# The Verdun Syndrome: simultaneous origin of protective armour and infaunal shelters at the Precambrian–Cambrian transition

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**Abstract:** All of the structurally identifiable latest Ediacaran and earliest Cambrian infaunal trace fossils represent shelters of animals feeding above the sediment surface. It is the case with the most complete and oldest radiometrically dated Precambrian–Cambrian transition strata along the Khorbusuonka River in northern Siberia, in the basal Cambrian succession at Meishucun in southern China, richest in small shelly fossils, as well as in the type succession of the Vendian in Podolia, Ukraine. The oldest traces of feeding within the mud are known from no earlier than the late Tommotian of Siberia, Mongolia, Sweden, and Poland. This suggests that the invention of hydraulic mechanisms of sediment penetration was enforced by predation, not by trophic needs. Various ways to protect the body by secretion of a mineral skeleton or building tubes by collected mineral grains were developed by other animals at the same time. Predation may thus appear to be the triggering mechanism for the 'Cambrian explosion'. Subsequent increase in the depth of bioturbation resulted in a profound change of taphonomic conditions, artificially enhancing the effects of evolution.

There are two primary sources of evidence on the Precambrian–Cambrian evolution of marine faunas: the 'Ediacaran biota' of imprints of soft-bodied organisms in sandstone facies and the 'small shelly fossils' assemblages of mostly secondarily phosphatized remains of mineral skeletons in limestone facies. Owing to recent progress in understanding the taphonomy of the Ediacaran fossils, significant anatomical data has rapidly emerged from the long-known fossil collections. Imprints of dorsal surfaces of decaying bodies, fixed by early diagenetic iron sulphide cementation of soft sand ('Ediacaran death masks'; of Gehling (1999)); may offer information on the distribution and mechanical properties of the internal organs (Dzik 2003). Impressions of animal bodies passively or actively settling on the surface of a microbial mat ('Shroud of Ediacara'; of Dzik (2003)) inform about the external morphology of Ediacaran animals. Among the minute phosphatic and secondarily phosphatized fossils, easy to extract from limestone samples with organic acids and frequently numerous, there are not only elements of the skeletal armour (scleritomes), but also phosphatized organic tissues or even whole embryos (e.g. Bengtson & Zhao 1997).

These highly valuable sources of palaeontological information have their limitations, however. Early diagenetic phosphatization was a rare phenomenon, except for the Early Cambrian, and gradually disappeared during the early Palaeozoic, probably the result of increased bioturbation depth in pelagic sediments (Dzik 1994). Fossilization of entirely soft bodies, not easily escaping scavengers and bacterial decay, is even less likely. After their Ediacaran abundance, such fossils became extremely rare. In the Ediacaran White Sea locality Zimnie Gory in northern Russia, the Devonian Bundenbach slates of the Hunsrück Mountains in Germany and the Jurassic Solnhofen lithographic limestone of Bavaria, 'death tracks' occur, represented by short (frequently spiral) trace fossils with the carcass of the animal at the end, apparently thrown into a toxic environment. These were thus extreme environments, in the Ediacaran time supporting only bizarre, and probably chemoautotrophic organisms in place (Dzik 2003). Even if the stratigraphic ranges of the Ediacaran biota and small shelly fossils may partially overlap, there is a wide gap in our knowledge of Precambrian–Cambrian organisms in between these two taphonomic windows. The gap exists not only in their time distribution, but also in a range of less unusual environments.

This gap can be filled partially with evidence offered by traces organisms left in their activities, where their bodies had no chance to fossilize. Much data on the latest Precambrian and earliest Cambrian trace fossils has accumulated, but the main difficulty in interpreting this data results

from their lack of precise dating. The situation has improved significantly with the acquisition of diverse and unusually informative trace fossil assemblages from the Mattaia Creek section at Khorbusuonka in northern Siberia (Dzik 2005). These occur primarily below the occurrence of the abundant *Manykodes* (=‘*Phycodes*’) *pedum*, the appearance of which defines the base of the Cambrian (although it probably also occurs somewhat below in the stratotype section of Newfoundland; Gehling *et al.* 2001), and from above a radiometrically dated volcanic breccia (Bowring *et al.* 1993). All are traces of infaunal activities of animals penetrating the sediment but feeding above it. Their burrows were, thus, protective shelters.

The first skeletal remains of a variety of organisms occur in the same rock unit (Khomentovsky & Karlova 1993), as well as in coeval strata elsewhere. Thus, it is likely that predation forced the latest Ediacaran animals to either seek shelter under the sediment surface or protect themselves with mineral skeletons (‘the Verdun Syndrome’; Dzik 2005). Such explanation of the sudden emergence of skeletonized animals at the beginning of the Cambrian was first proposed by Evans (1912).

