Paleobiology, 31(3), 2005, pp. 503–521

Behavioral and anatomical unity of the earliest burrowing animals and the cause of the "Cambrian explosion"

Jerzy Dzik

Abstract.—All interpretable trace fossils from the Ediacarian–Cambrian transition strata of northern Siberia, Ukraine, and elsewhere represent shelters of infaunal animals feeding from the sediment surface. There is a gradation of forms ranging from (1) makers of horizontal galleries in soft sand with bilobed lower surface and proboscis extended to the surface, through (2) linear or zigzag series of short, widely U-shaped burrows in firm clay with bilobed or three-lobed lower surface, to (3) series of cylindrical chambers dug completely inside the sediment but opening to its surface. At the same time, protective skeleton originated in animals living above the sediment surface. Apparently, the diversification of predators in the earliest Cambrian forced other animals to invest energy either in digging or in a protective armor (''the Verdun Syndrome''). True mud-eaters appeared later, as documented by the late Tommotian horizontal spreite structures from central Siberia. Most, if not all, of those infaunal traces of activity were produced probably by relatives of priapulid worms. It appears that body cavities and segmentation in the Metazoa (diverse already in the Ediacarian) evolved independently of, and prior to, hydraulic burrowing.

Jerzy Dzik. Instytut Paleobiologii PAN, Twarda 51/55, 00-818 Warsaw, Poland. E-mail: dzik@twarda.pan.pl

Accepted: 27 July 2004

Introduction

Whatever the exact time of the first diversification of animal phyla (Wray et al. 1996; Conway Morris 1997; Ayala et al. 1998), it no doubt significantly preceded the ''Cambrian explosion'' of skeletal animals and even the emergence of soft-bodied Ediacaran faunas. The fossil record in both cases was strongly biased by the profound change in the conditions of sedimentation, at least partially influenced by the evolving animals themselves. The Ediacaran biota was connected with microbial mats (Gehling 1999; Seilacher 1999), and their decrease perhaps resulted from the advent of bioturbation, which destroyed their environment (McIlroy and Logan 1999; Dzik 2003). Further evolutionary and ecological expansion of bioturbators probably also altered the environment of phosphatization of the early Paleozoic ''small shelly fossils,'' eventually leading to their disappearance (Dzik 1994). The origin of animals with abilities to penetrate sediment and their subsequent diversification are thus of much importance to understanding the Ediacarian–Cambrian transition.

The main task of many paleontologists is to determine function from the morphology of extinct animals. Trace fossils offer an opportunity to proceed in the opposite direction: from the effects of biological activity and behavior to the anatomy, which allowed the animal to leave a specific trace. This reasoning is used here to hypothesize about the body plans of the oldest animals, which were not represented in the Ediacaran biota or among the earliest Cambrian ''small shelly fossils.'' In this paper the structurally most complex trace fossils are used to determine basic anatomical features of those ancient metazoans, which invented the infaunal mode of life.

This specific line of inference is especially appealing for two reasons: First, the taphonomic bias hiders any direct access to anatomical evidence of these non-skeletonized earliest animals. Well-preserved macroscopic fossils of soft-bodied animals are unknown from before the emergence of the trilobites (Atdabanian). The Ediacaran biota, although prolific and highly informative, seems to be an extreme environment not representative of the mainstream of animal life in the Precambrian (Dzik 2003). The second challenge is phylogenetic in nature. Many zoologists believed that internal body cavities originated in connection with hydraulic locomotion and bur-

© 2005 The Paleontological Society. All rights reserved.

0094-8373/05/3103-0011/$1.00

rowing (Clark 1964, 1979). If so, the oldest traces of locomotory activities of the metazoans should be connected with their infaunal life. But this is clearly inconsistent with the fossil evidence.

If the burrowing worms were not the first, what then was the original anatomy of the metazoans? Why did some of them choose infaunal life at approximately the same time that other organisms developed mineralized skeletons? The evidence, which is here used to answer these questions, comes mostly from the Khorbusuonka River section in northernmost Siberia. This section is of special importance because both skeletal and trace fossils occur there in abundance, and also because it offered the first reliable radiometric dating of the base of the Cambrian (Bowring et al. 1993).

Material

The fossil material used in this work comes from various horizons of the Cambrian. The youngest in geological age is that already described by Orłowski and Żylińska (1996) from the latest Cambrian Klonówka Shale at Wiśniówka in the Holy Cross Mountains, Poland (housed at the Institute of Geology of Warsaw University; IGPUW). The Middle Cambrian trace fossils from the Kaili Formation of Guizhou Province, China come from beds described by Dzik et al. (1997) and are deposited at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (ZPAL). I collected a small collection of trace fossils in Tommotian limestone of the Lena River section (ZPAL) in 1987 during an expedition of the Paleontological Institute, Moscow. The earliest Cambrian trace fossils from Podolia, Ukraine, were studied in 2002 at the Geological Institute of the Ukrainian Academy of Sciences in Kiev (GIK). The material of major importance to the conclusions presented below (ZPAL) was collected from the topmost Ediacarian to basalmost Cambrian unit, the Nemakit-Daldynian (Manykayan) Kessyusa Formation in 2001 during an expedition to the Khorbusuonka River section in polar Siberia. The fossil site is located near the mouth of the Mattaia Creek (Fig. 1A).

Diversity of Infaunal Life at the Beginning of Cambrian

The beginning of the Cambrian is now defined in the lower part of the Chapel Island Formation in Newfoundland to coincide with the first appearance of the infaunal trace fossil *Manykodes* (''*Phycodes*'' or ''*Treptichnus*'') *pedum* (see Appendices 1 and 2 for taxonomic nomenclature) showing a complex arrangement of burrows (which makes its determination relatively easy). However, this species, as well as several other trace fossils, including elaborate *Spiroscolex*, occurs in the Newfoundland section also in the part underlying the Chapel Island Formation (Gehling et al. 2001). This means that the base of the Kessyusa Formation in northern Siberia may be significantly older than the beginning of the Cambrian as currently defined (Zhuravlev 1995). *M. pedum* appears there not far from the top of the formation (Fig. 1D).

It seems likely that the distribution of trace fossils in each of these successions was controlled mostly by ecological factors and had little to do with the evolutionary emergence of their makers. Until independent evidence of their real succession is obtained, only the most general aspects of the evolutionary events can be relied on. Thus, it appears certain that the oldest traces of animal life activity are known from the Ediacarian and were restricted to the sediment surface (Droser et al. 2000a; Vidal et al. 1994). Shallow burrows with a three-lobed lower surface widely occur in strata generally believed to be latest Precambrian in age, for instance in the Okuniec Formation of Ukraine (Gureev 1986; Velikanov 1990), Scandinavian strata with *Sabellidites* (Jensen and Grant 1998), and the Urusis Formation of Namibia (Jensen et al. 2000). Such traces are abundant in the middle part of the Kessyusa Formation.

Within the spectrum of trace fossils represented in the Kessyusa Formation there is a gradation from three-lobed shallow burrows to fully submerged burrows with a round cross-section to horizontal trails with a bilobed lower surface. This series can be extended further to trace fossils from younger Cambrian strata. Their morphology and possible ways of formation are reviewed below.

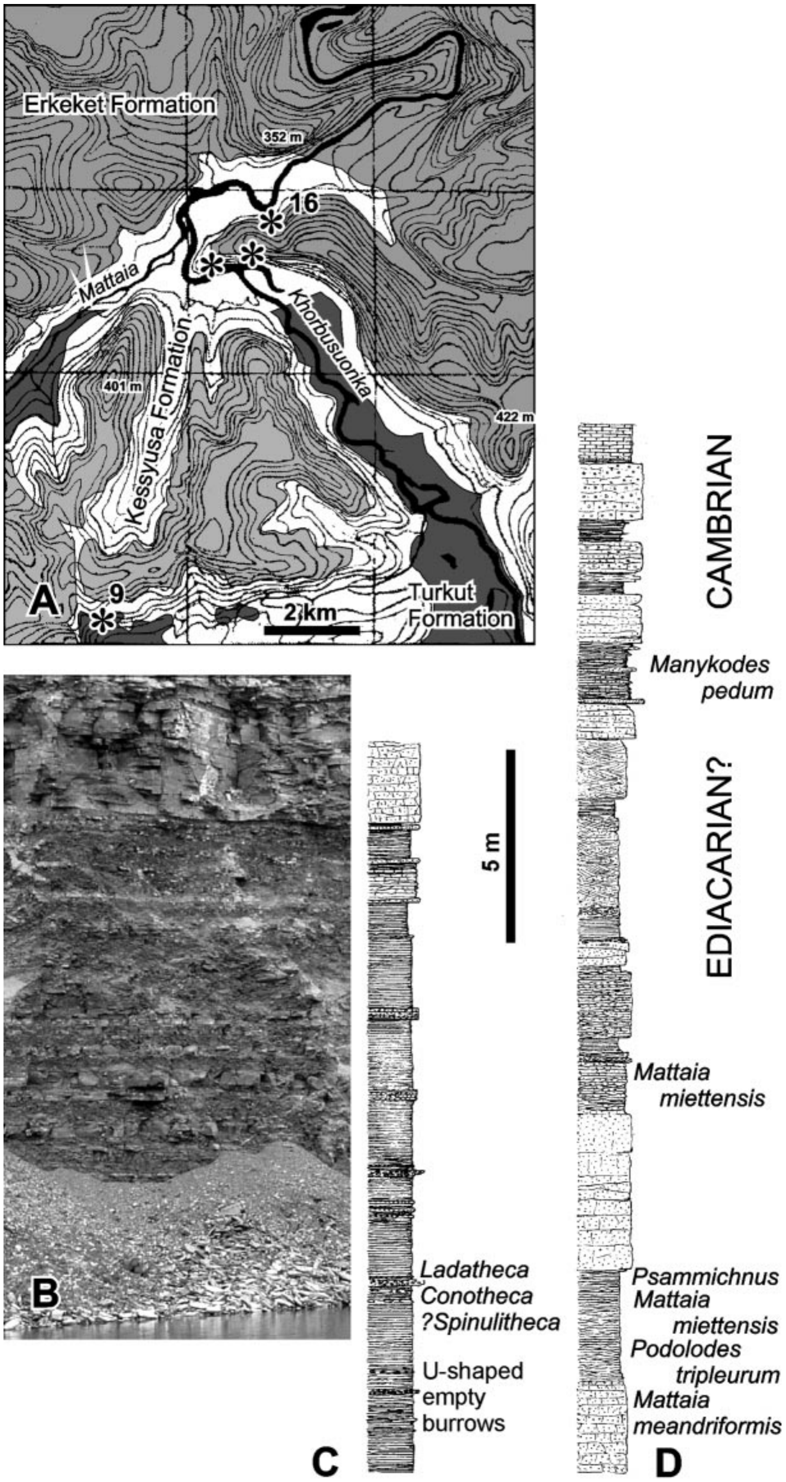

FIGURE 1. Location and stratigraphy of the earliest Cambrian strata at the mouth of Mattaia Creek in the Khorbusonka section (71°25′N,123°35′E). A, Map showing position of exposures; dark gray areas are outcrops of the latest Vendian (possibly also Nemakit–Daldynian) dolomitic Turkut Formation; light gray are exposures of the Tommotian Erkeket Formation and younger strata; numbers refer to localities of Karlova and Vodanjuk (1985). B, Cliff at the turning point of Khorbusuonka exposing the lower part of the mudstone unit of the Kessyusa Formation and the stratigraphic column of exposed mudstone with calcareous concretions and dark sandstone at the top. C, Stratigraphic column of strata exposed at the southern slope of the hill (locality 16). D, Same for locality 17.

