 30-80 μm; mode 60 μm), with the strongly convex upper surface ornamented by 4-10 (usually 6-7) sharply pointed cones (diameter of 5-10 μm) arranged in circles (Text-figs 5F, 11B). Some rare plates bear a central node surrounded by circlet of spiny cones (Text-figs 5I; 6E, G-J) or arranged in rows (Text-fig. 6L), resembling *Milaculum*-type sclerite (cf. WRONA & HAMDI 2001) or *Kaimenella* MÄRSS, 1988. Plates located on the ventral side of the trunk are ornamented with outwardly directed high sharp cones, protruding as a circlet of spines (Text-fig. 6E, G). Outer margin of plate forms a distinct marginal brim which can be covered with radial striae (Text-figs 5E, 6K-L). The broken plates (Text-fig. 6D, F) show their two layered internal structure: the thick lower unit of basal core, covered by a thin hyaline central crown bearing spines.

REMARKS: New species differs from the others of this genus in having one or two rows of variable in size and ornament, loosely arranged spiny plates, and no platelets nor microplates (Text-fig. 11B). The exact arrangement of the differently sized plates within each annulus is not easy recognizable since plates have been displaced (e.g., Text-fig. 5G, I) and disordered (Text-fig. 6H) by post-mortem shrinkage. Plates ornamented with high and sharp spines are similar to the isolated sclerites of *Hadimopanella*? *coronata* described by VAN DEN BOOGAARD (1989a). They are also similar to plates of *Rhomboscolex chaoticus* MÜLLER & HINZ-SCHALLREUTER, 1993, described as "plates ornamented with four to five strikingly high cones" (MÜLLER & HINZ-SCHALLREUTER 1993, p. 575, fig. 9E-F). The location of plates bearing long "coronata-type" spines (Text-figs 6A-D) seems to be restricted to the ventral side of the trunk. This location strongly reveal the distinction between the dorsal and ventral sides, and may suggests that worms of *P. spinosus* sp. nov. were adapted for a level-bottom epifaunal mode of life.

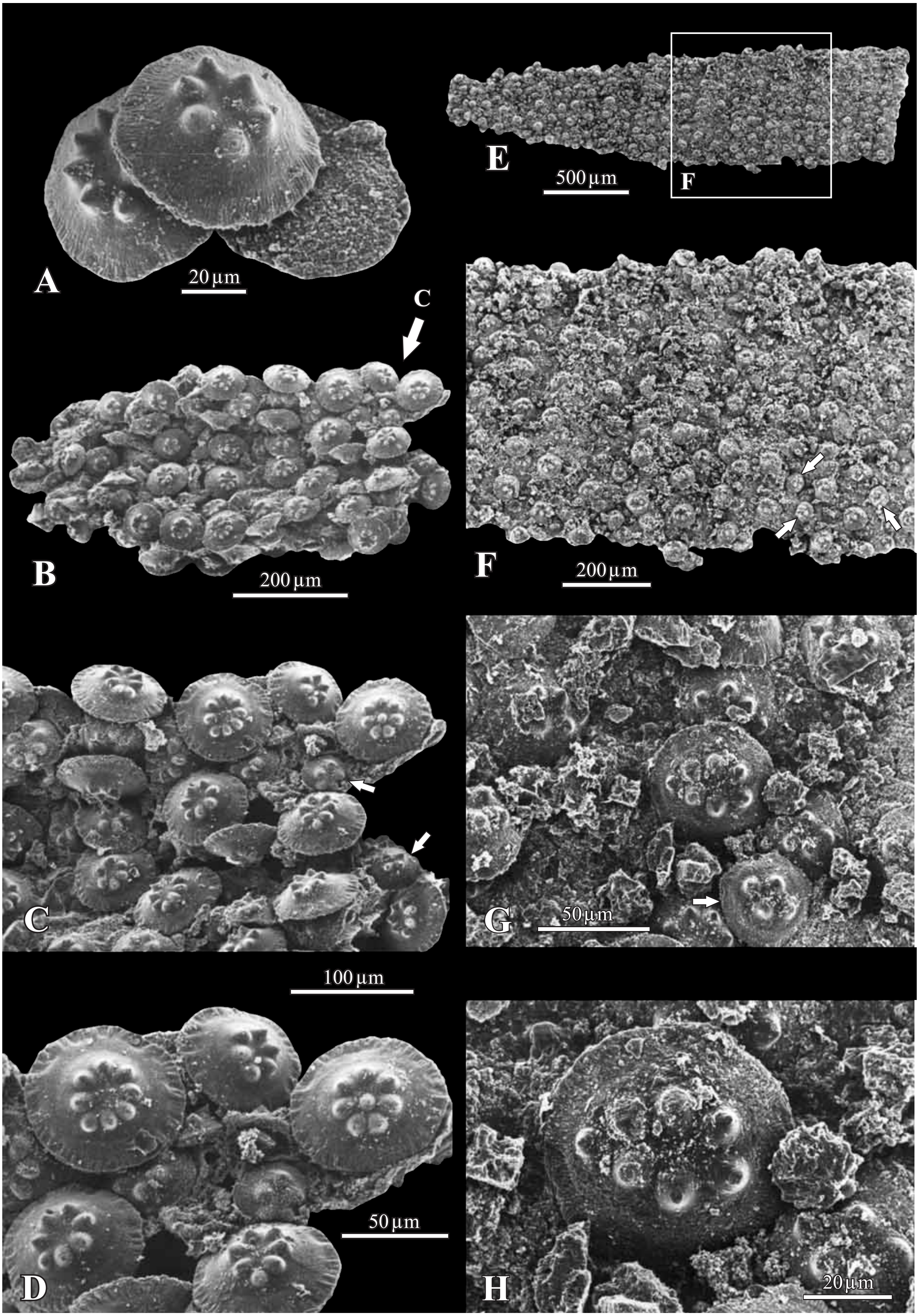
Palaeoscolex sp.
(Text-figs 7-8, 11C)