In the present paper this idea is developed further, with a more specific presentation of the probable anatomy of the earliest producers of infaunal trace fossils. Additional evidence on the succession of specific modes of infaunal penetration, as reflected by trace fossils from Podolia, Ukraine, and the Meishucun locality in Yunnan, China is also presented.

## The late Ediacaran infaunal trace makers

The Olenek River region in polar Siberia is among the few sites in the world where the Precambrian–Cambrian transition is documented by radiometric dating (Bowring *et al.* 1993), a stable isotope record (Pelechaty *et al.* 1996; Kouchinsky *et al.* 2001), Ediacaran biotas (Fedonkin 1985), skeletal remains (Khomentovsky & Karlova 1993), and trace fossils (Fedonkin 1985). As in fossiliferous successions elsewhere, traces of infaunal activity are missing in strata with Ediacaran fossils in Siberia. Although Seilacher (1999) suggested that most Ediacaran trace fossils makers fed below the microbial mat, this was falsified by the discovery of intact mats in the Zimnie Gory section (Dzik 2003). Both body and trace fossils occur there on the upper surface of the mat. Only shallow surface burrows are known from deposits of such age elsewhere (Jensen 1995, 2003; Jensen *et al.* 2005). The oldest common traces of deep sediment penetration by worm-like animals have been recovered from the middle part of the Nemakit-Daldynian

(Manykayan) Kessyusa Formation in exposures near the mouth of the Mattaia Creek in the Khorbusuonka River section of the Olenek region.
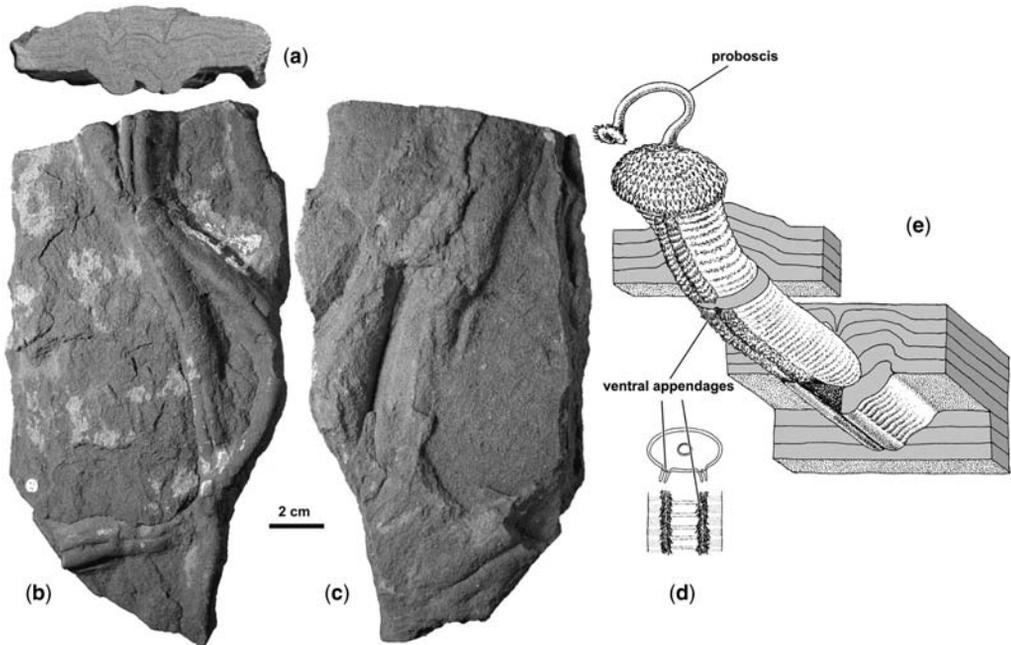
Many types of trace fossils occur in the Kessyusa Formation. Virtually all bedding plane trace fossils assemblages there are monospecific, and it is difficult to separate results of evolutionary change from changes controlled by purely ecological and environmental factors. Different species seem to be restricted to specific kinds of sediments. Narrow U-shaped, shallow burrows are found in thin layers of dark mudstone intercalated with siltstone and sandstone. The mud was apparently firm, because the burrows remained open during life of their makers, preserving a cylindrical cross-section (Dzik 2005). Synsedimentary faults offer proof that the light-grey quartz mud, in which serial cylindrical burrows of *Manykodes pedum* were dug, was firm in its whole bed volume already before deposition of the overlying pure sand layer. Also, the small trilobate burrows of *Podolodes* were produced in a relatively firm, fine-grained mud. In a softer, but coarser, sediment trace makers tended to dig deeper and make burrows circular in cross-section (Dzik 2005). The horizontal galleries of *Mattaia miettensis* were excavated in green glauconitic sand.