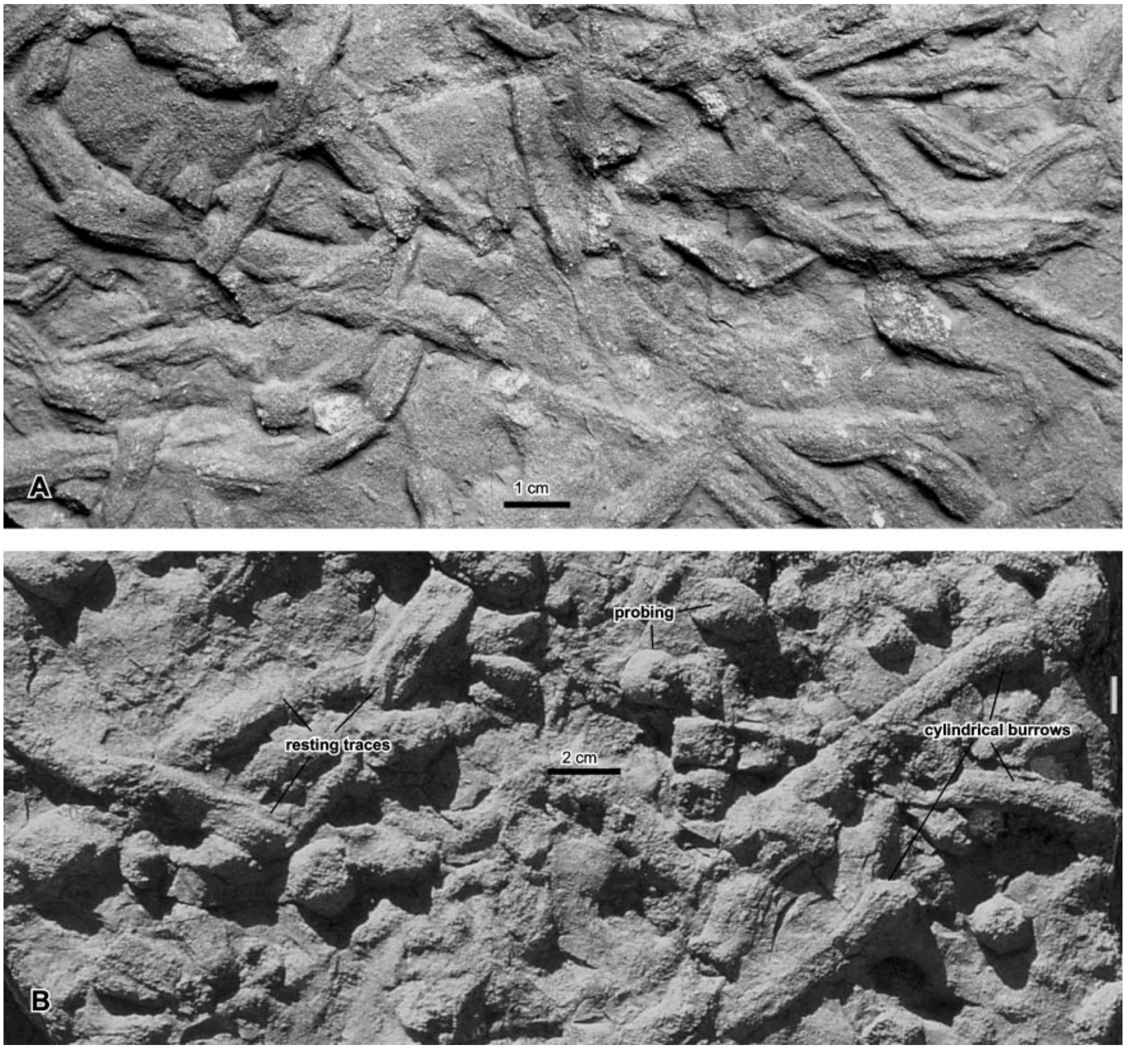

FIGURE 2. Lower surface of slabs of green glauconitic sandstone with three-lobed traces of *Podolodes tripleurum* (Geyer and Uchman 1995) from the middle part of the Kessyusa Formation collected at the northern slope of the hill near the mouth of Mattaia Creek. A, Shallow resting traces dug in probably firm clay; ZPAL A 7/7. B, Deeper galleries and probing from above the surface of somewhat coarser clay (perhaps softer), probably made with hydraulically swelling bulbous prosoma; ZPAL A 7/3.

Three-Lobed Furrows and Chambers in Firm Clay.—The lower surface of glauconitic sandstone beds in the middle part of the Kessyusa Formation in the Khorbusuonka section is in places densely covered with molds of shallow burrows in the underlying claystone. They range from 3 mm up to 8 mm in width and are usually 1.5–2.0 cm long. They are thus larger than the probably older three-lobed traces from the Urusis Formation of Namibia (Jensen et al. 2000). Narrow, smooth longitudinal ridges are visible on both sides of a wide, more or less elevated central convexity with a rather irregular surface (Fig. 2). In profile view the burrow molds are gently convex, with both ends smoothly disappearing at the bedding plane. Rarely they penetrated the clay to attain a roughly elliptical cross-section with a rounded upper side.

The burrows are frequently arranged in series, each behind the other, apparently dug by the same animal. Usually their orientation differs and burrows overlap slightly at their ends. This means that these were not trails of the animal moving continuously. Instead, both ends of the body extended above and the

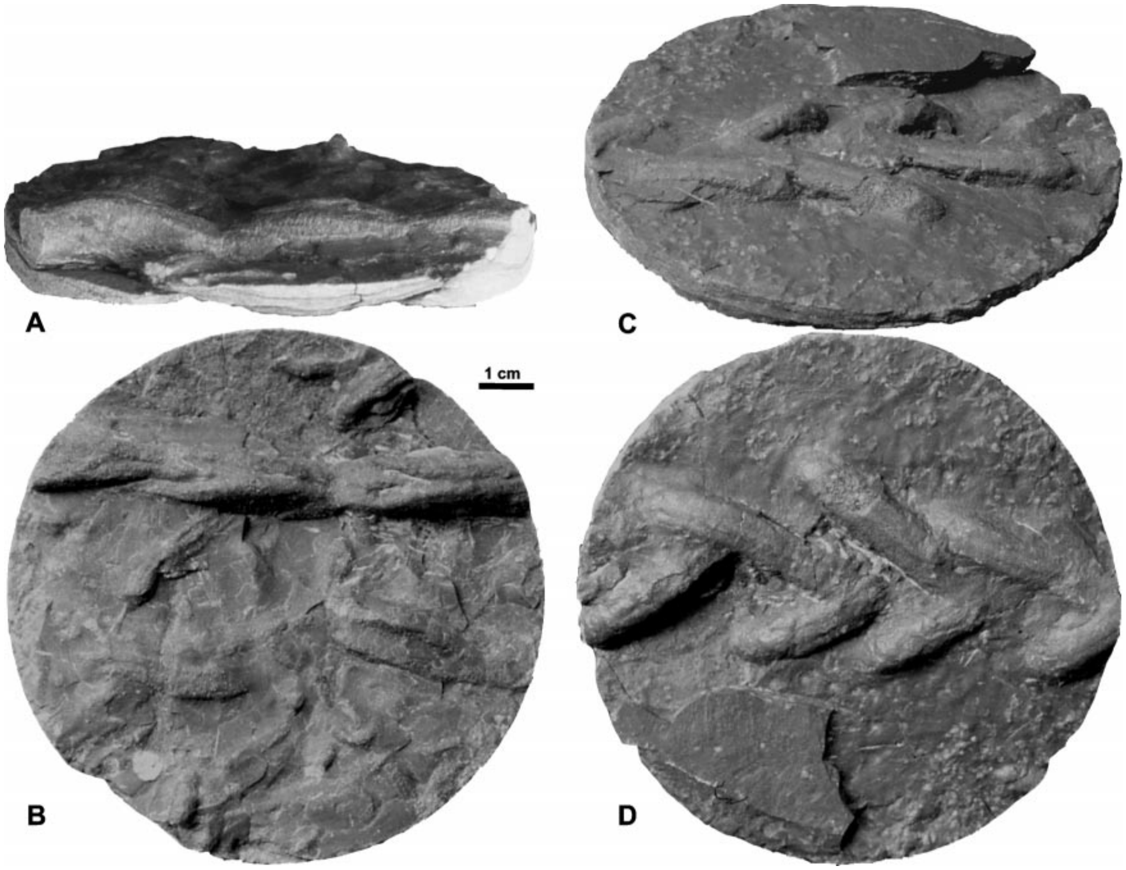

FIGURE 3. Lower surface of core slices of sandstone intercalations in the lower part of the Chmielnicki Formation from Podolia, Ukraine. A, B. Linear series of chambers of *Podolodes* sp. dug completely under the sediment surface; note transverse wrinkles on sides; specimen GIK 1907/25 (Geological Institute, Kiev), borehole 12607, Olchowcy village in Chmielnicki district, depth 268.0–270.0 m. C, D, Series of alternately oriented chambers of *Podolodes triplex* (Palij 1976) with each chamber initiated separately from the sediment surface; specimen GIK 1907/13 (holotype), borehole 561 in Kamieniec Podolski, depth 167.7–168.0 m.

fine sediment was removed from below with some organs located at the ventral surface of the body. Probably the animal was resting on the bottom partially hidden in the sediment. These were thus analogues of the trilobite ''rusophycus.'' The rather clear-cut course of the lateral ridges suggests that these were produced by longitudinally arranged series of appendages. Indistinct transverse wrinkles in the central belt of the trace may reflect a peristaltic wave moving along the body.

On some slabs of sandstone covering somewhat more silty clay, the three-lobed burrows tend to penetrated the sediment deeper (Fig. 2B). Although now somewhat more petrified, the sediment could have been originally softer or better oxygenated than in the case of shallower traces. Some of the burrows attain an almost circular cross-section and are closely similar to *Podolodes* (''*Treptichnus*'') *tripleurum* of Geyer and Uchman (1995) from the Nababis Formation of Namibia. Near the cylindrical part, the medial convex belt disappears or is replaced with a narrow furrow. The burrow terminates by turning vertically and opening to the surface. The same pattern is shown by the serially arranged partially three-lobed and partially bilobed burrow from the lower part of the Chmielnicki Formation of Ukraine (Fig. 3A,B) (Palij 1976; Palij et al. 1983). Lateral sides of the burrow show transverse wrinkles possibly related to peristaltic movement of the body. Probably burrowing was done hydraulically with a frontal organ of circular cross-section. Judging from the section of the burrow, the middle part of the worm was round only dorsally, with its venter showing three convex longitudinal belts of equal height. Among burrows from Mattaia there are numerous shallow probing traces almost hemispherical in shape that grade into regular burrows of this kind.