MATERIAL: Six phosphatized cuticle fragments of flattened cylindrical trunks (PIN 4349/852 [1S3], 854 [1S5], 856 [1S8], 857 [1S9], 858 [1S10], 859 [1S11], 862 [4S6]) and several aggregated (PIN 4349/853 [1S4]) and numerous disarticulated plates.

DESCRIPTION: Cylindrical cuticle fragments, compressed laterally (Text-figs 7B-H, 8A-I), show regular broad annulations through the entire length. Each annulus is covered with plates arranged in densely spaced duplicate rows (Text-figs 7E-F; 8A-C, F, H), accompanied by platelets (Text-figs 7C-D; F-G; 8E, G). The plates are circular to slightly elongate (diameter 60-75 μm), with a strongly convex upper surface ornamented by 4-8 (usually 6-7) coarse nodes (maximum diameter 10 μm) arranged in a circlet (Text-figs 7A-D, G-H; 8E, G, I), sometimes also with a central node (Text-fig. 7D). These are consistent in their ornamentation, but vary in diameter. All sclerites are embedded in cuticular tissue visible in intersclerite spaces. Outer margins of plates form a broad marginal brim, which is radially ribbed and striated (Text-figs 7A, D; 8E, G). Platelets are minute and often simplified (bearing fewer nodes, usually 4) versions of a plate (Text-figs 7C-D; 8E, G). Plates : platelets ratio about 1:2 or 1:1.5. Platelets were, probably, located internally to the plates in the central zone of annulus (Text-fig. 11C).

REMARKS: The arrangement of plates and platelets in the cuticular fragments is disordered and sclerites are jammed together (Text-figs 7B-H; 8C, I) by decay processes and post-mortem shrinkage. Some plates ornamented with central node surrounded by a circlet of nodes (Text-figs 7D) are closely similar to the isolated sclerites of *Hadimopanella oezgueli* GEDIK, 1977, especially those illustrated by VAN DEN BOOGAARD (1983, e.g., fig. 4a) from the Middle Cambrian of the Láncara Formation in northwestern Spain. However, the latter