## Continuous horizontal galleries in sand

Probably the most bizarre Early Cambrian traces of infaunal activity are those produced by *Psammichnites*. As interpreted by Seilacher (1995) and McIlroy & Heys (1997; referred to as *Plagiogmus*), these were made by animals horizontally penetrating sandy sediment at a stable depth. Sediment stripes were left behind as a result of their movement with retrograde peristaltic wave. An organ exposed to the surface was cutting the sediment while the worm moved (Seilacher 1995; Jensen 1997) and collecting food together with the sediment from the surface.

Continuous burrows of *Mattaia miettensis* are similar to those of *Psammichnites*. They occur within the glauconitic sandstone beds in the Mattaia section, as well as in the coeval strata exposed along the Olenek River in the same region of northern Siberia (Fedonkin 1985). Owing to a clear delimitation of particular rock layers by clay-rich laminae (possibly representing remnants of microbial mats), the cross-section of the rock shows the internal structure of the trail (Fig. 1a).

The lack of deformation of layers below the trail indicates that it was not produced by action of any hydraulic pushing mechanism, but the sediment was simply abraded by the organism. The trace itself is filled with two bands of a homogenized sediment, laterally raised and depressed in the centre, where the bands are separated by a vertical fissure filled with clay (cf. Young 1972). The

**Fig. 1.** Reconstruction of *Mattaia miettensis* (Young 1972) from the latest Ediacaran Kessyusa formation at Mattaia Creek, inferred from the structure of its horizontal bilobed galleries. (**a**–**c**) Cross-section, lower, and upper surface of a glauconitic sandstone slab with two associated galleries. (**d**–**e**). Diagram showing the arrangement of sediment layers while the trail was made. The morphology of the inserted priapulid worm is based on the mid-Cambrian *Louisella* (data from Conway Morris 1977).

volume of these bands corresponds roughly with the volume of sediment removed from the channel. This means that all the material removed mechanically from below was transported behind. The smooth surface of the double ventral furrow at the lower surface of the gallery suggests that this was the route of the sediment transport. In well-preserved specimens the outer lateral bevel consists of series of transverse, slightly oblique folds suggesting that the animal was propelled by retrograde peristaltic wave (Dzik 2005).
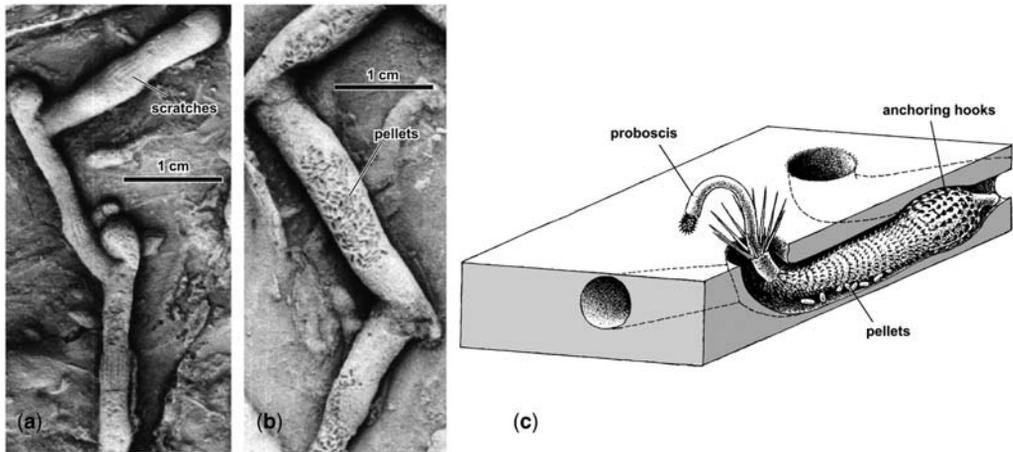
The clay laminae above the trail remained intact, but are folded and raised evidently as a result of a gentle hydraulic elevation of sand by the organism. Sediment above the trail first appears to have been pushed upwards to flow on both sides and then collapsed in the middle behind the animal. In the centre of the trail, the laminae dip down to form a vertical zone where the organ exposed to the surface was apparently cutting the sediment while the organism moved, collecting food together with the sediment from the surface (Hofmann & Patel 1989).