The same morphology is exhibited by particular units of the plait-like alternating series of burrows of *Podolodes* (''*Treptichnus*'') *triplex* with a three-lobed lower side, from the lower part of the Chmielnicki Formation of Podolia (Fig. 3B,C) (Palij 1976). They occur also in the earliest Cambrian *Platysolenites* Zone of eastern Poland (Paczešna 1996). The burrows open vertically to the surface, which suggests that the organism fed over the sediment surface using the burrow as a shelter, not deposit feeding as suggested by Uchman et al. (1998). Although these burrows were generally deeper than in the case of the linearly arranged three-lobed traces, burrowing of each successive unit was still initiated from the sediment surface. The animal had to retreat from its previous burrow basally and start burrowing again nearby.

In the upper part of the Chmielnicki Formation, trails of *Mattaia* (''*Didymaulichnites*'') *tirasensis* occur at the sole of sandstone beds. In places they are arranged into series of separate burrows, but in others show continuous burrows parallel to the sediment surface (Palij 1974; Palij et al. 1983). In short separate burrows, a three-lobed ventral surface may be developed in their central parts, although generally the irregular appearance of the fossil makes observation difficult. Definitely ends of such units show only a ventral furrow and traces of continuous burrowing are always bilobed. Trails in another specimen (GIK 1831/7; Palij 1974) are somewhat wider and closely resemble horizontal galleries well represented in the glauconitic sandstone unit at Mattaia. These shallow continuous burrows in clay show a possible transition from temporary hidings of *P. triplex* to permanent penetration of sandy sediment.

Unroofed Galleries in Soft Sand.—The interior of green glauconitic sandstone beds of the Kessyusa Formation at Mattaia is penetrated with bilobate trails about 2–3 cm wide, gently curved and crossing each other (Fig. 4). They are virtually identical with *Mattaia* (''*Didymaulichnus*'') *miettensis* from the top of Miette Group near Mt. Buchanan in British Columbia (Young 1972).

The trail is composed of four belts: a smooth double furrow in the middle and gently sloped convex outer lateral bevels (as named by Young [1972]) on both sides, with relatively rough surface. It was dug in the sediment without any deformation of layers below the bevels' margins. The lamination remains intact and horizontal. The lack of deformation of layers below the preserved trail margins indicate that this was not done by the action of any hydraulic pushing mechanism. Instead, the sediment was probably abraded with a frontal grazing organ.

The trail itself is filled with two bands of homogenized sediment, laterally raised and depressed in the center, where they are separated by a vertical fissure filled with clay. The volume of these belts roughly corresponds to the volume of sediment removed from the channel delimited by bevels. This means that all the material mechanically removed from below by the frontal grazing organ was transported behind. The smooth surface of the double ventral furrow suggests that this was the route of transportation (Fig. 4C), possibly with a paired belt of some ventral appendages. These may have been homologous to organs producing lateral furrows in *Podolodes tripleurum* or *P. triplex*.

In well-preserved specimens the outer lateral bevel consists of series of transverse, slightly oblique folds that terminate at the boundary between the bevel and the central double furrow. As seen from below, the folds are convex and separated by fissures. They at least remotely resemble stripes of *Plagiogmus arcuatus* Glaessner 1969 (Jaeger and Martinsson 1980; in Seilacher 1995 classified in *Psammichnites*; McIlroy and Heys 1997). In both cases these were probably effects of anchoring of the body and its movement with retrograde peristaltic waves.

The layer 1.5 cm thick above the mechanically removed channel (as measured from its margins) is gently deformed. From above the

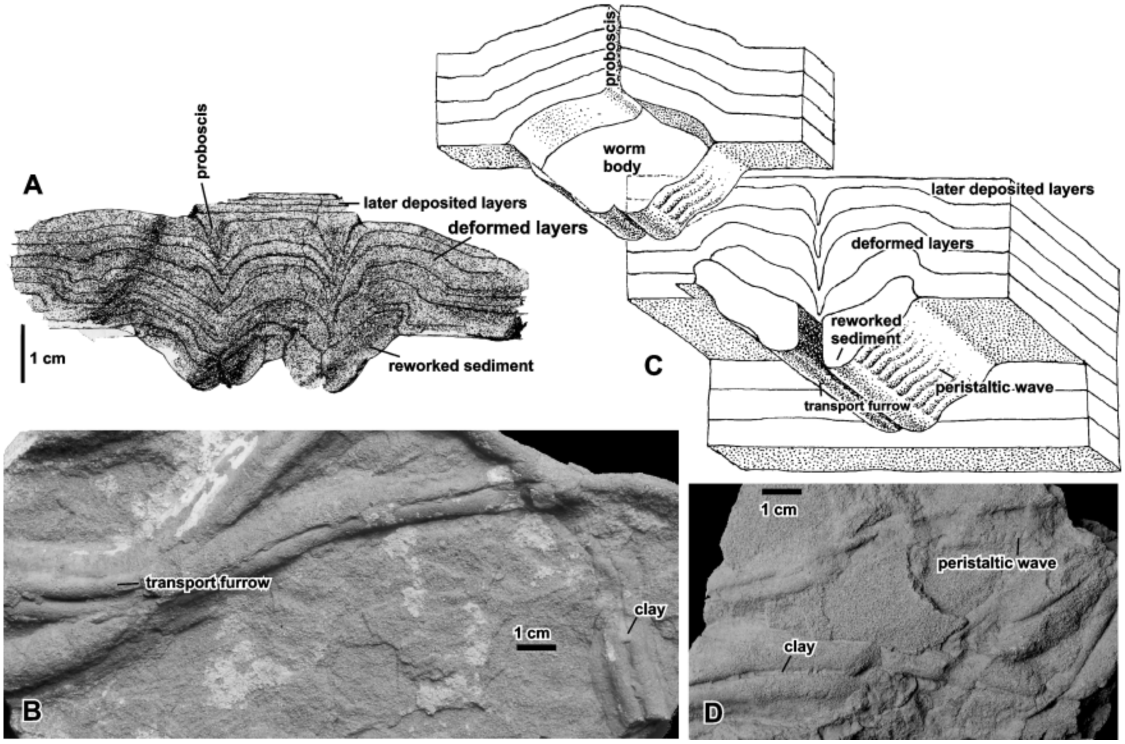

FIGURE 4. Bilobed horizontal galleries of *Mattaia miettensis* (Young 1972) in a glauconitic sandstone slab from the middle part of the Kessyusa Formation collected at the northern slope of the hill near the mouth of Mattaia Creek. A, B, Two associated galleries in cross-section and seen on the lower surface of slab ZPAL A 7/14. C. Diagrammatic presentation of the arrangement of sediment layers while the trail was made and after collapse of its roof. The lower part of gallery was excavated mechanically by the worm, whereas the layers above it were elevated hydraulically. The worm fed with its proboscis permanently extended to the sediment surface, as shown by the continuous fissure in the roof. D, Galleries from slab ZPAL A 7/2 showing transverse folds probably resulting from peristaltic movement of the animal

trail this is visible as a somewhat wider elevated belt with a furrow in the middle, which follows the course of the trail underneath. Undisturbed horizontal sediment layers above were deposited after the passage of the animal (Fig. 4A). Owing to clear delimitation of particular rock layers by clayish laminae, the cross-section of the rock shows rather well the internal structure of the trail (similar to that of the trail attributed to *Psammichnites gigas* by Hofmann and Patel [1989]). The clayish laminae remain intact, showing folded and raised external margins. This suggests a gentle hydraulic elevation by the worm. Such a precise horizontal splitting of sediment layers at a constant depth required that the worm was equipped with a rather narrow, horizontal cutting edge immediately above the grazing organ. The sand was quite soft, as shown by the ease of deformation of the sediment resulting from the *Mattaia* activity.

The sediment above the trail was thus first pushed upwards to fold on both sides and then collapsed in the middle behind the animal, as already inferred by Hofmann and Patel (1989). In the center of the trail the laminae dip down to form a vertical zone of discontinuity. Apparently, an organ exposed to the surface was cutting the sediment in the middle while the worm moved. It appears thus that the animal producing these trails had a body plan similar to that producing *Plagiogmus-Psammichnites*-type trails as restored by Seilacher (1995) and McIlroy and Heys (1997), except for having sediment grazing and transporting organs instead of a mollusc-like foot. Both these burrowers had a proboscis permanently penetrating to the surface and, at least in the case of the detritus feeding by *Psammichnites*, collected food together with sediment from the surface. Possibly, as suggested by Hofmann and Patel (1989), the clay concentrated between the central furrows in *Mattaia miettensis* came from excrements.

Although such a body organization is not similar to any Recent animal and seems rather ridiculous at first glance, there were similar organisms in the Cambrian. The Burgess Shale priapulid *Louisella pedunculata*, as restored by Conway Morris (1977) had a long eversible proboscis, the prosoma armed with hooks, annulated body, and, most interestingly, two ventral belts of minute appendages. Moreover, its cross-section was significantly depressed. Using *Louisella* as a prototype, not much transformation would be necessary to have a body organization necessary to produce all the above discussed trails.

Only small segments of *M. miettensis* were found in the green glauconitic sandstone at Mattaia. In a slab of a somewhat finer dark glauconitic sandstone of the Kessyusa Formation at the same locality, two superimposed trails (at different levels) of principally the same morphology but of significantly smaller size (12 mm wide) were collected (Fig. 5A). The geometrically regular appearance of meanders, closely similar to those from the same formation exposed at the shore of the Olenek River (Fedonkin 1985) and from the Ratcliffe Brook Formation of New Brunswick (Hofmann and Patel 1989), indicates a high efficiency in exploitation of sediment surface with proboscis.

Unlike the gallery floor, the roof of those trails was weakly, if at all, strengthened with mucus and apparently collapsed immediately behind the animal. Different construction, to some degree more similar to the zigzag-shaped Cambrian burrows, was applied to galleries by *Psammichnites* and related organisms.

Roofed Galleries in Soft Sand.—Together with wide bilobed trails, in the glauconitic sandstone of the Kessyusa Formation at Mattaia roofed galleries occur, similar to those from the Arumbera Sandstone of Australia attributed to *Plagiogmus arcuatus* by McIlroy and Heys (1997), but smaller. The Siberian galleries are only 16 mm wide and probably they were dug only a few millimeters below the sediment surface. The backfill is of the same sediment as around the gallery and the proboscis cut is straight (Fig. 5B).