Fig. 7. Isolated sclerites and cuticle fragments of *Palaeoscolex* sp. from the Early Cambrian Sinsk Formation, Achchagyy Tuoydakh section; **A** – Aggregate of three adhering sclerites (PIN 4349/ 853 [1S4]), with two juxtaposed back-to-back reflecting two cuticle layers of the compressed trunk; sclerites considerably elongated with 6-7 nodes arranged in two rows, closely similar to plates of *P. piscatorum* (CONWAY MORRIS 1997, figs 2-11); **B** – Cuticle portion of *Palaeoscolex* sp., (PIN 4349/ 859 [1S11]), strongly compacted by shrinkage, arrowed portion is position of Fig. C; **C** – Magnified portion of the same cuticle showing dimorphism in sclerite size: - plates and platelets (arrowed) clearly miniaturized equivalents of the larger plates; **D** – Magnified portion of C, showing intersclerite tissue connecting plates with elongate elliptic node rings (bottom left), and with central node (upper right); this ornamentation approaches fairly closely those recorded in *P. piscatorum* (CONWAY MORRIS 1997, figs 8-9); **E** – Cuticle portion of a flattened cylindrical trunk of *Palaeoscolex* sp. (PIN 4349/ 862 [4S6]), showing crowded arrangement of plates as result of post-mortem shrinkage, with annulations still recognizable; frame indicates position of enlargement in Fig. F; **F** – Detail of sclerite arrangement with annuli covered by two rows of large sclerites and two rows of small sclerites (arrows); **G** – Another cuticle portion of a similar flattened cylindrical trunk of *Palaeoscolex* sp., (PIN 4349/ 863 [4S7]), showing crowded arrangement of the plates caused by post-mortem shrinkage; arrow points to a small sclerite; **H** – Higher magnification of sclerites, showing elongate elliptic arrangement of node rings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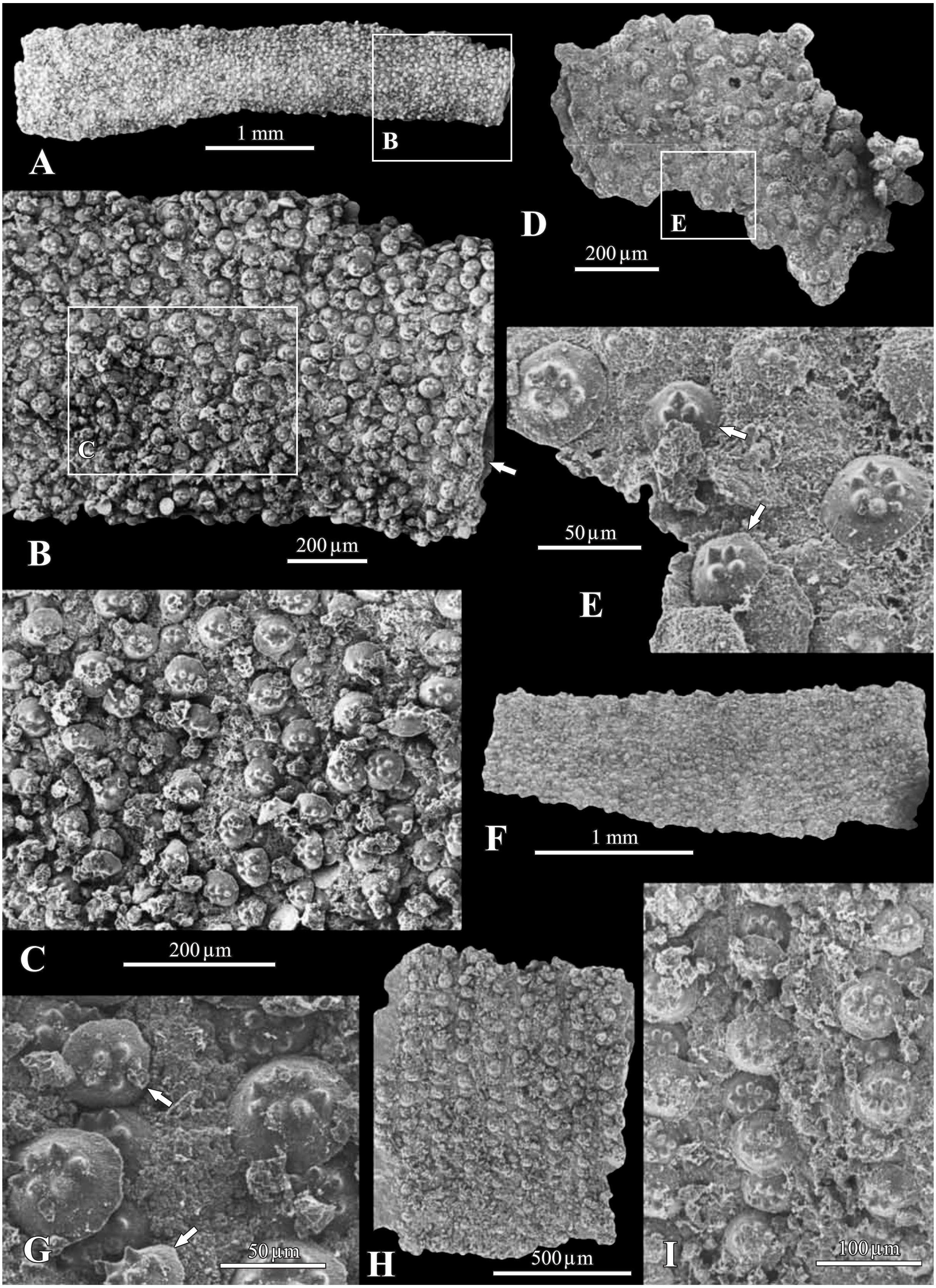
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are much larger, with diameters of 80-250 μm. They are also similar to sclerites of *H. acollaris* Märss, 1988 from Cambrian/Ordovician boundary beds of the Kallavere Formation in Estonia (Märss 1988, pl. 2, fig. 6). Plates bearing a series of nodes arranged in elongate circle are oval-shaped and thus most similar to the plates of *Palaeoscolex*, *P. piscatorum* Whittard, 1953 redescribed by Conway Morris (1997). However, the latter are much smaller, with a maximum diameter of only 30 μm, and are ornamented by up to 12 nodes. The surface structure of the crumpled cuticular tissue underlaying sclerites and filling intersclerite spaces is difficult to recognize, because of its poor preservation (Text-fig. 7C-D).

Genus *Sahascolex* gen. nov.

TYPE SPECIES: *Sahascolex labyrinthus* sp. nov.

DERIVATION OF NAME: Referring to its occurrence in the Saha Republic (Yakutia) and from the Greek *scolex* – worm.

DIAGNOSIS: Annulation moderately broad, intercalations absent. Annuli with two rows of sparsely spaced plates and platelets. Plates with central node surrounded by circlet of sharply pointed nodes. Platelets perfectly miniaturized version of plates, and arranged loosely in rows alternate to the plates. All sclerites are embedded in cuticular tissue, with a characteristic superficial labyrinthine pattern. Genus differs from the others palaeosolecid genera in having two rows of identically ornamented sclerites which differ in size (plates and platelets) embedded in an inter-sclerite cuticular tissue, which has labyrinthine surface structure.