In the glauconitic sandstone of the Kessyusa Formation such galleries were dug in so sophisticated a manner that much anatomical information can be extracted from the observed deformations of the sediment layers. Although the inferred body organization is unlike any living animal and seems strange at a 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, an annulated body and, most interestingly, two ventral strips of minute appendages. Moreover, its cross-section was significantly depressed (Fig. 1d). Using *Louisella* as a prototype, not much transformation would be necessary to have the body organization necessary to produce all those trails (Fig. 1e).

### Cylindrical branching burrows

The earliest Cambrian clay-rich sediment surface was probably firm enough that empty burrows in it did not collapse without additional impregnation (Droser *et al.* 2002). These most likely permanently open shelters of a surface detritus feeder subsequently filled with sand (Jensen 1997). That they were empty during life of the producer is convincingly demonstrated by an aggregation of clay-rich faecal pellets at the bottom of burrows of related *Manykodes rectangulare* from the latest Cambrian of the Holy Cross Mountains, Poland (Fig. 2; Orłowski & Żylińska 1996).

**Fig. 2.** Biology of *Manykodes rectangulare* (Orłowski & Żylińska 1996) from the latest Cambrian Klonówka Shale at Wiśniówka in the Holy Cross Mountains, Poland, inferred from the morphology of its serial burrows. (**a**, **b**) Specimens showing scratches left by hooks covering the animal (a) and faecal pellets at the bottom of chamber (b). Such traces indicate that the burrow was originally empty and that the animal was deposit feeding above the sediment surface (originals of Orłowski & Żylińska 1996). (**c**) The Early Cambrian priapulid *Corynetis* (data from Huang *et al.* 2004) situated in the burrow of *Manykodes* to demonstrate the correspondence in distribution of scratch marks in the burrow and anchoring hooks in the animal's body.

These Late Cambrian trace fossils provide important information about the anatomy of their makers, which can be extrapolated also to older, earliest Cambrian species. Swollen parts of the burrow are marked with a ring of 15–20 longitudinal striae. Digging was apparently performed with hooks surrounding the body, such as those in the priapulid prosoma. Such swellings developed most probably when the animal retreated to the burrow, contracted and, as a result, widened its body.

The recently published information on the anatomy of the Early Cambrian priapulid *Corynetis* from the Chengjiang Fauna (Huang *et al.* 2004) suggests that it was not necessarily the prosoma, but rather anchoring hooks at the posterior part of the body which were responsible for scratches noted on the burrow wall. The long proboscis of *Corynetis* and the circle of long setae near its base suggest that this trace maker lived in a shelter with only its proboscis and protective setae extending from it, exactly what is suggested by the burrows of *Manykodes*, likely excavated by a related priapulid (Fig. 2c).
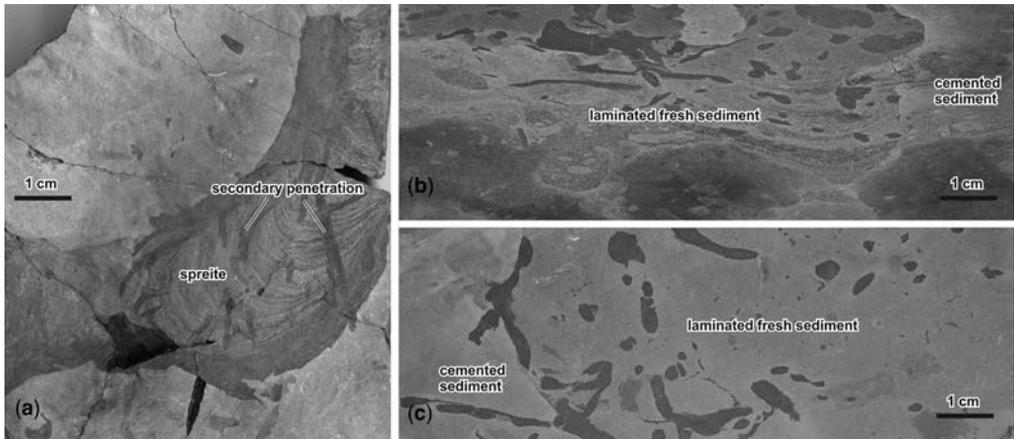
## First mud eaters

It is commonly argued that internal body cavities originated in connection with hydraulic locomotion and burrowing (Clark 1964) and that it was the search for food which forced early animals to begin infaunal life. If so, the oldest traces of peristaltic activities of the metazoans should be connected with their infaunal lifestyle. The fossil evidence does not support this.

