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Forum

The New Zealand *Zoophycos* revisited: morphology, ethology, and paleoecology—some notes for clarification

Andreas Wetzel

Geologisch-Paläontologisches Institut der Universität
Bernoullistrasse 32, CH 4056 Basel, Switzerland

Zoophycos is a highly organized and morphologically variable trace fossil found in Cambrian to Holocene sediments (Häntzschel, 1975; Alpert, 1977; Ekdale and Berger, 1978; Bottjer et al., 1988). The organisms producing this trace are unknown but have been subjected to much speculation, as noted by Ekdale and Lewis (1991).

Is it really necessary to know the taxonomic affinity of a trace-producing animal if mainly the organism's behavioral response to environmental changes has implications in understanding the paleoecologic significance of a deposit?

At first glance the taxonomic affinity of a burrowing animal seems to be unimportant. However, the deduction of a behavioral program responsible for trace formation is closely related to anatomical requirements of the trace-producing organism, including aspects of feeding and respiration. In consequence a dilemma arises: if the identity of the trace-producing organism is not known, the anatomical requirements of the animal normally are based on the deduced behavioral program which normally is affected by the paradigm representing increased efficiency by the animal. But how can we determine what is "efficient" if we do not understand clearly *why* a *Zoophycos* was produced (Bromley, 1991)?

Consequently any attempt to identify a single animal taxon as the producer of all forms of *Zoophycos* obviously can present pitfalls for the ecologic interpretation of different *Zoophycos* of varying morphologies, ages, or environments. To accept or reject a certain model for a type of *Zoophycos* actually studied, careful analyses of nearly all aspects are needed, such as geometry, characteristics of the host sediment and fill sediment, co-occurring traces, and so forth.

In their recent paper, Ekdale and Lewis (1991) rejected a number of *Zoophycos* ethologic models for various reasons. Some of their arguments are valid, but some others may not be. Especially, their arguments against a sipunculid behavioral program are not convincing, because their observations of the Amuri *Zoophycos* do not really preclude sipunculids as *Zoophycos* producers. Ekdale and Lewis (1991, p. 188) gave the following explanations:

(1) "Sipunculids worms are common in the sea, yet none has been found in the process of creating incipient *Zoophycos*, nor have they ever been found in *Zoophycos* bearing sediments" Ekdale and Lewis (1991, p. 188). It is fair to say that *no* organism has been observed producing a *Zoophycos*, including worm-like animals with straight digestive tracts, the favorites of Ekdale and Lewis (1991, p. 192), or echiurans, the favorites of Kotake (1989). Sipunculids (as well as polychaete annelids and echiurans) occur in the water depth range in which *Zoophycos* occurs. Furthermore, (A) the population density of the *Zoophycos*-producing animals typically is extremely low; in the case studied by Wetzel and Werner (1981), one animal per 100 m^2 was calculated. (B) Jumars et al. (1990) illustrated a sipunculid worm in situ in a modern spreiten structure. The structure figured by Jumars et al. (1990) is morphologically similar to the burrows described by Wetzel and Werner (1981) from which they deduced sipunculids as *Zoophycos* producers. However, the trace figured by Jumars et al. (1990) can also be grouped into the ichnogenus *Teichichnus*.

(2) "A lobate spreite outline would not be produced by this ethologic explanation" (Ekdale and Lewis, 1991, p. 188). A lobate spreite results from a discontinuous behavioral program, in which the burrower creates a spreite, stops, and then constructs a new spreite alongside the previous one when the former is completed. Any highly thigmotactic organism could easily burrow in this way, it is a question of behavior program (discontinuous U-shaped spreiten construction) rather than of anatomy (e.g., polychaete versus sipunculid).

In the case of sipunculids as possible *Zoophycos* producers, the spreite lobes may represent maximum exten-

sion of the proboscis. However, one also needs to explain why a smooth or a lobate spreite is constructed. Does lobe formation indicate maximum use of a certain sediment volume that is valuable for food or living space, or may lobe formation indicate the animal's probing to explore additional sediment? In the case of the Amuri *Zoophycos*, it would be interesting to know the ecologic meaning of this type of behavioral program in comparison to other *Zoophycos*.

(3) "Feeding movements cannot be explained in this way for the U-form *Zoophycos*" (Ekdale and Lewis, 1991, p. 188). In the sipunculid model, the *Zoophycos* producer stays upside down within the central part of a burrow, while the proboscis is moved to-and-fro during construction of the spreite. The animal stays at a fixed position, and only occasional excursions of the animal to clean out the marginal tube (in case of a basic U-shaped tube) are necessary. In the case of a basic J-shaped tube, the organism can stay at a nearly fixed position in the central part of the burrow as long as it lives.

(4) "Water circulation through deep, distal parts of the tunnel in the 'J-form' of *Zoophycos* cannot be explained" (Ekdale and Lewis, 1991, p. 188). Sipunculids producing a 'J-form' *Zoophycos* stay in the central part of the burrow and constructs a spreite by a to-and-fro motion of its proboscis. At the same time, respiration water is pumped throughout the burrow by peristaltic body motions, while the burrower respires through its body surface. The movements of the proboscis support the pumping of respiration water. When the proboscis moves forward, water is sucked into the tube; when the proboscis moves backward, the water is expelled, in each case along the respiring cuticule of the burrower.

In summary, *Zoophycos* may be constructed by polychaetes, as suggested by Ekdale and Lewis (1991), and they described a plausible behavioral program for the construction of a system of multiple spreiten burrows. However, their explanation does not preclude the possibility that other groups of animals, such as sipunculids, can construct *Zoophycos* of the Amuri type.

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