Sahascolex labyrinthus sp. nov.
(Text-fig. 9-10, 11D)

HOLOTYPE: Fragment of the trunk with in situ sclerite array, PIN 4349/864 [4S8], illustrated in Text-fgs 9A-D, 10F.

TYPE HORIZON: Early Cambrian, Botoman Stage, *Bergeroniellus gurarii* Biozone, Sinsk Formation.

TYPE LOCALITY: Achchagy-Tuoydakh section, on the right bank of the Lena River, opposite the Sinsk village, 2.5 km below the mouth of the Achchagy-Tuoydakh creek, eastern Siberia, Russia.

DERIVATION OF NAME: From the Latin *labyrinthus* – labyrinth, referring to the labyrinthine surface structure of the inter-sclerite cuticular tissue.

DIAGNOSIS: As for the genus.

MATERIAL: Five incomplete, cuticle fragments (PIN 4349/860 [4S1], 861 [4S2], 864 [4S8]. 865 [4S10]), and a numerous aggregated and isolated plates.

DESCRIPTION: The fragments of cylindrical large worm cuticles are compressed laterally and folded (Text-figs 9A; 8A-B). Flattened specimens show juxtaposed back-to-back sclerites in two layers (Text-fig. 10A-B); with the ornamented surfaces facing outwards. All cuticle fragments show regular, moderately broad annulations through the entire length. No intercalations were observed. Each annulus consists of two rows of sparsely spaced plates (Text-fig. 9A), accompanied by small platelets (Text-figs 9B, F; 10C). The plates are circular, equal in size (diameter 40-50 μm), with strongly convex upper surface ornamented by 7-10 (usually 8) sharply pointed coarse nodes (maximum diameter of 10 μm) arranged in a circle surrounding a central node (Text-figs 9, 10). The plates are consistent in size and ornamentation. Their outer margins form a broad, convex marginal rim, with a distinct radial

Fig. 8. Cuticle fragments of *Palaeoscolex* sp. from the Early Cambrian Sinsk Formation, Achchagyy Tuoydakh section; **A** – Cuticle portion of a flattened trunk (PIN 4349/858 [1S10]), showing crowded arrangement of plates due to post-mortem shrinkage, with annulae indistinct, but sclerites still keeping arrangement in rows; frame indicates position of enlargement in Fig. B; **B** – Detail of cuticle, showing sclerites arranged in rows; at the right end two layers of flattened cylindrical trunk are visible (arrow); frame indicates position of enlargement in Fig. C; **C** – Detail of the same cuticle surface in Fig. B. **D** – Cuticle portion (PIN 4349/852 [1S3]), with disordered and crowded plates caused by post-mortem shrinkage; left margin shows contact of two layers of the flattened trunk (arrowed); frame indicates position of enlargement in Fig. E; **E** – Disordered sclerite embedded in intersclerite cuticular tissue; showing dimorphism in the sclerite size, small sclerites are arrowed; plates are slightly elongated sclerites with 6-7 nodes arranged in two rows and platelets are smaller (with four nodes) equivalent of the plates; **F** – Another cuticle portion of a flattened trunk (PIN 4349/856 [1S8]), showing crowded arrangement of the plates caused by post-mortem shrinkage, with annulations recognizable, plates and platelets still keeping arrangement in double rows; **G** – Enlargement of one segment in F; showing dimorphism in the sclerite size, small sclerites are arrowed; plates are elliptically elongated sclerites with 6-7 nodes arranged in two rows; **H** – Another cuticle portion of flattened trunk (PIN 4349/ 854 [1S5]), with crowded plates by post-mortem shrinkage; annuli recognizable, plates and platelets still keeping arrangement in double rows; **I** – Detail of the same cuticle, showing crowded arrangement of the plates due to post-mortem contraction; plates show arrangement of nodes in two rows; this ornamentation approaches fairly closely the circlet arrangements of *P. piscatorum* (Conway Morris 1997, figs 8-9)