The geologically oldest evidence of purposeful penetration of sediments for feeding are the horizontal 'rhizocorallium' spreite structures in a marly limestone facies of the late Tommotian (or early Atdabanian) in the Tiktirikteekh section on the Lena River near Jakutsk (Fig. 3a; Dzik 2005). Such feeding traces are known also from roughly coeval sandstones of northern Poland (Pacześna 1996) and Mongolia (Goldring & Jensen 1996). More sophisticated spreite structures, apparently produced by related organisms in the Atdabanian of Sweden, show a helicoidal organization (Jensen 1997).

In the late Tommotian marly limestone at the Zhurinsky Mys locality along the Lena River section, narrow, linear burrows of probable mud-eaters are restricted to the laminated sediment fill of earlier meandering furrows in the firm ground surfaces, 2–3 cm wide and deep. The already bioturbated sediment was probably softer and easier to penetrate (Fig. 3b–c). It may also have been richer in organic matter, the actual impetus for digging.

Even among the infaunal burrows of the Late Cambrian, those produced by organisms feeding above the sediment surface are the most common (e.g. Orłowski & Żylińska 1996). Not before the

**Fig. 3.** The oldest infaunal mud-eaters from the Tommotian to earliest Atdabanian Pestrotsvetnaya Formation of the Lena River section near Yakutsk. (**a**) Horizontal spreite structure ('rhizocorallium') from the Tiktirikteekh Locality, probably produced by a relative of *Diplocraterion*. Note secondary burrows penetrating the reworked sediment of the spreite. (**b**, **c**) Vertical and horizontal section across the sedimentary discontinuity surface at Zhurinsky Mys with minute horizontal burrows preferably penetrating the soft sediment filling the network of older and wider horizontal burrows.

Ordovician do feeding burrows dominate the trace fossils assemblages.

## Transitions between various forms of the Ediacaran infaunal behaviour

At first glance, the difference between the short, tri-lobed and depressed shallow burrows in firm clay, continuous galleries in sand and serial U-shaped cylindrical burrows in firm clay from the latest Ediacaran of the Olenek River region look like a fundamental and abrupt change. However, traces indicative of transitional behaviours are known from other Ediacaran–Cambrian localities.

### Intermediates between cylindrical and trilobed burrows

About 15 m above the base of a mudstone series exposed at Khorbusuonka near the mouth of the Mattaia Creek, the lower surface of glauconitic sandstone beds is densely covered with casts of generally shallow burrows in the underlying claystone (referred to *Podolodes tripleurum* in Dzik 2005). The dominant morphology is three-lobed. Similar traces are known also from Namibia (Geyer & Uchman 1995; Jensen *et al.* 2000) and Mongolia (Goldring & Jensen 1996). In profile view, the burrow casts are gently convex, with both ends smoothly disappearing at the bedding plane. Rarely, they are arranged in linear series. On sandstone slabs covering a more sand-rich clay, burrows have nearly circular cross-section. Similar burrows are known from the Chmielnicki Formation of Podolia, Ukraine, usually exhibiting a medial fissure along their ventral surface and arranged in linear series (Palij *et al.* 1983; Dzik 2005). Sometimes, the fissure splits, giving the ventral surface of the burrow a three-lobate appearance.

The similarity of the three-lobed burrows of *Podolodes* to a branching series of cylindrical burrows of *Manykodes* is highlighted by the plait-like arrangement of alternating series of shallow burrows of *Podolodes triplex* from Podolia (Palij *et al.* 1983; Dzik 2005) and eastern Poland (Pacześna 1996). In both the specimens from Khorbusuonka and Podolia there is a gradation from three-lobed shallow to fully submerged burrows with a round cross-section and a smooth or bilobed lower surface. They may alternate but may also be arranged linearly (Jensen & Mens 2001).

There is, thus, a gradation of morphologies of trace fossils from shallow U-shaped burrows with circular cross-section to even shallower burrows with a three-lobed ventral surface. Although the burrows do not offer much information about the detailed anatomy of their producers, some inferences can be attempted. Indistinct, transverse wrinkles in the central belt of the trace may reflect a peristaltic wave moving along the body. The clear-cut course of the lateral ridges suggests that they were produced by longitudinally arranged series of appendages. This is not unlike the body plan inferred for *Mattaia*, which is represented by horizontal galleries in sand from the same strata.

