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Title

Paleobiology of the Climactichnites Trackmaker: An Enigmatic Late Cambrian Animal Known Only from Trace Fossils

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Abstract

Based on a thorough examination of museum and field Climactichnites specimens, two species of this trace, which is restricted to North America, are recognized, each representing a unique behavioral variant. *C. wilsoni* represents surface-produced trackways, whereas *C. youngi* is erected for subsurface burrows. Burrowing behavior is supported by the presence of *C. youngi* within beds, the orientation of burrows inclined to bedding, and the presence of distinct burrow fills. Burrows are distinguished from surface traces by characteristics including the absence of lateral ridges and the presence of mm-sized striations superimposed on the trace. Burrowing behavior was previously unknown and represents a new behavior for the animal. A new ichnospecies, *Musculopodus sedentarius*, is erected for sedentary impressions of the animal. In the future *Musculopodus* may be expanded to include the resting traces of other soft-bodied animals known from fossils.

Analysis of Climactichnites indicates that the trackmaker was elongate, bilaterally symmetric, dorsoventrally flattened, and soft-footed. These characteristics are consistent with the trackmaker being a primitive mollusk or mollusk-like animal. Unlike other Neoproterozoic and Cambrian mollusks, such as *Matthevia*, *Wiwaxia*, and *Odontogriphus*, the Climactichnites trackmaker could reach considerable size. At up to 29 cm wide and possibly 67 cm long, it was one of the largest animals of its time.

During locomotion, the animal generated muscular waves along the sole of its foot, which was extended and clamped into the substrate. Contraction of pedal muscles then pulled the body forward. This method of locomotion is similar to that employed by some gastropods, including *Bullia* and *Polinices*, which make Climactichnites-like trackways in exposed intertidal settings today. However, these modern trackways are not preserved because they are eroded by wind, waves, tides and subsequent bioturbation, as experiments confirm. Abundant microbial sedimentary structures associated with Cambrian occurrences suggests that microbial binding may have mediated the preservation of Climactichnites.

Two lines of evidence suggest that the Climactichnites trackmaker may have been one of the first animals to venture onto land: the co-occurrence of subaerially-produced sedimentary structures, such as adhesion structures and raindrop impressions, and trackways that span shoreline depth gradients and exhibit variable preservation quality along their length.

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