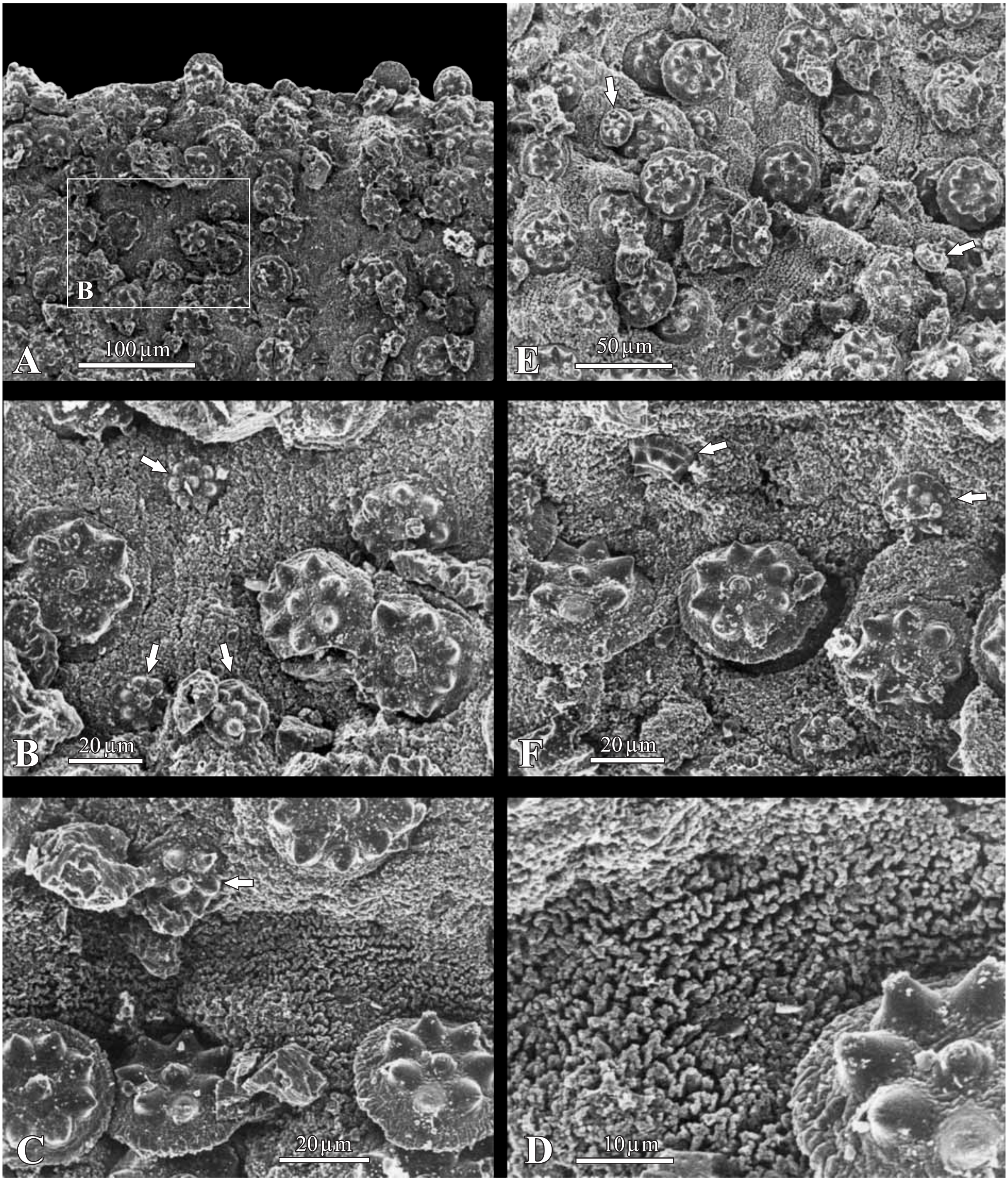

Fig. 9. Phosphatized cuticle of flattened cylindrical trunks of *Sahascolex labyrinthus* gen. et sp. nov. from the Early Cambrian Sinsk Formation, Achchagyy Tuoydakh section. **A** – Cuticle portion of holotype (PIN 4349/864 [4S8]), showing sclerites arranged in rows (or belts); but annulations indistinct, since lacking intersegmental furrows; frame indicates position of enlargement in Fig. B; **B** – Enlarged cuticle portion of holotype specimen, showing intercalary zone with platelets (arrowed) and phosphatized intersclerite tissue; **C** – Higher magnification of the same cuticle portion with plates and platelets (arrowed) partly peeled-off; **D** – Enlargement of C, showing vermicular (labyrinthine) pattern of the upper surface of intersclerite tissue formed by regularly arranged convex ridges separated by deep grooves; **E** – Another cuticle portion (PIN 4349/865 [4S10]), showing phosphatized intersclerite folded tissue, and disordered plates caused by post-mortem shrinkage; arrows point to some platelets; **F** – Enlargement of the same surface portion with densely packed plates and platelets (arrowed)

