The Verdun Syndrome: Simultaneous Origin of Protective Armor and Infaunal Shelters at the Precambrian-Cambrian Transition

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Abstract

In the most complete and first radiometrically dated Precambrian-Cambrian transition strata along the Khorbusuonka River in northern Siberia, a succession of fossilized traces of activity of the earliest infaunal animals has been identified. As supplemented by a similar record in Podolia, the Ukraine and elsewhere. This collection demonstrates that thus far all of the structurally identifiable trace fossils of infaunal life from the earliest Cambrian represent shelters of animals feeding above the sediment surface. The oldest traces of feeding within the mud are known from no earlier than the Late Tommotian. This suggests that the invention of hydraulic mechanisms for sediment penetration was forced by predation, not by trophic needs. Various ways to protect the body, by secretion of a mineral skeleton or the building of tubes with collected mineral grains, were developed by other animals at about the same time. Predation thus appears to be the triggering mechanism for the “Cambrian explosion”. Subsequent increase in the depth of bioturbation resulted in a profound change of taphonomic conditions.

The Khorbusuonka River section of polar Siberia is one of the very few sites in the world where the Precambrian-Cambrian transition is documented with radiometric dating (Bowring *et al.* 1993), a stable isotope record (Pelechaty *et al.* 1996), Ediacaran body impressions (Fedonkin 1985), as well as skeletal (Khomentovsky & Karlova 1993) and trace fossils. The latter are of special interest, because their appearance, well represented in the exposure of the Nemakit-Daldynian (Manykayan) Kessyusa Formation near the mouth of Mattaia Creek, extends well below

the first appearance of "*Phycodes*" *pedum*, the index fossil defining the base of the Cambrian and probably occurring also somewhat below this boundary in the stratotype section of Newfoundland (Gehling, *et al.*, 2001).

Not unlike fossiliferous successions elsewhere, traces of infaunal activity are missing in strata hosting Ediacaran fossils at Khorbusonka. Only shallow surface burrows occur widely in strata of such an age (Jensen, 2003). The oldest traces of sediment penetration by worm-like animals at the base of the Mattaia exposure of the middle part of the Kessyusa Formation are shallow burrows of rather indifferent morphology.

A more informative record begins about 15 m above this boundary (Fig. 1a). The lower surfaces of glauconitic sandstone beds are densely covered with moulds of shallow burrows in the underlying claystone (Fig. 1b). Similar, although somewhat smaller, three-lobed traces occur in approximately coeval strata in Namibia (Jensen, *et al.*, 2000). In the profile view, burrow moulds are gently convex, with both ends smoothly disappearing at the bedding plane. Rarely they penetrate 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 resting on the bottom and partially hidden in the sediment, analogous to the trilobite *Rusophycus* traces. 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 sandstones overlying coarser clays, three-lobed burrows tend to be more elevated to attain an almost circular cross section similar to "*Treptichnus*" *tripleurus* from Namibia (Geyer & Uchman 1995) and Podolia, and the Ukraine (Palij, *et al.*, 1983). This is an expression of variability, which can be extended into series of morphologies linking these traces with more elaborate forms from strata of similar or younger age elsewhere. One of such series leads to alternating series of shallow U-shaped burrows with circular cross sections, the other to continuous galleries below the sediment surface.

Three-lobed traces on the lower side of certain units characterizes the plait-like alternating series of burrows of "*Treptichnus*" *triplex* from Podolia (Palij *et al.* 1983) and eastern Poland

(Paczena 1996). Both in the specimens from Khorbusuonka and Podolia there is a gradation from three-lobed shallow burrows to fully submerged burrows with round cross sections and smooth or bilobed lower surface. They may alternate, but may also be arranged linearly (Jensen & Mens, 2001).

Branching burrows with round crosssections of "*Phycodes*" *pedum* appear not far from the top of the Kessyusa Formation. These were apparently permanently open shelters of a surface detritus feeder, burrows (Jensen, 1997) in partially cemented clay (as indicated by synsedimentary faults) that subsequently filled with sand. In apparently related "*Treptichnus*" *rectangularis* from the latest Cambrian of the Holy Cross Mountains, Poland, an aggregation of clay-rich fecal pellets were found at the bottom of burrows (Orowski and Yliska, 1996), suggesting that they were empty during the life of the producer. The walls may have been stiffened with mucus, but the earliest Cambrian clay-rich sediment surface was probably firm enough to prevent collapse without additional impregnation (Droser, *et al.*, 2002). Swollen parts of the burrow marked with a ring of longitudinal striae indicate that the excavation was carried out by means of hooks surrounding the body, like those in the priapulid prosoma.

A bilobed lower surface characterizes trails of "*Didymaulichnites*" *tirasensis* on the soles of sandstone beds in Podolia. In some places these are arranged in a series of separate burrows, but others show continuous burrows parallel to the sediment surface. These all represent sandstone replicas of burrows in clay.