Molluscan-Type Trails.—Somewhat surprisingly, among the earliest Cambrian trails none seem to be produced by a mollusc, despite the abundance of their shells in the ‘‘small shelly fossils’’ assemblages. Perhaps molluscan in origin is the large (about 5 cm wide) trail from the Poleta Formation of California (*Nevadella* Zone, Botomian) classified within *Taphrhelminthopsis* by Hagadorn et al. (2000). It does not show any evidence of roof or lining of the walls with mucus and the lower surface seems to be gently convex. It may be similar to the even larger *Climactichnites* from the Late Cambrian Potsdam Sandstone of New York, misinterpreted by Yochelson and Fedonkin (1993) but elegantly explained by Seilacher (1995: p. 46). Perhaps molluscs large enough to produce trails with identifiable effects of retrograde peristaltic waves of the foot did not appear earlier than close to the end of the Early Cambrian. Molluscs of relatively large size are known from the Tommotian (Dzik 1991), but their adaptation to active locomotion on soft sediment surface may possibly be an even later invention than the truly infaunal feeding.

Zigzag-Arranged Tubular Chambers in Firm Clay.—The branching burrows with round cross-section from the Kessyusa Formation at Mattaia do not show any signs of successive deepening of individual burrows (spreite structures). Instead, these were apparently permanently open burrows in partially compacted clay (as indicated by synsedimentary faults) subsequently filled with the glauconitic sand from the overlying bed. Traces of this kind from the earliest Cambrian are usually referred to *Manykodes* (‘‘*Phycodes*’’) *pedum*. Jensen (1997) has proposed that *M. pedum* was not a feeding burrow but rather a shelter of a surface detritus feeder.

However, incipient spreite structures have been reported to occur in the population of *M. pedum* from the Gross Aub Formation of Namibia (Geyer and Uchman 1995). If these are not just marks left on the wall of the burrow by the worm deepening it, this would mean

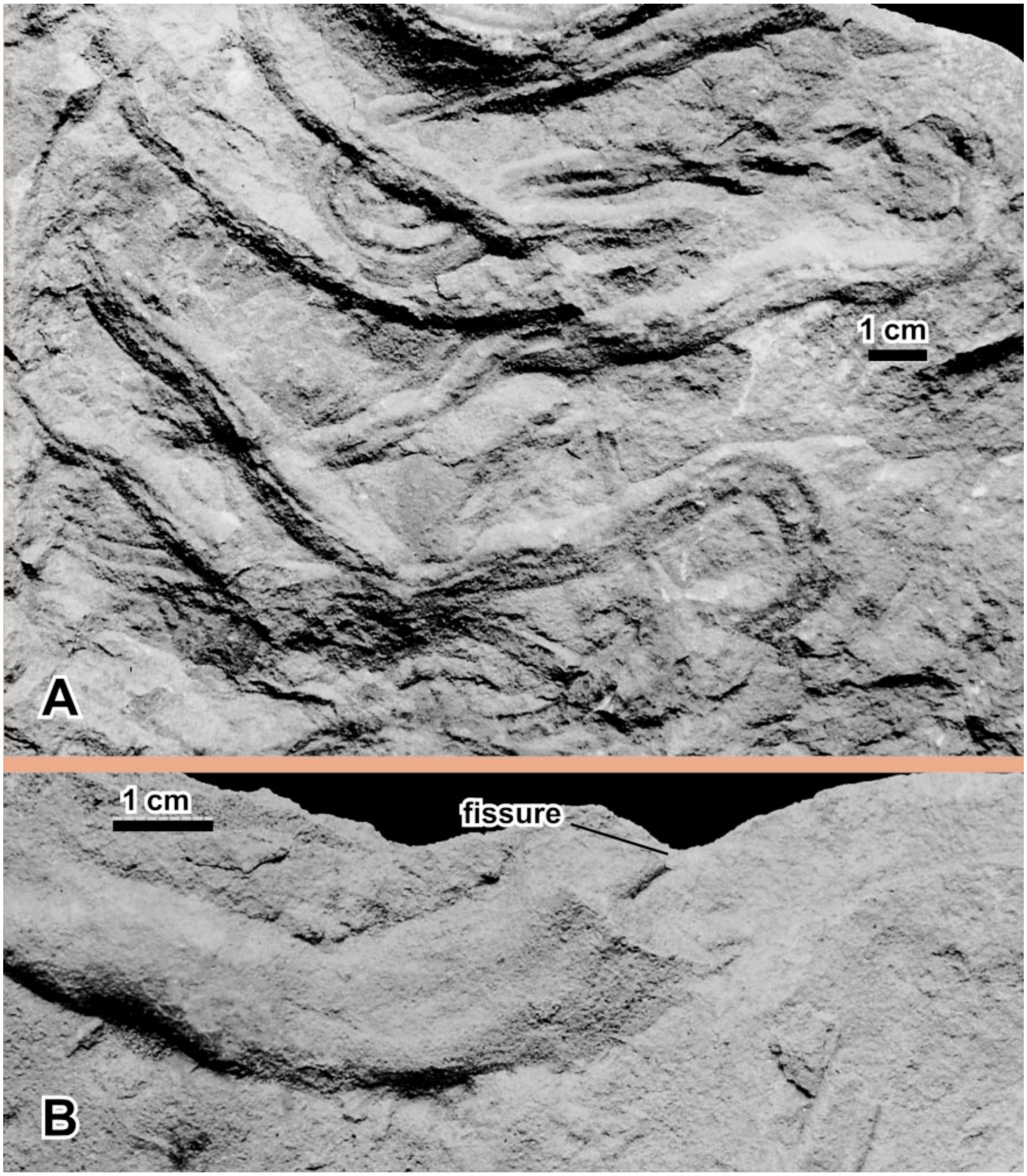

FIGURE 5. Lower surface of slabs of glauconitic sandstone from the middle part of the Kessyusa Formation collected at the northern slope of the hill near the mouth of Mattaia Creek. A, Dark muddy sandstone slab ZPAL A 7/13 with *Mattaia meanderiformis* (Fedonkin 1985), probably from the upper glauconitic sandstone bed. B, Green sandstone slab ZPAL A 7/4 with *Psammichnites* sp. occurring in association with *M. miettensis*. Note straight course of fissure in the gallery roof.

that the burrows were produced under sand cover. Some of burrows are rather deeply U-shaped; in others, palmately arranged, new burrows started from the deepest part of the preceding burrow (Geyer and Uchman 1995: Fig. 7.6). This is not the case with the Mattaia material, in which burrows are more horizontal, with their turning-upward ends hemispherical. In this respect the behavior of the Siberian animal was similar to geologically younger species with alternating burrows. In fact, alternation sometimes occurs there (Fig. 6C), similarly as in specimens from the Chmielnicki Formation of Ukraine (Velikanov et al. 1983). Unfortunately, the behavioral and anatomical information content in these traces is not great and they may represent various species of earliest Cambrian worms.

The much more informative exquisite material of apparently related *Manykodes* (''*Treptichnus*'') *rectangulare* from the latest Cambrian Klonówka Shale in the Holy Cross Mountains offered the conclusive support to Jensen's (1997) idea. A specimen was found with aggregation of fecal pellets visible at the bottom of burrows (Fig. 6B) (Orłowski and Żylińska 1996). This leaves little doubt that the burrows were empty during the life of the producer, with walls stiffened with mucus, and they subsequently were filled with sand. Clay-rich pellets suggest feeding on detritus around the opening of the burrow. Similar pellets are known to be associated with the Late Carboniferous echiurid *Caprinoscolex* from the Essex fauna of Illinois (Jones and Thompson 1977). Any affinity to echiurids, at least of morphology known from the Carboniferous and Recent seas, is excluded by traces left on walls of *M. rectangulare* burrows (Fig. 6A) (Orłowski and Żylińska 1996). These are swollen parts of the burrow marked with a ring of longitudinal striae. They are well visible only on the basal surface so their number can only be estimated as 15–20 in the circle. Such morphology is consistent with that of priapulids, known to burrow in the early Cambrian clay and sand (Jensen 1990). The swellings develop in the middle length of the burrow or somewhat proximally to it. This suggests that the animal, while retreating to the burrow, contracted its body and in effect widened its prosomal (or posterior; see Huang et al. 2004) part, which resulted in markings on the burrow walls.

The intrinsic control of burrowing behavior was apparently not very strict and a great variety of arrangements of chamber can be seen in particular populations. Still, they may substantially differ from each other in the way the new burrow is initiated. Whereas in the earliest Cambrian *M. pedum* each next chamber is rooted in the proximal part of the preceding one (Seilacher 1955; Geyer and Uchman 1995), in the latest Cambrian *M. rectangulare* it was dug laterally in the distal half of the chamber (Orłowski and Żylińska 1996). In the Middle Cambrian Kaili Formation an unnamed species of *Manykodes* occurs that was digging new chambers distally, from the vertical bulbous opening of the preceding chamber. Even in spiral series of chambers this way of origination is maintained, although new chambers are there attached to lateral sides of the opening or immediately behind it (similarly to *M. rectangulare*). This may be a case of directional evolution of behavior, with the animal retreating less and less deeply into the chamber while initiating a new burrow.

Even in long series of chambers in the Kaili and Klonówka Shale Formations there is no systematic change in size of chambers (Orłowski and Żylińska 1996), which means that the animal changed location frequently. Series of burrows of different size co-occur, suggestive of a stable population, not periodically recruited. Probably food resources around the chamber opening were limited and the energetic costs of burrowing reduced efficiency even more. The burrows are similar to borings by Ordovician ctenostome bryozoans, but the analogy seems superficial as there is no special reason to suggest that each chamber belonged to a new asexually produced individual of *Manykodes*.

U-shaped Empty Burrows.—The oldest traces of sediment penetration by wormlike animals in the Kessyusa Formation at Mattaia are shallow burrows resembling incipient *Diplocraterion parallelum*. The burrows are round in cross-section, about 2 mm in diameter, and in their central parts they were completely submerged in the sediment. Some are in contact but this may be accidental and their distribution seems chaotic (Fig. 2). Because of their rather indifferent morphology little can be said about the way they were produced. Similarly shallow burrows not showing any spreite structure occur also in the latest Cambrian Klonówka Shale (Orłowski and Żylińska 1996). Some burrows were partially filled with clay before sand entered, which means that they were originally empty.