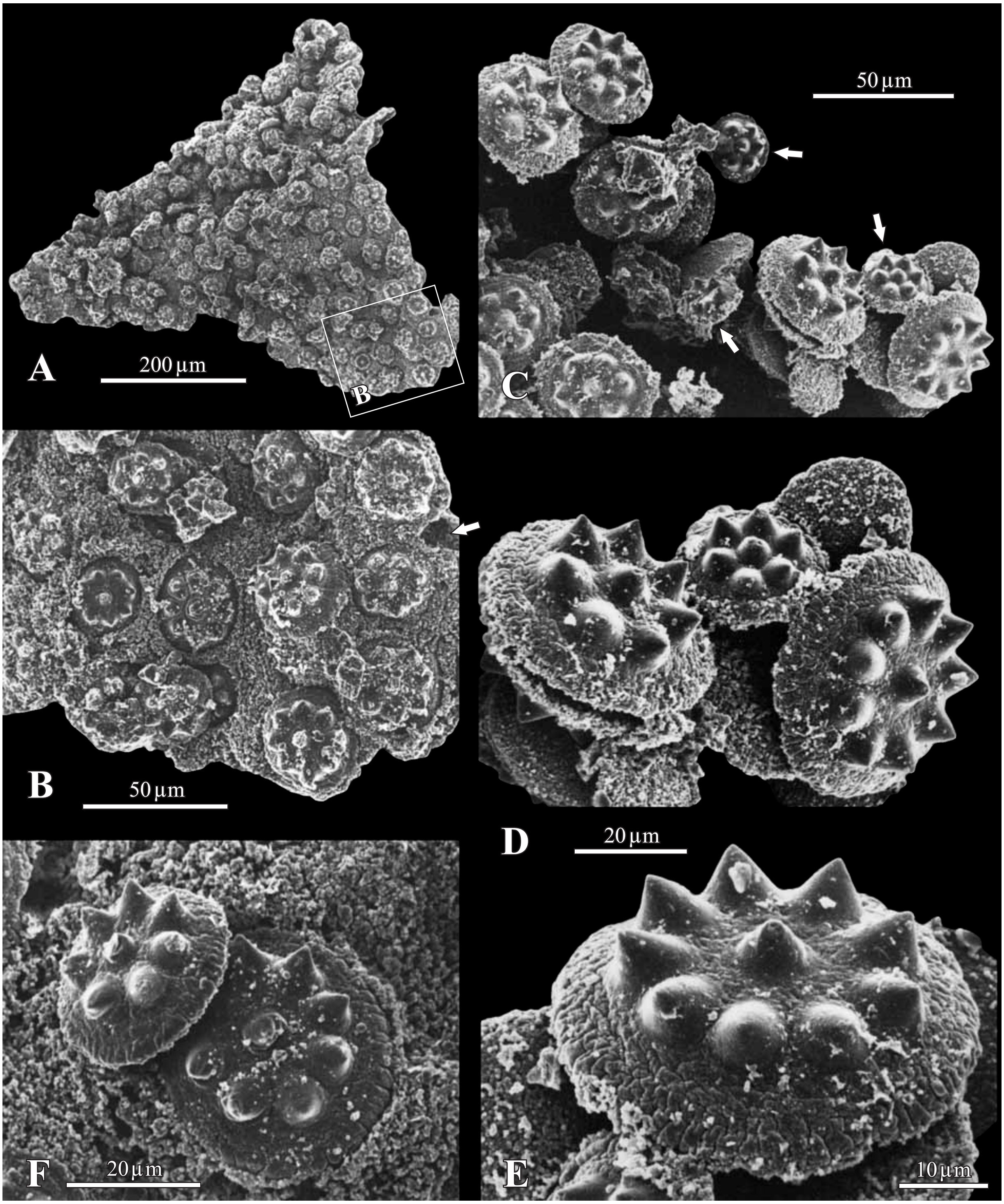

Fig. 10. Phosphatized cuticle portion of flattened cylindrical trunks of *Sahascolex labyrinthus* gen. et sp. nov. from the Early Cambrian Sinsk Formation, Achchagyy Tuoydakh section. **A** – Folded cuticle portion (PIN 4349/860 [4S1]), with disordered plates caused by post-mortem shrinkage; frame indicates position of enlargement in Fig. B; **B** – Detail of A, showing sclerite arrangement and intersclerite tissue; note sclerites with circlet of 6-9 nodes surrounding central node, which are similar to plates of *H. cassiniana* (Repetski, 1981, pl. 1, figs 1-2); arrow points to a contact of two layers of the flattened, primarily cylindrical trunk; **C** – Cluster of aggregated sclerites (PIN 4349/861 [4S2]), with plates juxtaposed back-to-back reflecting two cuticle layers of the compressed cylindrical trunk; arrows indicate platelets; **D** – Enlargement of the same as in Fig. C; **E** – Single plate of Fig. D, with labyrinthine ornamentation in the basal margin; **F** – Plate and platelet of holotype specimen (PIN 4349/864 [4S8]), showing sclerite embedding into surrounding cuticular tissue