## Intermediates between bilobed horizontal galleries and trilobed burrows

The collapsing galleries of *Mattaia miettensis* were dug horizontally between sand layers. In this respect they differ rather markedly from other trace fossils recognized in the terminal Ediacaran strata of northern Siberia. However, in the Chmielnicki Formation of Podolia, Ukraine, similar horizontal galleries occur on the sole of sandstone beds covering claystone.

The lower surface of the trails of *Mattaia tirasensis* from Podolia is bilobed (Fig. 4; Palij *et al.* 1983). In places the traces are arranged into series of separate burrows, but in others the burrows are continuous and parallel to the sediment surface. In the short burrows with a three-lobed ventral surface, sometimes developed centrally, the generally irregular appearance of the traces makes observation difficult. These shallow, continuous burrows in clay, possibly produced at the clay-sand interface, demonstrate a transition from the temporary shelters of *Podolodes* to more permanent penetration of sand, resulting in continuous galleries below the sediment surface.
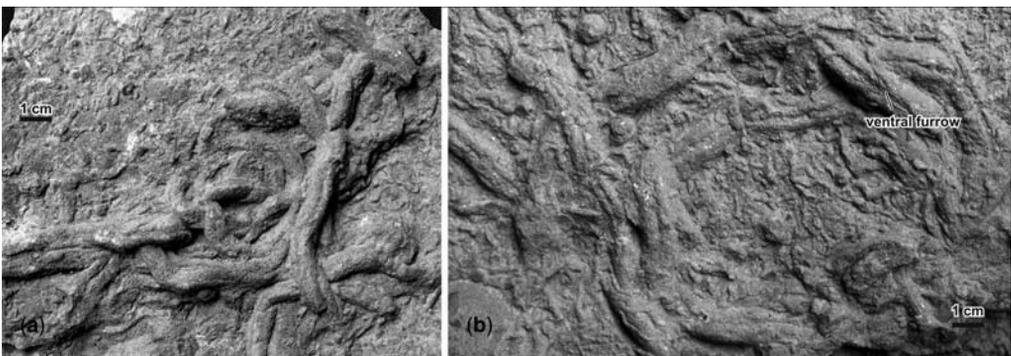
## Correlation of earliest infaunal traces and small shelly fossils

There are two reasons to think that the advent of skeletonization was related to the function of the external skeleton, rather than to it resulting simply as a response to the geochemical environment of the Precambrian–Cambrian oceans: (1) skeletons of calcitic, aragonitic, phosphatic, and siliceous composition emerged virtually simultaneously, although not necessarily in the same environment; (2) amongst the first protective skeletal innovations were agglutinated tubes built of foreign objects by the animals inhabiting them—exemplified by the worm *Onuphionella*, with its collection of mica flakes lining its shelter (Signor & McMenamin 1988). Such particle collecting behaviour required not only anatomical adaptations allowing organisms to pick out and glue together skeletal debris with organic secretions, but also an advanced neural system enabling such sophisticated behaviour.

In order to explain the origin of skeletonization in early animals, it is necessary to establish the chronological relationship between first mineralized armours and the fossil traces of activity of these early 'arms manufacturers'. The first calcareous tubular fossils occur in strata of similar age to those containing the Ediacaran fauna (Bengtson & Yue 1992), as is also true in the Khorbusuonka section (Khomentovsky & Karlova 1993). However, the metazoan nature of the tubes cannot be established yet. The oldest taxonomically identifiable skeletal fossils of undoubted animal affinity remain the phosphatic small shelly fossils.

In Siberia, the Kessyusa Formation has yielded the oldest record of phosphatic conchs and tubes of unquestionable metazoan affinities. In the section at Mattaia, horizons within the dark, laminated mudstone unit containing winnowed concretions have yielded numerous calcareous tubes. In acid-resistant residue, phosphatic internal moulds of their apices with swollen tips demonstrate that these are laterally compressed conchs of a hyolith-like
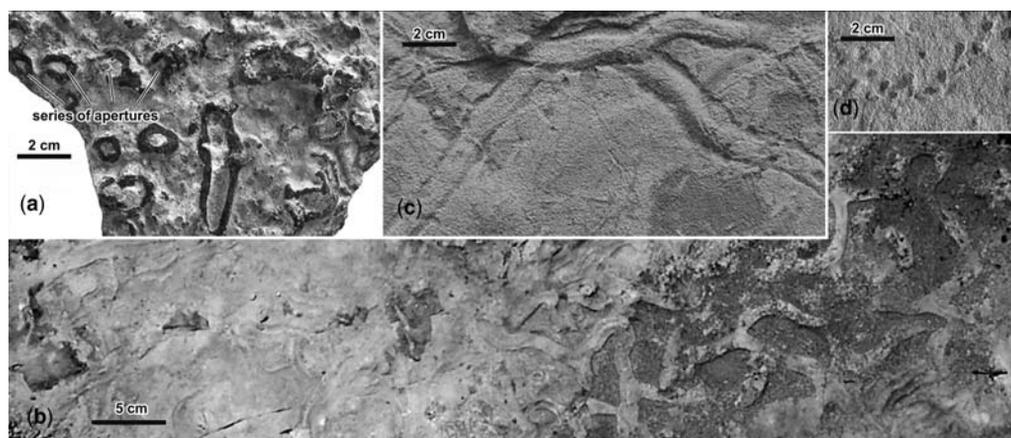