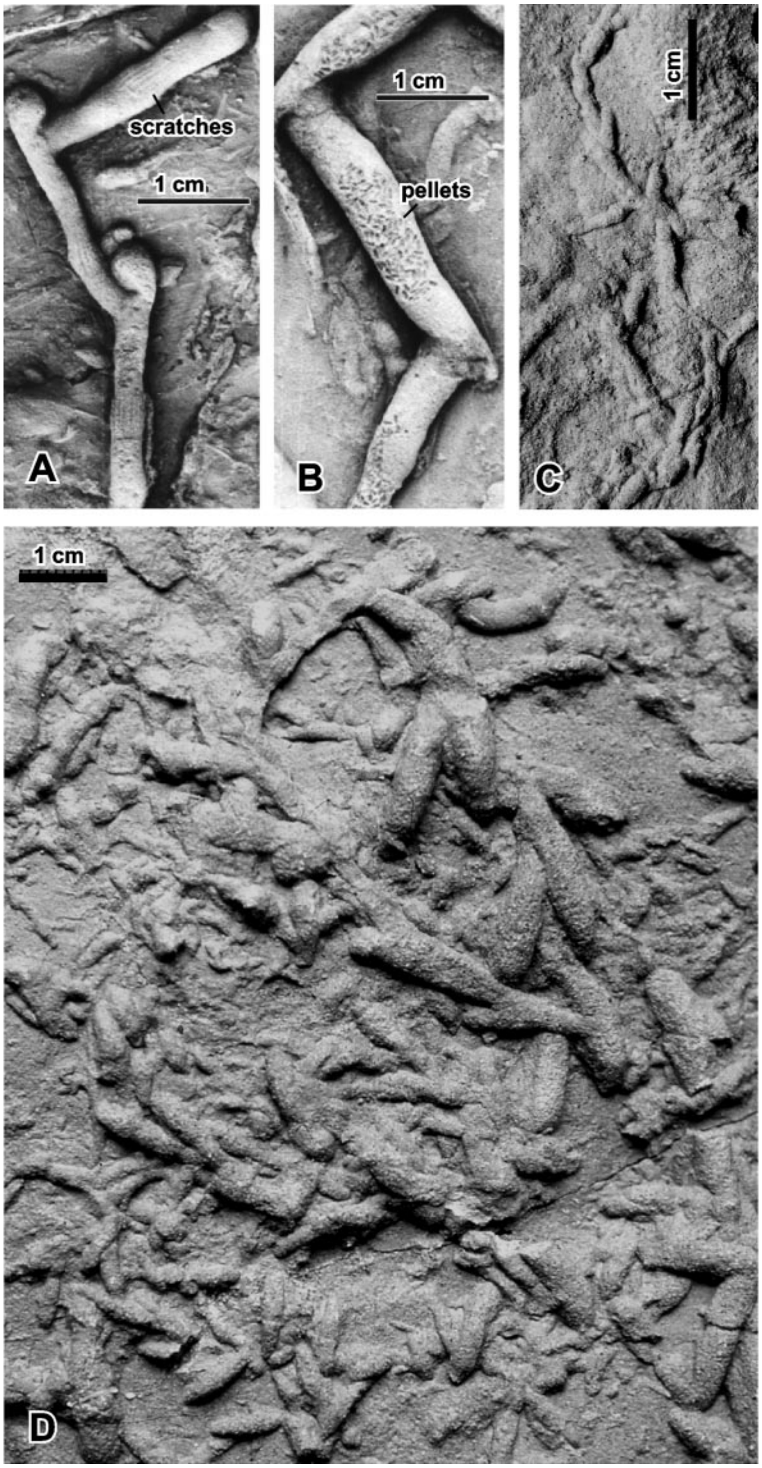

FIGURE 6. Cylindrical horizontal chambers dug hydraulically by probable priapulids feeding with proboscis on the sediment surface. A, B, Specimens of *Manykodes rectangulare* (Orłowski and Żylińska 1996) from the latest Cambrian Klonówka Shale at Wiśniówka in the Holy Cross Mountains, Poland, showing scratches left by proboscis of retreated animal (A; IGPUW/Tf/1/592) and fecal pellets at the bottom of chamber (B; IGPUW/Tf/1/605) proving that it was originally empty (Orłowski and Żylińska 1996). C, D, Lower surface of slabs ZPAL A 7/8 (C)and 15 (D) of light-colored sandstone with *Manykodes pedum* (Seilacher 1955) from the upper part of the Kessyusa Formation collected at the southern slope of the hill near the mouth of Mattaia Creek.

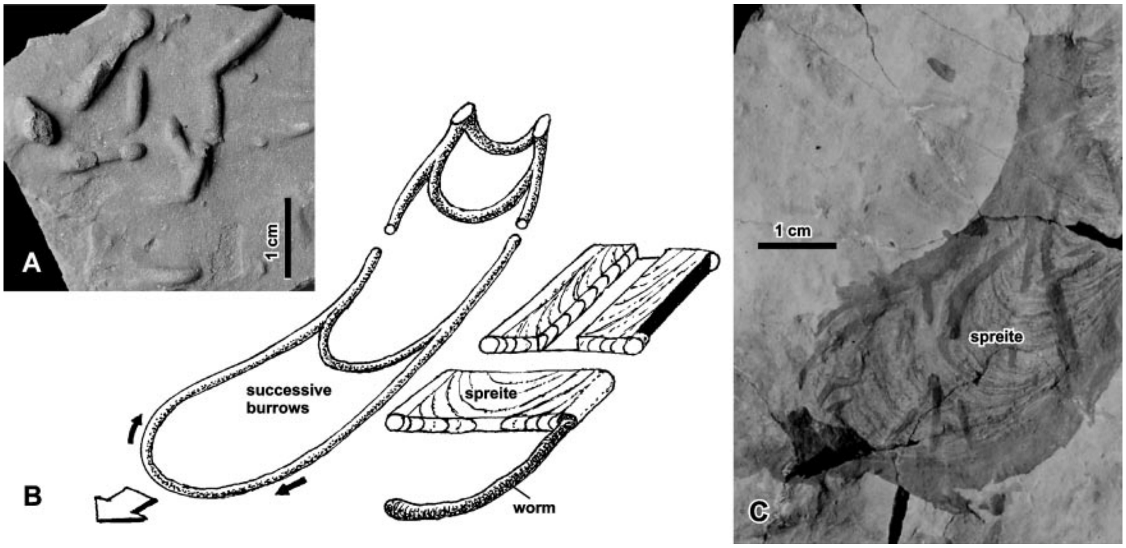

FIGURE 7. U-shaped burrows of earliest Cambrian infaunal worms. A, Irregularly distributed shallow burrows ZPAL A 7/5, probably of *Diplocraterion*, from the base of the mudstone unit of the Kessyusa Formation exposed at the cliff of Khorbusuonka near the mouth of Mattaia Creek. B, C, Horizontal burrow related to *Diplocraterion* showing spreite structure and subsequent penetration by a similar-size possible sediment eater from the late Tommotian (or early Atdabanian) of central Siberia. Schematic presentation of the way the trace was made and its internal structure (B) and the original slab ZPAL A 7/16 of red marly limestone (C) collected on the shore of the Lena River near the mouth of Tiktirikteech Creek.

Even if a spreite structure developed in such burrows, this does not prove infaunal feeding. Instead, it was rather a case of keeping balance with the surface erosion by deepening the burrow, or retreat of the animal in conditions of high sedimentation rate.

Spreite Feeding Traces in Soft Sediment.—A proof for purposeful penetration of the sediment for feeding is offered by horizontal spreite structures occurring in a marly limestone facies of the late Tommotian (or early Atdabanian) at the Tiktirikteekh section on the Lena River near Jakutsk (Fig. 7B,C). These are results of serial burrowing by the same animal, of about 3 mm diameter, with each subsequent gallery being produced along, and partially within, the previous one. The producer of the horizontal spreite structure directed its main effort at drilling in the middle length of the burrow. As a result, a tongue-like appearance of the whole structure (''rhizocorallium'') developed, with its lateral parts much stronger homogenized by repeated penetration. This connection between earlier and later burrows may have had a purely mechanical cause. The already bioturbated sediment was probably softer and easier to penetrate. This is suggested by a common restriction of narrower linear burrows, possibly made by juvenile individuals of the same species of worms, to the earlier produced spreite structure. In the Atdabanian marly limestone at the nearby Zhurinsky Mys locality, such burrows are restricted to laminated sediment fill of earlier made meandering furrows, 2–3 cm wide and deep, at the firm ground surface.

The great length of the U-shaped channel along the structure makes feeding from the sediment surface unlikely. Instead, exploitation of organic matter from the sediment is likely. The presence of two openings suggests some way of ventilation, although there is no direct evidence that the burrow was empty.

Such feeding traces are known also from roughly coeval strata in sandstone facies, for instance the ''rhizocorallium'' from the *Mobergella* Zone of northern Poland preceded *Spiroscolex* (Pacześna 1996). Already in the basal trilobite-bearing strata (Atdabanian) in Sweden (Mickwitzia sandstone) a helicoidal organization of U-shaped empty burrows with horizontal spreite structure developed (Jensen 1997). The abundance of priapulids in the Cambrian localities with soft-bodied organ-

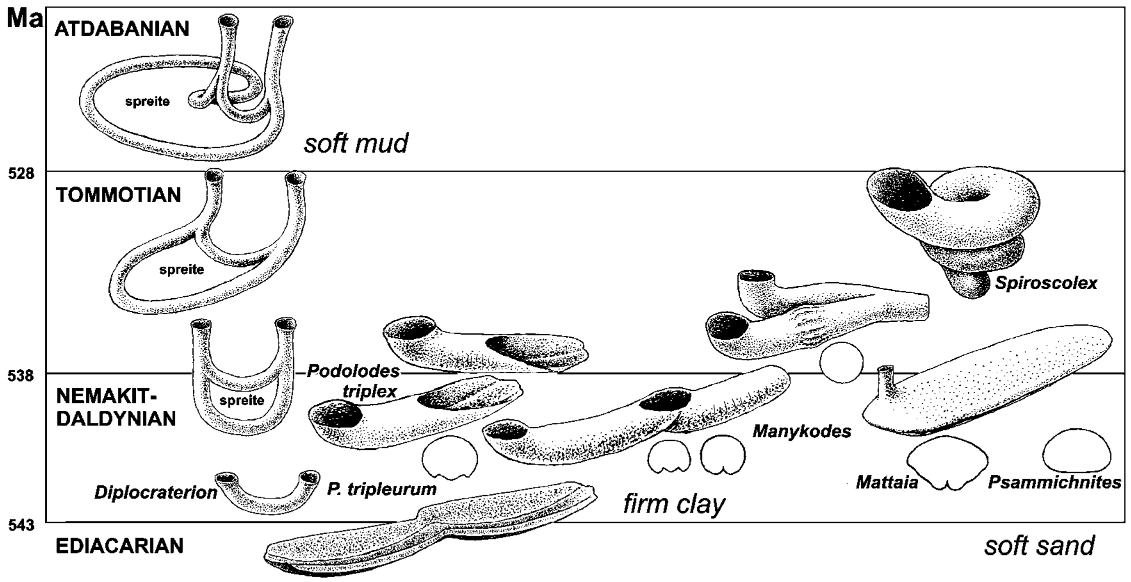

FIGURE 8. Time and sediment substrate distribution of the first known occurrences of animal trace fossils discussed in the text. Drawings show shape of burrows; two successive burrows in cases of serial burrowing. Note that various calcareous tubes of uncertain affinities are known already from the late Ediacarian. The beginning of the Nemakit–Daldynian is marked by the appearance of triradial tubes of the metazoan anabaritids; the oldest molluscs are known from the middle of this unit, and close to its end diverse skeletonized animal communities existed, with the oldest gastropods and numerous phosphatic problematica.

isms (Conway Morris 1977) suggests that they were producers of the Siberian spreite structures.