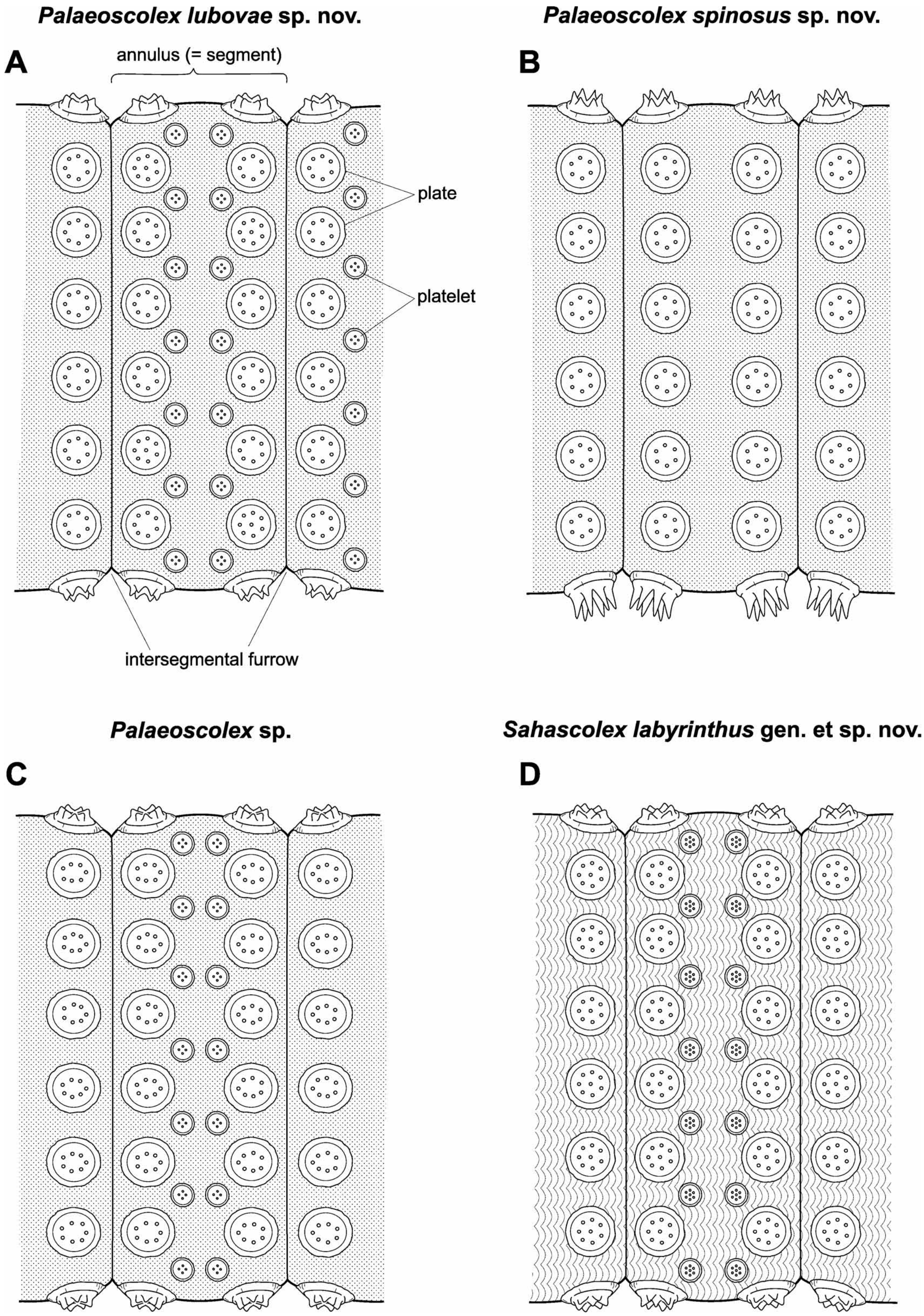

Fig. 11. Idealized reconstruction of the cuticle fragments showing sclerite arrangement in the annuli: **A** – *Palaeoscolex lubovae* sp. nov., **B** – *Palaeoscolex spinosus* sp. nov., **C** – *Palaeoscolex* sp., **D** – *Sahascolex labyrinthus* gen. et sp. nov.

labyrinthine sculpture (Text-fig. 10E), corresponding to the surface pattern of the inter-sclerite cuticle. Marginal rim jagged (Text-fig. 10F). Platelets are perfectly miniaturized version of plates, and are arranged loosely in rows alternating with the plates (Text-figs 9B, E-F; 11D). Plates and platelets are embedded in cuticular tissue, a matrix for overlying sclerites. This inter-sclerite cuticular tissue has characteristic pattern of labyrinthine surface structure. Plates : platelets ratio about 1:2 or 1:3 (Text-fig. A). Platelets are arranged alternately to the plates in the central zone of annulus (Text-figs 9A-B, 11D).