Similar, but larger in size continuous burrows of "*Didymaulichnus*" *miettensis* (Young 1972) occur within the green glauconitic sandstone beds higher above in the Mattaia section (Fig. 1c), as well as in coeval strata exposed along the Olenek River in the same region of northern Siberia (Fedonkin 1985). These were animals which permanently penetrated sandy sediments. The lack of deformation of layers below the trail indicates that this was not due to action of any hydraulic pushing mechanism, but the sediment was abraded by the organism. 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, suggesting that all the material mechanically

removed from below was transported behind. The smooth surface of the double ventral furrow suggests that this was the route of transport. In well-preserved specimens the outer lateral bevel consists of series of transverse, slightly oblique folds. They at least remotely resemble stripes of *Plagiogmus*, probably produced by anchoring of the body of an organism and its movement with retrograde peristaltic wave (McIlroy and Heys, 1997).

Owing to clear delimitation of particular rock layers by clay laminae, the cross-sections preserve, rather well, the internal structure of the trail. The clay laminae remain intact, exhibiting folded and raised external margins. This suggests a gentle hydraulic elevation of sand by the passage of the worm. The sediment above the trail evidently was first pushed upwards to fold on both sides and then collapsed in the middle behind the animal (Hofmann & 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 (Jensen 1997; Seilacher 1995) and collecting food together with the sediment from the surface (Hofmann & Patel 1989).

The geologically oldest evidence for purposeful penetration of sediments for feeding are the horizontal *Rhizocorallium*-like spreite structures occurring in marly limestone facies of the Late Tommotian (or Early Atdabanian) in the Tikiriteekh section along the Lena River near Yakutsk. Such feeding traces are known also from roughly coeval sandstone facies of northern Poland (Pacze na, 1996). In the Atdabanian of Sweden such spreite structures show a helicoidal organization (Jensen 1997).

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 that forced early animals to start infaunal life. If so, the oldest traces of locomotory activities of the metazoans should be connected with their infaunal life. The fossil evidence does not support this idea. All interpretable trace fossils from the Ediacaran-Cambrian transition strata of northern Siberia, the Ukraine, and elsewhere represent shelters of infaunal animals collecting food from above. It is a paradox that these animals wasted energy by burrowing in search of organic detritus on the sediment surface (McIlroy and Heys, 1997).

Figure 1. Trace fossil record in the Precambrian-Cambrian transition strata exposed at the mouth of Mattaia Creek in the Khorbusonka section (71° 25' N, 123° 35' E) (localities 16 and 17); **a**, stratigraphic column, distribution of skeletal and trace fossils, and photograph of the cliff at the turning point of Khorbusonka where the lower part of the mudstone unit of the middle Kessyusa Formation is exposed; **b**, lower surface of a slab with three-lobed traces of '*Treptichnus*' *tripleurus* (Geyer and Uchman, 1995); **c**, transverse section of two associated galleries of '*Didymaulichnus*' *miettensis* (Young, 1972).

A possible explanation is offered by the sequence of events in the process of skeletonization of the early animals. The first calcareous tubular fossils of unknown affinities occur in strata of the same age as those containing the Ediacaran fauna (Bengtson and Yue, 1992), also in the Khorbusonka section (Khomentovsky and Karlova, 1993). The Kessyusa Formation is the oldest occurrence of taxonomically identifiable animal skeletal fossils in Siberia, and probably also in the world. In the section exposed at Mattai, horizons with winnowed concretions in glauconite-

quartz sand matrix within the dark laminated mudstone unit yielded numerous calcareous tubes. In the acid-resistant residue, phosphatic internal moulds of their apices with swollen tips demonstrate that these laterally compressed conchs are like the hyolith mollusc *Ladatheca annae*. Other tubular fossils (enigmatic *Conothea*), probably anabaritids like *Spinulitheca* and phosphatized coprolites, helically wound or meandering, are associated. In coeval strata exposed along the Olenek River, planispiral conchs of the bellerophontid mollusc *Latouchella*, a probable sinistral gastropod *Barskovia*, and low-conical probable monoplacophoran *Purella* occur (Khomentovsky and Karlova, 1993).

Various explanations have been offered for the Cambrian “explosion” of skeletonized organisms. Notably, protective effects were achieved by the earliest Cambrian, not necessarily by secretion of mineral skeleton, as exemplified by the worm *Onuphionella*, which purposely collects mica flakes from surroundings to build tubes for protection (Signor and McMenamin, 1988). The synchronicity of appearance of so many sorts of protective armor and the origin of the infaunal mode of life suggests a similar cause. It seems likely that such 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.

Apparently, the diversification of predators in the earliest Cambrian forced other animals to invest significant energy either in digging or in a protective armor (“the Verdun Syndrome”). True mud-eaters appeared later (McIlroy & Logan 1999). Eventually, the expansion of infaunal life destroyed at first the widespread and vast cyanobacterial mats that prospered in shallow oceans (Dzik, 2003) and, gradually, the small shelly fossils environment in deeper regions (Dzik, 1994). The fossil record at the Precambrian-Cambrian transition was strongly biased by the profound change in the conditions of sedimentation, at least partially influenced by the evolving animals themselves.

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