Evolution of the Earliest Cambrian Infaunal Animals

Some of the trace fossils from the Cambrian are so indifferent structurally that they could be works of various unrelated animals. Taxonomic identification of their producers is hardly possible. However, in several cases, the behavior of the trace maker is so specific that it may be more taxonomically informative than the animal's fossilized remains, if found.

There is no doubt about the polarity of evolutionary change in behavior of the earliest Cambrian mud burrowers (Fig. 8). Until the end of the Vendian (Ediacarian), only traces produced by few-millimeters-wide organisms moving over the sediment surface are known (e.g., Glaessner 1969; Crimes and Zhiwen 1986; Narbonne and Aitken 1990; Vidal et al. 1994; Droser et al. 2000a; Jensen 2003), the oldest of them being chains of pellets dated as more than 595 Ma (Brasier and McIlroy 1998) but their organic origin is in question (Brasier and Shields 2000). Seilacher (1999) suggested that the Vendian traces were left by ''undermat miners'' but this idea does not fit the evidence from the Vendian of the White Sea where imprints, however rare, originated at the mat surface during prolonged episodes of non-deposition (Dzik 2003).

Close to the end of the Vendian (early Nemakit-Daldynian) animals emerged that were able to hide partially the middle part of their bodies in the sediment while not moving (*Podolodes* gen. n.; see Appendix 2). They removed sediment from below mechanically, probably because penetrating it by a hydraulic action was difficult. The animal changed its position periodically, digging new resting traces in linear series (Jensen and Mens 2001). The depth of penetration increased in their relatives from the Vendian–Cambrian transition (middle Nemakit–Daldynian) and they started to use a bulbous anterior part of the body to penetrate at least in a softer sediment. The originally lateral belts of hypothetical appendages moved admedially to give the trail a bilobed appearance in deeper-digging Nemakit–Daldynian forms.

As suggested by Droser et al. (2000a) and supported by observations at Mattaia, the earliest Cambrian clayish sediment surface was relatively firm and its penetration required much energy. This is probably why the earliest infaunal organisms dug series of chambers from where they searched for food. Continuous locomotion under the sediment surface was easier in soft sand and this opportunity was explored by the lineage of large worms making continuous horizontal galleries (*Mattaia* gen. n.). Their permanently exposed proboscis explored the sediment surface. In even more advanced forms the proboscis rhythmically moved from one side of the trail to another (Seilacher 1995; McIlroy and Heys 1997). Probably the final step of this process was to reduce appendages and to rely completely on peristaltic locomotion and sediment transportation (*Psammichnites-Plagiogmus*).

Increased hydraulic efficiency of prosoma armed with hooks enabled the emergence of worms burrowing cylindrical chambers from under the sediment surface (*Manykodes* gen. n.). The chamber wall was impregnated with mucus. If this evolutionary interpretation is correct, this change in behavior marks the origin of infaunal priapulid worms from those crawling at the sediment surface with ventral appendages. The helical empty burrows of *Spiroscolex spiralis* (= *Gyrolithes polonicus*) (Jensen 1997; Droser et al. 2002b) from the earliest Cambrian may have been made by related animals.

Yet another lineage originated, probably from peristaltically digging roundworms increasing the depth of their U-shaped burrows (*Diplocraterion*). These were relatively small animals of a couple of millimeters in diameter; they were apparently cylindrical but no additional anatomical information can be extracted from the morphology of their burrows. They evolved toward infaunal feeding during the Tommotian, being initially adapted to searching for food in soft sediment (or softened by bioturbation).

This sequence of evolutionary events of behavioral diversification is evidently an expression of a more general trend. During the early Paleozoic surficial, horizontal exploitation of the benthic food resources was replaced by vertically oriented bioturbation (Hagadorn and Bottjer 1999). The problem remains whether this was a result of opening a new environment as a result of destruction of microbial mats by grazers, or rather bioturbators themselves destroyed the mats and liquidized the bottom clay surface. The latter is suggested by the disappearance of the Cambrian firm-ground assemblage of trace fossils (Droser et al. 2000a), which, beginning from the Ordovician, has its analogy only in the assemblages of borings in limy substrate.

The Verdun Syndrome: Predation as the Cause of Infaunal Life and Skeletogenesis

It is generally assumed that it was search for food that forced early animals to start infaunal life (e.g., Seilacher 1999) and that the hydraulic burrowing behavior was crucial to developing the basic metazoan body plan (Clark 1964, 1979). The above-presented evidence from the fossil record contradicts both these concepts. The major metazoan body plans had emerged already in the Ediacarian (e.g., Dzik 2003), whatever was the background of the process (e.g., Dewel et al. 2001; Valentine 2002). McIlroy and Heys (1997) have addressed the paradox (in reference to *Plagiogmus arcuatus*): ''Why an animal should waste energy by burrowing when the organic detritus that it seeks to exploit is on the sediment surface?'' One of the alternative interpretations they offered is that this was a peculiar (and rather expensive) way of anchoring in a high-energy environment; the other was that this resulted from predation pressure. That predation was a problem even to infaunal Early Cambrian organisms was elegantly shown by Jensen (1990) in his documentation of trilobite-priapulid encounters.

The Kessyusa Formation is the oldest occurrence of taxonomically identifiable skeletal fossils in Siberia, and probably also in the world. In the section at Mattaia, horizons with winnowed concretions in glauconite-quartz sand matrix within the dark laminated mudstone unit 2 yielded numerous calcareous tubes. In acid-resistant residue, phosphatic internal molds of their apices with swollen tips show that these are laterally compressed conchs of hyolith-like molluscs *Ladatheca annae* (cf. Dzik 1994). Other tubular fossils (enigmatic *Conotheca*, probably anabaritids *Spinulitheca*; see Bengtson et al. 1990; Dzik 1994) and phosphatized coprolites, helically wound or meandering, are associated. In the section of the Kessyusa Formation along the Olenek River, limestone intercalations occur in the middle of unit 3 and yielded phosphatized internal molds of the oldest planispiral conchs of the bellerophontid molluscs *Latouchella*, trochospiral conchs of the probable sinistral gastropod *Barskovia*, and the low-conical probable monoplacophoran *Purella* with a caplike embryonic conch (Valkov 1987; Vodanyuk 1987; Missarzhevsky 1989; Khomentovsky and Karlova 1993). No taxonomically identifiable skeletal fossils occur in the calcareous sandstone with oolites of the upper part of unit 3, but it is dated as the earliest Tommotian (Khomentovsky and Karlova 1993), which elsewhere yields the oldest dextrally coiled gastropods *Aldanella* and diverse assemblage of problematic halkieriids and tommotiids. The red marly limestone of the Tommotian-age Erkeket Formation overlies the sandstone with a sedimentary discontinuity, its cavities being filled with phosphatized skeletal fossil (including abundant gastropods *Aldanella*).

Various explanations have been offered for the Cambrian ‘‘explosion’’ of skeletonized organisms, among others that it was triggered by lateral gene transfer or sudden use of earlier silenced biomineralization mechanisms (Kirschvink and Hagadorn 2000). However, a protective skeleton was not necessarily produced in the earliest Cambrian by the protected organism itself. Especially significant seems to be the appearance of the worms *Onuphionella* at that time, purposely collecting mica flakes from surroundings to built tubes (Areń and Lendzion 1978; Signor and McMenamin 1988). This shows not only the emerging need to construct skeletal structures in any possible way but also high behavioral abilities of the earliest Cambrian animals. It appears that they were not only able to recognize food at the sediment surface and collect it with a proboscis (as was the case with all those burrowers discussed above) but also to find the necessary building materials. In fact, this suggests also that these organisms were related to each other and had a similar anatomy, not only behavior (burrows of *Spiroscolex* are lined with mica flakes, too [Jensen 1997)]. The synchroneity of so variously achieved skeletonization with the origin of the infaunal mode of life suggests the same cause. It seems likely that the selective pressure resulted from the origin of predatory organisms feeding on large metazoans. This was the initiation of an arms race, giving the choice to either shield behind a strong mineralized skeleton or to hide in the sediment.

Exploitation of food resources in the sediment probably required improvement of digestive functions and developed somewhat later. Perhaps also the lack of oxygen in deeper layers of the organic-rich sediment was an obstacle and this required the evolutionary invention of efficient oxygen transport, although anaerobic metabolism is widely used by digging worms (Portner 2002).

Eventually, the expansion of infaunal life destroyed first the widespread and vast cyanobacterial mats in shallow regions of the sea and, gradually, the small shelly fossils’ environment in deeper regions (Dzik 1994).

Acknowledgments

The expedition to the Khorbusuonka River section in 2001 (guided by Andrey Yu. Ivantsov from the Paleontological Institute, Moscow) was financed with research grant 6 PO4D 010 13 from the Polish Committee of Scientific Research. The opportunity to take part in the Paleontological Institute, Moscow expedition to the Lena River section in 1987 I owe to A. Y. Rozanov. I am thankful to S. Orłowski and W. M. Palij for introducing me to their collections of Cambrian trace fossils. My special thanks are to S. Jensen for the constructive criticism in his review and for understanding my point also in the cases where his opinion differs.

Literature Cited

Adrianov, A. B., and V. V. Malakhov. 1996. Priapulidy (Priapulida) stroyenie, razvitie, filogenia i sistema. KMK Scientific Press, Moscow.

Areń, B., and K. Lendzion. 1978. Charakterystyka stratygraficzno-litologiczna wendu i kambru dolnego. Prace Instytutu Geologicznego 90:7–50.

Ayala, F. J., A. Rzhetsky, and F. J. Ayala. 1998. Origin of the metazoan phyla: molecular clocks confirm paleontological estimates. Proceedings of the National Academy of Sciences USA 95:606–611.

Bengtson, S., S. Conway Morris, B. J. Cooper, P. A. Jell, and B. N. Runnegar. 1990. Early Cambrian fossils from South Australia. Memoirs of the Association of Australasian Palaeontologists 9:1–364.

Bowring, S. A., J. P. Grotzinger, C. E. Isachsen, A. H. Knoll, S. M. Pelechaty, and P. Kolosov. 1993. Calibrating rates of early Cambrian evolution. Science 261:1293–1298.

Brasier, M. D., and D. McIlroy. 1998. *Neonereites uniserialis* from c. 600 Ma year old rocks in western Scotland and the emergence of animals. Journal of the Geological Society, London 155:5–12.

Brasier, M. D., and G. Shields. 2000. Neoproterozoic chemostratigraphy and correlation of the Port Askaig glaciation, Dalradian Supergroup of Scotland. Journal of the Geological Society, London 157:909–914.

Buatois, L. A., and M. G. Mángano. 1993. The ichnotaxonomic status of *Plangtichnus* and *Treptichnus*. Ichnos 2:217–224.

Clark, R. B. 1964. Dynamics in metazoan evolution: the origin of the coelom and segments. Clarendon, Oxford.

———. 1979. Radiation of the Metazoa. *In* M. R. House, ed. The origin of major invertebrate groups. Systematic Association Special Volume 12:55–101. Academic Press, London.

Conway Morris, S. 1977. Fossil priapulid worms. Special Papers in Palaeontology 20:1–97.