REMARKS: Plates in general are similar in ornamentation and structure to the isolated sclerites of *Hadimopanella oezgueli* GEDIK, 1977; in particular, striking similarity is seen to specimens from the Middle Cambrian Láncara Formation (VAN DEN BOOGAARD 1983, fig. 4a), as well as to single sclerites in the cuticular structure of *Utahphospha cassiniana* REPETSKI, 1981; reported from the El Paso Group, Lower Ordovician of western Texas (REPETSKI 1981, pl. 1, fig. 14). This latter species has no characters of the hollow coniform scleritome typical for *Utahphospha* MÜLLER & MILLER, 1976, but has more in common with armoured cuticle fragments, with similar plates and without annulation, ascribed to aff. *Hadimopanella oezgueli* GEDIK, 1977 form II by MÜLLER & HINZ-SCHALLREUTER (1993, p. 567, figs 7H-K). Similar sclerites were discovered in many different configurations (MÜLLER & HINZ-SCHALLREUTER 1993; CONWAY MORRIS 1997; WRONA & HAMDI 2001), and may occur in scleritomes of different palaeocolecid taxa. The radial labyrinthine sculpture on the broad marginal brim of plates *S. labyrinthus* gen. et sp. nov. is somewhat similar to the sculpture observed at the base of the sclerites of *Rhomboscolex chaoticus* MÜLLER & HINZ-SCHALLREUTER, 1993, described as "crumpled cuticular structure" (MÜLLER & HINZ-SCHALLREUTER 1993, p. 575, fig. 9E). Similar radial labyrithic pattern can also be observed on the steep lateral girdle of the single plates of *Utahphospha kazahstanensis* ESAKOVA, 1990 (in KONEVA & *al*. 1990, pl. 15, figs 1, 5). The labyrinthine structure of the matrix tissue supporting the overlying sclerites is also similar to the mineralized inter-sclerite wall fused to the basal brim of *Hadimopanella apicata* WRONA, 1982 recovered from the Lower Cambrian Aftenstjernesø Formation of North Greenland (BENDIX-ALMGREEN & PEEL 1988, p. 86, figs 5-6), as well as to the reticulate or labyrinthine structure that appears in the inner cuticular layer of *Corallioscolex gravitus* MÜLLER & HINZ-SCHALLREUTER, 1993 (p. 563, fig. 5L-M).

DISCUSSION AND CONCLUSIONS

Palaeoscolecid worms were first recovered mainly from shales as flattened, partially complete, individuals with annulation of transverse rows of papillae or tubercles, later recognized as sclerites (e.g., ULRICH 1878; BATHER 1920; WHITTARD 1953; ROBISON 1969; GLAESSNER 1979; CONWAY MORRIS & ROBISON 1986; HOU & SUN 1988; HOU & BERGSTRÖM 1994; GÁMEZ VINTANED 1995; LIN 1995). Disarticulated palaeoscolecid sclerites were subsequently found to be common isolated phosphatic microfossils of the *Hadimopanella-Kaimenella-Milaculum* morphotype in early Palaeozoic rocks over the world (e.g., MÜLLER 1973a,b; GEDIK 1977, BENGTSON 1977, ETHINGTON & CLARK 1981, VAN DEN BOOGAARD 1983, 1988, 1989a,b; WRONA 1982, 1987, 1989, 2004; CHERCHI & SCHROEDER 1984, PEEL AND LARSEN 1984, HINZ 1987, BENDIX-ALMGREEN & PEEL 1988, MÄRSS 1988, WANG 1990, DZIK 1994, FERNÁNDEZ-REMOLAR 2001, SARMIENTO & *al*. 2001, WRONA & HAMDI 2001). Despite extensive study of well-preserved secondarily phosphatized more or less complete cuticular structure of palaeoscolecid worms, including three-dimensional sclerite arrays (KRAFT & MERGL 1989; HINZ & *al*. 1990; MÜLLER & HINZ-SCHALLREUTER 1993; HOU & BERGSTRÖM 1994; ZHANG & PRATT 1996; CONWAY MORRIS 1997), their taxonomic relationships are still incompletely resolved. Their systematic position has been considered to be within the nematomorphs (HOU & BERGSTRÖM 1994) or the priapulids (CONWAY MORRIS 1993, 1997; MÜLLER & HINZ-SCHALLREUTER 1993). Unfortunately, the material from Sinsk Formation is imperfectly preserved to contribute to this discussion, and does not clarify a more exact systematic position for the Palaeoscolecida. We propose to include palaeoscolecids into the superphylum Ecdysozoa, containing moulting animals, such as arthropods, tardigrades, onychophorans, nematodes, nematomorphs, kinorynchs and priapulids (see AGUINALDO & *al*. 1997; AGUINALDO & LAKE 1998; GAREY & SCHMIDT-RHAESA 1998). The utility of isolated sclerites for biostratigraphy remains low, because of the same morphology may occur in different palaeoscolecid taxa (MÜLLER & HINZ-SCHALLREUTER 1993), and the different type-species of isolated sclerites may occur in one scleritome (Text-figs 3-4, 5A, 6, 7D; MÜLLER & HINZ-SCHALLREUTER 1993), and in a single sample (WRONA & HAMDI 2001). Palaeoscolecid worms were a common constituent of Cambrian level-bottom marine communities that often inhabited inter-reef environments, and most of them were probably infaunal (e.g., CONWAY MORRIS & ROBISON 1986; KRAFT & MERGL 1989; ZHANG & PRATT 1996, CONWAY MORRIS 1997; BURZIN & *al*. 2001), but some, with differentiated dorsal and ventral sides (seen by nipple-like ?appendages) may have been adapted for an epifaunal mode of life (e.g., MÜLLER & HINZ-SCHALLREUTER 1993; ZHANG & PRATT 1996). *Palaeoscolex lubovae* sp. nov. and *P. spinosus* sp. nov., showing distinction between the ventral side of the trunk, covered with spiny sclerites, and the dorsal side, covered with coarse ornamented sclerites, may have represent a similar adaptation to a vagile, epifaunal mode of life.

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