**Fig. 4.** Burrows of *Mattaia tirasensis* (Palij 1974) from the lower part of the Chmielnicki Formation at the village Subocz on the right bank of the Dniester River, Podolia, Ukraine, dug in clay and morphologically transitional between horizontal bilobed galleries of *Mattaia* and three-lobed series of *Podolodes* (originals of Palij *et al.* 1983 housed at the Geological Institute, Kiev). (**a**) Sole face of sandstone slab with deep, bilobed burrows tending to develop a separation between ventral furrows, similar to partially three-lobed linearly short burrows of *Podolodes* sp. from the same formation (cf. Dzik 2005, Fig. 3a–b). (**b**) Slab with shallow burrows more similar to *Mattaia miettensis*; note than in both cases the animal tended to produce short burrows instead of truly continuous galleries.

mollusc—*Ladatheca annae*. Other tubular fossils (enigmatic *Conotheca* and probable anabaritid *Spinulitheca*) are associated (Dzik 2005). In coeval strata exposed along the Olenek River, planispiral conchs of the bellerophontid mollusc *Latouchella*, the probable sinistral gastropod *Barskovia*, and the low-conical possible monoplacophoran *Purella* occur (Khomentovsky & Karlova 1993). The first infaunal traces of activity in the area are thus coeval with the oldest occurrences of small shelly fossils.
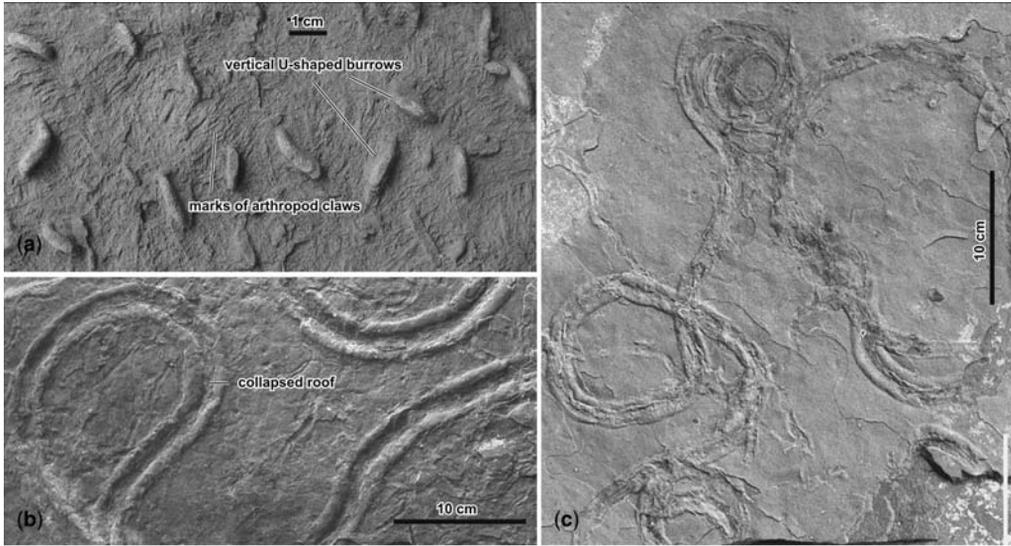
The earliest Cambrian succession at the Meishucun section in Yunnan, China, is the richest in phosphatic fossils. However, its correlation with the Cambrian units of Siberia, is highly controversial. The lowest unit containing skeletal fossils in China is Bed 3 at the base of the Zhongyicun Member of the Dengying Formation (Qian & Bengtson 1989). Qian & Bengtson (1989) recovered small shelly fossils in Beds 3–6, insufficient to assign a precise age correlation with strata elsewhere, but probably about the same age as the Nemakit-Daldynian (Manykayan) strata in Siberia. This is consistent with the occurrence of the first infaunal trace fossils which occur in a phosphate-rich oolite of Bed 3—serially branching circular tubes with openings at the surface (Fig. 5a, b). Most tubes are enveloped in phosphorite, which obliterates details of their morphology. The mode of branching and circular cross-section is similar to *Manykodes*, although diameters (5–7 mm) are larger than in *M. pedum* from Siberia.