———. 1997. Molecular clocks: defusing the Cambrian ''explosion''? Current Biology 7:R71–R74.

Crimes, T. P., and J. Zhiwen. 1986. Trace fossils from the Precambrian-Cambrian boundary candidate at Meishucun, Jinning, Yunnan, China. Geological Magazine 123:641–649.

Dewel, R. A., W. C. Dewel, and F. K. McKinney. 2001. Diversification of the Metazoa: Ediacarans, colonies, and the origin of eumetazoan complexity by nested modularity. Historical Biology 15:93–118.

Droser, M. L., S. Jensen, and J. G. Gehling 2000a. Trace fossils and substrates of the terminal Proterozoic-Cambrian transition: implications for the record of early bilaterians and sediment mixing. Proceedings of the National Academy of Sciences USA 99:12572–12576.

Droser, M. L., S. Jensen, J. G. Gehling, P. M. Myrow, and G. M. Narbonne. 2002b. Lowermost Cambrian ichnofabrics from the Chapel Island Formation, Newfoundland: implications for Cambrian substrates. Palaios 17:3–15.

Dzik, J. 1991. Is fossil evidence consistent with traditional views of the early Metazoan phylogeny? Pp. 47–56 *in* S. Conway Morris and A. Simonetta, eds. The early evolution of metazoa and significance of problematic taxa. Cambridge University Press, Cambridge.

———. 1994. Evolution of 'small shelly fossils' assemblages of the early Paleozoic. Acta Palaeontologica Polonica 39:3,247–313.

———. 2003. Anatomical information content in the Ediacaran fossils and their possible zoological affinities. Integrative and Comparative Biology 43:114–126.

Dzik, J., Y.-l. Zhao, and M.-y. Zhu. 1997. Mode of life of the Middle Cambrian eldonioid lophophorate *Rotadiscus*. Palaeontology 40:385–396.

Fedonkin, M. A. 1985. Paleoikhnologia vendskich Metazoa. Pp. 112–117 *in* B. S. Sokolov and A. B. Ivanovsky, eds. Vendskaya Sistema. Istoriko-geologicheskoye i paleontologicheskoye obosnovanie. 1 Paleontologia. Nauka, Moscow.

Gehling, J. G. 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. Palaios 14:40–57.

Gehling, J. G., S. Jensen, M. L. Droser, P. M. Myrow, and G. Narbonne. 2001. Burrowing below the basal GSSP, Newfoundland. Geological Magazine 138:213–218.

Geyer, G., and A. Uchman. 1995. Ichnofossil assemblages from the Nama Group (Neoproterozoic-Lower Cambrian) in Namibia and the Proterozoic-Cambrian boundary problem revisited. Beringeria Special Issue 2:175–202.

Glaessner, M. 1969. Trace fossils from the Precambrian and basal Cambrian. Lethaia 2:369–393.

Gureev, Y. A. 1986. O perpektivach paleoikhnologicheskogo metoda v stratigrafii. Tektonika i Stratigrafia 27:42–47.

Hagadorn, J. W., and D. J. Bottjer. 1999. Restriction of a late Neoproterozoic biotope: suspect-microbial structures and trace fossils at the Vendian-Cambrian transition. Palaios 14:73–85.

Hagadorn, J. W., S. A. Schellenberg, and D. J. Bottjer. 2000. Paleoecology of a large Early Cambrian bioturbator. Lethaia 33: 42–156.

Hofmann, H. J., and I. M. Patel. 1989. Trace fossils from the type 'Etcheminian Series' (Lower Cambrian Ratcliffe Brook Formation), Saint John area, New Brunswick, Canada. Geological Magazine 126:139–157.

Hou, X.-G., and W.-G. Sun. 1988. Discovery of Chengjiang fauna at Meishucun, Jinning, Yunnan. Acta Palaeontologica Sinica 27:1–9.

Huang, D.-y., J. Vannier, J.-Y. Chen. 2004. Anatomy and lifestyles of Early Cambrian priapulid worms exemplified by *Corynetis* and *Anningvermis* from the Maotianshan Shale (SW China). Lethaia 37:21–33.

International Commission on Zoological Nomenclature. 1999. International code of zoological nomenclature, 4th ed. Natural History Museum, London.

Jaeger, H., and A. Martinsson. 1980. The Early Cambrian trace *Plagiogmus* in its type area. Geologiska Föreningens i Stockholm Förhandlingar 102:117–126.

Jensen, S. 1990. Predation by early Cambrian trilobites on infaunal worms—evidence from the Swedish Mickwitzia Sandstone. Lethaia 23:29–42.

———. 1997. Trace fossils from the Lower Cambrian Mickwitzia sandstone, south-central Sweden. Fossils and Strata 42:1–110.

———. 2003. The Proterozoic and earliest Cambrian trace fossil record: patterns, problems and perspectives. Integrative and Comparative Biology 43:219–228.

Jensen, S., and S. W. F. Grant. 1998. Trace fossils from the Dividalen Group, northern Sweden: implications for Early Cambrian biostratigraphy of Baltica. Norsk Geologisk Tidsskrift 78:305–317.

Jensen, S., and K. Mens. 2001. Trace fossils *Didymaulichnus* cf. *tirasensis* and *Monomorphichnus* isp. from the Estonian Lower Cambrian, with a discussion on the early Cambrian ichnocoenoses of Baltica. Proceedings of the Estonian Academy of Sciences, Geology 50:75–85.

Jensen, S., J. G. Gehling, and M. Droser. 1998. Ediacara-type fossils in Cambrian sediments. Nature 393:567–569.

Jensen, S., B. Z. Saylor, J. G. Gehling, and G. J. B. Germs. 2000. Complex trace fossils from the terminal Proterozoic of Namibia. Geology 28:143–146.

Jones, D., and I. Thompson. 1977. Echiura from the Pennsylvanian Essex Fauna of northern Illinois. Lethaia 10:317–325.

Karlova, G. A., and S. A. Vodanjuk. 1985. Novyie dannyie o perekhodnych k kembriu otlozheniach basseina r. Khorbusuonki (olenekskoie podniatie). Pp. 3–13 *in* V. V. Khomentovsky, A. A. Terleyev, and S. S. Bragin, eds. Stratigrafia pozdniego dokemebria i ranniego paleozoja Sibiri. Vend i rifej. Institut Geologii i Geofiziki SOAN SSSR, Novosibirsk.

Khomentovsky, V. V., and G. A. Karlova. 1993. Biostratigraphy of the Vendian-Cambrian beds and the lower Cambrian boundary in Siberia. Geological Magazine 130:29–45.

Kirschvink, J. L., and J. W. Hagadorn. 2000. A grand unified theory of biomineralization. Pp. 139–149 *in* E. Baeurlein, ed. Biomineralization: from biology to biotechnology and medical application. Wiley-CCH, Weinheim.

Książkiewicz, M. 1977. Trace fossils in the flysch of the Polish Carpathians. Palaeontologia Polonica 36:1–208.

Maples, C. G., and A. W. Archer. 1987. Redescription of early Pennsylvanian trace-fossil holotypes from the nonmarine Hindostan Whetstone beds of Indiana. Journal of Paleontology 61:890–897.

McIlroy, D., and G. R. Heys. 1997. Palaeobiological significance of *Plagiogmus arcuatus* from the lower Cambrian of central Australia. Alcheringa 21:167–178.

McIlroy, D., and G. A. Logan. 1999. The impact of bioturbation on infaunal ecology and evolution during the Proterozoic-Cambrian transition. Palaios 14:58–72.

Missarzhevsky, V. V. 1989. Drevneyshije skeletnyie okamenelosti i stratigrafia pogranichnykh tolshch dokembria i kembria. Trudy Geologicheskogo Instituta AN SSSR 443:1–237.

Narbonne, G. M., and J. D. Aitken. 1990. Ediacaran fossils from the Sekwi Brook area, Mackenzie Mountains, northwestern Canada. Palaeontology 33:945–980.

Orłowski, S., and A. Żylińska. 1996. Non-arthropod burrows from the Middle and Late Cambrian of the Holy Cross Mountains, Poland. Acta Palaeontologia Polonica 41:385–409.

Osgood, R. G., Jr. 1970. Trace fossils from the Cincinnati area. Palaeontographica Americana 6:281–444.

Pacześna, J. 1996. The Vendian and Cambrian ichnocoenoses from the Polish part of the East-European Platform. Prace Państwowego Instytutu Geologicznego 152:1–77.

Palij, W. M. 1974. Podvijny slidy (bilobity) u vidkladach baltijskoj serii Pridniestrovia. Dopovidi AN USSR, seria B, 1:499–503.

———. 1976. Ostatki bezskeletnoj fauny i sledy ziznedeyatelnosti iz otlozhenii verkhnego dokembria i nizhnego kembria Podolii. Pp. 63–77 *in* P. L. Shulga, ed. Paleontologia i stratigrafia dokembria i nizhnego paleozoia jugo-zapada Vostochno-Evropejskoy Platformy. Naukova Dumka, Kiev.

———. 1983. Soft-bodied Metazoa and animal trace fossils in the Vendian and early Cambrian. Pp. 56–93 *in* A. Urbanek and A.Y. Rozanov, eds. Upper Precambrian and Cambrian Palaeontology of the East European Platform. Wydawnictwa Geologiczne, Warsaw.

Portner, H. O. 2002. Environmental and functional limits to muscular exercise and body size in marine invertebrate athletes. Comparative Biochemistry and Physiology A 133:303–321.

Seilacher, A. 1955. Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan). V. Spuren und Fazies im Unterkambrium. Abhandlungen der mathematisch-naturwissenschaftlichen Klasse der Akademie der Wissenschaften und der Literatur in Mainz 1955:372–399.

———. 1995. Fossile Kunst. Albumblätter der Erdgeschichte. Goldschneck, Korb.

———. 1999. Biomate-related lifestyles in the Precambrian. Palaios 14:86–93.

Seilacher, A., and C. Hemleben. 1966. Beiträge zur Sedimentation und Fossilführung de Hunsrückschiefers, Teil 14. Spurengfauna und Bildungstiefe der Hunsrückschiefer (Unterdevon). Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden 94:40–53.

Signor, P. W., and M. A. S. McMenamin. 1988. The Early Cambrian worm tube *Onuphionella* from California and Nevada. Journal of Paleontology 62:233–240.

Uchman, A., R. G. Bromley, and S. Leszczyński. 1998. Ichnogenus *Treptichnus* in Eocene flysch, Carpathians, Poland: taxonomy and preservation. Ichnos 5:269–275.

Valentine, J. W. 2002. Prelude to the Cambrian explosion. Annual Review of Earth and Planetary Sciences 30:285–306.

Valkov, A. K. 1987. Biostratigrafia nizhnego kembria vostoka Sibirskoi platformy. Yudomo-Olenekskij region. Nauka, Moscow.

Velikanov, V. A., ed. 1990. The Vendian of Podolia. Excursion guide for III International Symposium on Cambrian System and Vendian/Cambrian boundary. Institute of Geological Sciences, Kiev.

