

## The oldest evidence of bioturbation on Earth

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Recently, Rogov et al. (2012) discovered dense bioturbation fabrics, the preserved depth of which reached 5 cm, from the Ediacaran Khatyspyt Formation of the northern Siberian Platform. The age of the bioturbated beds is estimated at ca. 555 Ma. The ichnotaxon itself is attributed to the meniscate ichnogenus *Nenoxites*.

A similar meniscate fabric was previously described from the coeval upper Aim Formation of the southern Siberian Platform as the ichnogenus *Gaojiashania* by Zhuravlev et al. (2009). The main differences between *Nenoxites* from the Khatyspyt Formation and *Gaojiashania* from the upper Aim Formation is in the restriction of the latter to horizontal bedding planes only, without vertical structures.

Whereas Rogov et al. preferred a bilaterian bioturbation model for their ichnofabrics, Zhuravlev et al. (2009) proposed a mycetozoan behavior model for the origin of *Gaojiashania*. The latter model suggests a combination of fossilized fruiting bodies of mycetozoan plasmodia, together with traces produced by slime molds moving within soft to soupy sediment as they extracted nutrients.

We agree with Rogov et al. regarding the Khatyspyt meniscate fossils as a bioturbation ichnofabric, and we do not intend to argue against the existence of Ediacaran triploblastic Eumetazoa ichnofossils generally. Nevertheless, in opposition to those authors' assertion (Rogov et al., 2012, p. 397) that "the Khatyspyt ichnofabric could only have been produced by a bilaterian," and that this "represents the most reliable paleontological evidence for the existence of triploblastic Eumetazoa," we propose a different approach to interpretation of such ichnofabrics.

Most bioturbating soft-bodied animals tend to form discrete burrows with approximately parallel walls (except in those forms with pelletoidal fillings or petaloid branches, which nonetheless tend to be symmetrical), and the burrow width is either constant or varies at the same rate on opposite sides. Width variations along the body of a trace-making individual do not correlate with changes in width of the resulting trace, as the latter is determined by the widest part of the trace-maker's body. This rule should be equally applicable to bioturbation structures of Neoproterozoic age if such structures were produced by bilaterian triploblastic eumetazoans.

However, several features of the traces described by Rogov et al. hint at a non-animal origin, namely, the eccentrically nested position of meniscus-like segments; the significant variation in shape and width of the menisci, both along straight segments and at abrupt or gentle bends of the trace; the association of such abrupt bends with either a widening or a narrowing of the trace; and the distinctly irregular margins of the trace (visible both in longitudinal and cross section). Furthermore, despite the presence of a few more or less regular intervals (Rogov et al., 2012, their figure DR2), this regularity seems to be exceptional rather than normal.

Additionally, the figured specimens do not show any type of wall (neither lining, nor compression zones around adjacent substrate), and even burrow boundaries cannot be established. A similar trace pattern, also exhibiting a complete absence of regularities in meandering—which is atypical for bilaterian traces—was observed by Zhuravlev et al. (2009). Observed silicification alone cannot explain the poorly defined aspect of the traces.

The presence of "a string of silicified material or pyrite globules connecting the menisci to each other" closely resembles the "continuous dark axial string" locally present in *Gaojiashania* specimens, which in turn seems to correspond to a longitudinal crest along eccentrically nested crescent segments (Zhuravlev et al., 2009, their figures 2e and 2g). It is hardly possible that such structure could be generated by the regular sediment ingestion typical of bilaterians.

Further, the interpretation of a flaring, almost vertical structure displaying heavy silicification (Rogov et al., 2012, their figure DR2) as an escape burrow does not conform with the slow sedimentation anticipated for such intensely bioturbated strata, since sediment processing that leaves an organic imprint is not expected at all when an organism escapes from burial.

According to the mycetozoan behavior model, a sluglike colony moving within soft to soupy sediment (i.e., in a confined environment) as it extracts chemical substances can be expected to leave traces of rapidly varying width—very much as figured by Rogov et al. (2012, their figure 3A and figure DR2)—and with frequent lateral offsets. The limited length of the traces observed on vertical sections may be due to three-dimensional path oscillations. A slug of the Recent slime mold *Dictyostelium polycephalum* is able to burrow through soil and even through agar over long distances, penetrating to a soil depth of 7 cm in the search for food (Bonner, 2006). Slime molds easily adapt their shape to the environmental topology (Nakagaki et al., 2000). Thus, moving on a substrate surface, such organisms would likely produce two-dimensional traces with paths of low regularity (as in the Aim Formation), whereas confined environments could allow slime molds to spread so as to produce a three-dimensional, highly irregular network (Khatyspyt Formation).

In summary, we agree with Rogov et al. in considering the *Nenoxites-Gaojiashania* group of meniscate trace fossils as bioturbation products, but not as bilaterian (animal) traces originating via ingestion and defecation. Rather, this ichnofabric pattern better fits the activity of mycetozoan plasmodia and slugs, which are driven by chemical stimuli across a soft to soupy carbonate seafloor of slow sedimentation rate to produce an intrastratal three-dimensional mesh. In contrast with these observations, the shallower "looping pattern" of similar ichnofossils, typical of the Aim Formation, resulted from a higher sedimentation rate.

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