Poorly preserved alternating serial burrows similar in size to *M. pedum* occur in Bed 5 of the same rock unit (Fig. 5d), thus it is definitely Cambrian in age (Tommotian according to Jenkins *et al.* 2002). Co-occurring horizontal galleries resemble *Mattaia* in showing a convex ventral surface, but the ventral furrow is not recognizable on the specimen (Fig. 5c). Undoubted *Mattaia* (*Didymaulichnus* in Crimes & Zhiwen 1986) occurs in Bed 7 of the Zhongyicun Member, in which small shelly fossils with a Tommotian aspect occur. In the same bed, the first arthropod resting traces occur (Crimes & Zhiwen 1986), associated with cylindrical U-shaped burrows (Fig. 6a). Although the trilobite nature has not been established, an Atdabanian age of the bed has been suggested. Large horizontal galleries with collapsing roof, representing *Mattaia* or *Psammichnites* (*Taphrhelminthopsis* in Crimes & Zhiwen 1986), emerge in Bed 9 at the base of the Badaowan Member and continue throughout the succession upwards to the Canglangpu Formation (Fig. 6b, c), which is located above the mudstone unit with the Chengjiang fauna, containing fossils of soft-bodied animals. According to Qian & Bengtson (1989), the Badaowan Member small shelly fossils suggest an age not older than Atdabanian, possibly Botomian.

In general, the Meishucun assemblages of trace fossils are similar to those from northern Siberia, although the specimens are not as informative. Their advent is roughly synchronous with the



**Fig. 5.** Trace fossils from the oldest unit containing small shelly fossils (Zhongyicun Member of the Dengying Formation) at Meishucun, Yunnan (specimens collected by Wang Zhongzhi, housed at the Kunyang Phosphorite Mine museum at Kunyang). (**a**, **b**) Horizontal cylindrical burrows from Bed 3 remotely resembling *Manykodes*, with serial apertures at the sediment surface; partially weathered out phosphoritic envelopes of the burrows with linearly arranged apertures (a) and branching on an upper bedding plane cut by erosion (b). (**c**) Horizontal galleries from Bed 3 with convex, possibly bilobed lower surfaces, resembling small-size *Mattaia*. (**d**) Alternating serial burrows of *Manykodes* from Bed 5.

**Fig. 6.** Trace fossils from the post-Tommotian Early Cambrian of the Meishucun section (specimens collected by Shishan Zhang, housed at the Kunyang Phosphorite Mine museum at Kunyang). (**a**) Cylindrical U-shaped burrows and marks of arthropod appendages from Bed 7 of the Zhongyicun Member; sole of the bed. (**b**) Wide horizontal galleries with collapsing roof of *Mattaia* or *Psammichnites* from Bed 12 of the Badaowan Member. (**c**) Similar but narrower gallery from the Canglangpu Formation.

appearance of phosphatized skeletal remains of unquestionable metazoan affinities. Also in this succession, infaunal feeding traces are unknown in the earliest Cambrian strata. All of the animals producing elaborate chambers and galleries in the sediment seem to have searched for food at the surface.

## Conclusion

All interpretable trace fossils from the Ediacaran–Cambrian transition strata of northern Siberia, South China, Ukraine and elsewhere represent shelters of infaunal animals which appear to have been collecting food from above. McIlroy & Heys (1997) found it paradoxical that these animals wasted so much energy in burrowing, while seeking for the organic detritus on the sediment surface. True mud-eaters appeared later (McIlroy & Logan 1999). The synchronicity of the development of various sorts of protective armour with the origin of the infaunal mode of life suggests a similar cause—probably the development of predatory organisms targeting large metazoans. This was the beginning of an 'arms race', giving the choice to either shelter behind a strong mineralized skeleton or to hide in the sediment. Eventually, the expansion of infaunal life destroyed the widespread and vast cyanobacterial mats in shallow regions of the sea

(Dzik 2003). Ironically, the profound change in conditions of sedimentation that so strongly biased the fossil record of the animal evolution near the Precambrian–Cambrian transition was at least partially caused by the evolving animals themselves.

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