Velikanov, V. A., E. A. Aseeva, and M. A. Fedonkin. 1983. Vend Ukrainy. Naukova dumka, Kiev.

Vidal, G., S. Jensen, and T. Palacios. 1994. Neoproterozoic (Vendian) ichnofossils from Lower Alcudian strata in central Spain. Geological Magazine 131:169–179.

Vodanyuk, S. A. 1987. Problemnyie voprosy stratigrafii vendskich otlozheni basseina r. Khorbusuonki (olenekskoie podniatie). Pp. 3–17 *in* V. V. Khomentovsky, ed. Pozdnij dokemebrij i rannij paleozoj Sibiri. Sibirskaya platforma i jejo juzhnoye skladchatoye obramlenie. Institut Geologii i Geofiziki SOAN SSSR, Novosibirsk.

Wray, G. A., J. S. Levinton, and L. H. Shapiro. 1996. Molecular evidence for deep Pre-Cambrian divergences among metazoan phyla. Science 274:568–573.

Yochelson., E. L., and M. A. Fedonkin. 1993. Paleobiology of *Climactichnites*, an enigmatic Late Cambrian fossil. Smithsonian Contributions to Paleobiology 74:1–74.

Young, F. G. 1972. Early Cambrian and older trace fossils from the southern Cordillera of Canada. Canadian Journal of Earth Sciences 9:1–17.

Zhuravlev, A. Y. 1995. Preliminary suggestions on the global Early Cambrian zonation. Beringeria Special Issue 2:147–160.

Appendix 1

Comments on Taxonomic Nomenclature of Fossilized Works of Animals

As long as one pretends to do science while classifying trace fossils, the two fundamental requirements of scientific methodology have to be obeyed: parsimony and testability. Parsimony requires that no being be introduced into considerations unless this is absolutely necessary. But is it necessary to name all traces of animal activity with Linnean binomens? The obvious answer is No. In most cases these are empty names of no heuristic value and it would be more honest to replace them with vernacular names expressing what we actually are dealing with (for instance: ''a trail of a worm on the sediment surface''). Testability (or rather falsifiability) requires that it has to be possible to confront deductions derived from a scientific concept with empirical evidence to support or refute it. This is the case with the biological species concept that claims some specific properties of gene flow within and between the populations, and it is expected that these genetic phenomena have their expression in morphology of fossils. For higher-rank taxa in biology it is required that they share common evolutionary ancestry. This kind of empirical testing is not possible in case of, say, species of *Gordia* or *Cruziana*, representing just similar marks on fossilized sand left by unrelated organisms of Paleozoic to Tertiary ages that use not similar and not homologous anatomical structures in various ways. I see no purpose to mislead the reader with false use of the Linnean nomenclature, which now has a clear connotation with modern biological methodology. I refuse thus to accept the typological ''ichnotaxonomy,'' despite its wide use in geology and the great value of trace fossils as a source of information important to evolutionary biology.

Following the opportunity offered by Articles 10.3 and 42.2.1 of the International Code of Zoological Nomenclature (1999), the taxa based on fossilized works of animals (trace fossils) are here used as referring to the animals that formed them, even if they do not compete in priority with names established on skeletal fossils (Article 23.7.3). Species of trace fossils are understood here in the same way as skeletal paleontological species. Both are hardly anything more than clusters of biological species, but both are assumed to represent monophyletic (or paraphyletic) taxa. Monophyly of a taxon can be tested in paleontology by proving (or rejecting) its continuity in time and space. To do this, populations (fossil samples) of different ages or geographic locations have to be arranged into a series of morphologic and/or behavioral identity or gradation. Behavior of an extinct organism producing trace fossils need not be of less value than morphology in approximating the organism's genome, which in principle is the ultimate basis of its classification in a species.

Actually, in many cases the distinction between skeletal and trace fossils is highly questionable. All Ediacaran fossils are imprints of the body with no skeleton preserved, whereas the skeleton of graptolite colonies is an elaborate work of organisms, built of a collagenous secretion of their preoral discs (whereas the rare ''true'' fossils of pyritized zooids are of little taxonomic value). In any case the content of biologically meaningful information is far more important than formal rules of ''ichnotaxonomy.'' This is why I prefer to follow the spirit of biological taxonomy rather than the geological tradition of naming sedimentary structures with Linnean names.

Appendix 2

Description of New Taxa

Class Priapula Delage and Herouard, 1897
Order Miskoida Walcott, 1911

Comment.—The body appearance of priapulid worms is usually cylindrical, with external expressions of dorsoventral axis rather difficult to discern (e.g., Adrianov and Malakhov 1996). At least two extinct priapulids show presence of ventral two rows of appendages: *Cricocosmia jinningensis* from the late Early Cambrian Chengjiang fauna of Yunnan (Hou and Sun 1988) and *Louisella pedunculata* from the Middle Cambrian Burgess Shale of British Columbia, the latter being also dorsoventrally depressed (Conway Morris 1977). They deserve separation at ordinal rank, so it is more than likely that some of the Early Cambrian burrows were dug by anatomically similar worms.

Family? Miskoiidae Walcott, 1911
Genus *Podolodes* new

Type Species.—*Treptichnus triplex* Palij, 1976, from the Chmielnicki Formation, borehole in Kamieniec Podolski, Ukraine.

Derivation of Name.—From Podolia, Ukraine, where the type species of the genus was first reported.

Diagnosis.—Animals producing series of short burrows in mud with cylindrical vertical openings and three-lobed lower surface; each burrow started in front of the preceding one or laterally to it from the sediment surface.

Comments.—The type horizon of *T. triplex* is within the subsurface Chmielnicki Formation but it occurs also in exposures in the same area on the Dnester River near the mouth of the Ternawa River. Also found at this locality, together with alternating burrows (Palij 1976: Pl. 24:4–5), are series of closely similar burrows arranged linearly (Palij 1976: Pl. 25:4). Closely similar traces occur in the basal Cambrian subsurface Mazowsze Formation of eastern Poland (Pacześna 1996) of the *Platysolenites* Zone.

Species Included.—*Podolodes tripleurum* (Geyer and Uchman 1995) and *P. triplex* (Palij 1976).

Family Mattaiidae new

Diagnosis.—Dorsoventrally depressed animals with vertical, permanently everted narrow proboscis adapted to probing the sediment surface.

Genera Included.—*Psammichnites* Torell, 1870; *Plagiogmus* Roedel, 1929 (for possible identity with *Psammichnites* see McIlroy and Heys 1997), and *Mattaia* gen. n.

Genus *Mattaia* new

Type Species.—*Didymaulichnus miettensis* Young, 1972, from the top of Miette Group in British Columbia.

Derivation of Name.—From Mattaia Creek, tributary of Khorbusuonka.

Diagnosis.—Animals burrowing wide horizontal galleries in sand; in its lower parts the sediment was mechanically removed and transported backward along a double furrow; the sediment above was hydraulically raised, cut vertically by a proboscis extending to the surface and collapsing behind the animal.

Comments.—Fedonkin (1985) classified traces of this kind from the Kessyusa Formation of the Olenek River in *Didymaulichnus*, as *D. meanderiformis*. Hofmann and Patel, 1989 questioned validity of the Fedonkin's (1985: pl. 24: 3–4) species and replaced it with *Taphrhelminthoida daylyi* allegedly because of incomplete description and lack of diagnosis, but there is a brief description sufficient to diagnose the species in the figure caption.

Both these proposals of generic affiliation are hard to accept from a biological point of view. The type species of *Taphrhelminthoida*, *T. convoluta* Książkiewicz, 1977, from the Eocene of the Carpathians shows neither the characteristic impregnation of the walls with clay and mucus nor a cross-section typical of the Cambrian forms (Książkiewicz 1977). Foraging in a meandering way obviously developed convergently in animals producing such trails. Zoological identity of the type species of *Didymaulichnus*, *D. lyelli* (Rouault, 1850) from the Ordovician of Portugal, with the earliest Cambrian specimens seems equally doubtful. These could have been produced by arthropods.

Species Included.—*Mattaia tirasenis* (Palij 1974), *M. miettensis* (Young 1972), and *M. meanderiformis* (Fedonkin, 1985).

Order Priapulida Shipley, 1896
Family? Corynetidae Huang, Vannier, and Chen, 2004
Genus *Manykodes* new

Type species.—*Treptichnus rectangularis* Orłowski and Żylińska, 1996, from the Klonówka Shale at Wiśniówka in the Holy Cross Mountains.

Derivation of Name.—From the Manykay Formation and Stage of the basal Cambrian, where the genus appears for the first time.

Diagnosis.—Probable priapulid worms burrowing series of cylindrical empty chambers in mud with walls strengthened with mucus; the burrowing started laterally from the preceding chamber to give a more or less regular zigzag pattern.

Comments.—Burrows of this kind are widely classified in *Phycodes*, the type species of which is *P. circinnatum* Richter, 1853, from the Ordovician of Germany. These are typical feeding traces, with each new burrow deepening the earlier made trace and transporting sediment from above (spreite structure).

Seilacher (1955: Fig. 4b) and Geyer and Uchman (1995) suggested that a spreite structure is represented also in the type material of *Phycodes pedum*, which is in the *Neobolus* Beds of Pakistan, located well within the trilobite Cambrian (Seilacher 1955). This would mean that the animal repeatedly moved its burrow to higher positions. To be preserved such structures require that the whole activity be in the same sediment bed (the case of *Teichichnus*), in which successive stages in formation of the burrow are preserved, or that the sandy sediment be transported by the animal from above. In the first case the tube could have been empty and the animal accommodated only its disposition in response to changes at surface caused by either sudden sedimentation or erosion. Even if these are truly locally developing spreite structures, *Phycodes pedum* differs from *P. circinnatum* in that its branches were added distally instead of emanating from a common area (Jensen and Grant 1998). The Pakistan *P. pedum* produced series of shallow burrows rather irregular in both size and shape, arranged obliquely to each other, mostly to one side of the branch.

Geyer and Uchman (1995) transferred *P. pedum* to *Trichophycus*, of which the late Ordovician type species, *T. lanosus* Miller and Dyer, 1878, is a large burrow several centimeters wide (Osgood 1970) with hardly any correspondence to the Cambrian structures.

Permanently open branching burrows are usually classified as *Treptichnus* and such taxonomic affiliation was proposed by Jensen (1997; Jensen and Grant 1998; Jensen et al. 1998). The type species of *Treptichnus*, *T. bifurcus* Miller, 1889, was originally described on the basis of late Namurian material from the continental strata of Illinois (Maples and Archer 1987; Buatois and Mángano 1993). These are millimeter-wide semicylindrical depressions on the upper bedding plane, probably not produced by a deposit-feeding trace-maker (Uchman et al. 1998). Even if they truly extended upwards with tubular peristomes, as was the case with similar structures from the relatively deep-water marine Early Devonian Hunsrück slates (Seilacher and Hemleben 1966), there is no doubt that these were produced by different organisms.

Species Included.—*Manykodes pedum* (Seilacher 1955) and *M. rectangulare* (Orłowski and Żylińska 1996).