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# Trace fossils in the Ediacaran–Cambrian transition: Behavioral diversification, ecological turnover and environmental shift

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**Abstract**

After taxonomic revision, trace fossils show a similarly explosive diversification in the Ediacaran–Cambrian transition as metazoan body fossils. In shallow-marine deposits of Ediacaran age, trace fossils are horizontal, simple and rare, and display feeding strategies related to exploitation of microbial matgrounds. Equally notable is the absence of arthropod tracks and sinusoidal nematode trails. This situation changed in the Early Cambrian, when a dramatic increase in the diversity of distinct ichnotaxa is associated was followed by the onset of vertical bioturbation and the disappearance of a matground-based ecology (''agronomic revolution''). On deep sea bottoms, animals have been present already in the Ediacaran, but ichnofaunas were poorly diverse and dominated by the horizontal burrows of undermat miners. As shown by the ichnogenus *Oldhamia*, this life style continued to be predominant into the Early, and to a lesser extent, Middle Cambrian. Nevertheless, there was an explosive radiation of behavioral programs during the Early Cambrian. When exactly the bioturbational revolution arrived in the deep sea is uncertain. In any case, the *Nereites* ichnofacies was firmly established in the Early Ordovician. The rich ichnofauna in the Early Cambrian Guachos Formation of northwest Argentina probably marks a first step in this ecological onshore–offshore shift.


*Keywords:* Ediacaran–Cambrian; Ichnology; Microbial mats; Diversification

## 1. Introduction

Difficulties to analyze the ichnologic record of the Ediacaran–Cambrian transition result from the taphonomic filter biogenic structures passed through, but also from taxonomic idiosyncrasies contained in published data. The latter bias applies particularly to Proterozoic trace fossils, whose rarity and antiquity raise the tendency to describe and name specimens that would otherwise pass as non-descript or be simply referred to as *Planolites* or *Palaeophycus*-like structures. In the present paper we critically review the ichnofauna of the Ediacaran shallow-marine biota

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and then discuss the development of deep-water ichnocoenoses in the Ediacaran and Early Cambrian, with new data from North Carolina (USA) and northwest Argentina. Subsequently, we raise the question of when the Cambrian agronomic revolution (Seilacher and Pflüger, 1994) reached the deep sea. Finally, the taxonomy of some Ediacaran–Cambrian trace fossils is addressed in the light of new discoveries and reanalysis of selected specimens.

## 2. Ediacaran shallow-marine trace fossils

While an earlier compilation (Crimes, 1994) lists 35 ichnogenera for the Ediacaran period, this number shrinks considerably in view of recent revisions (Gehling et al., 2000; Jensen, 2003; Seilacher et al., 2003). In addition, some members of the Ediacaran ichnofauna (*Yelovichnus*, *Palaeopascichnus*, *Intrites* and *Harlaniella*) are no longer considered trace fossils.

### 2.1. Pseudofossils

The ubiquity of biomats on Precambrian sea bottoms accounts for certain sedimentary structures that are rare in later deposits (Seilacher and Pflüger, 1994; Seilacher, 1997). Sinusoidal shrinkage cracks (''manchuriophycus'') and small-scale load casts ("elephant-skin structures"), as well as various wrinkle patterns (e.g., "chloephycus", "kinneyia"), are now generally recognized as pseudofossils (Pflüger, 1995; Hagadorn and Bottjer, 1999; Chakrabarti, 2001). In Neoproterozoic and Cambrian rocks, some of these structures have been repeatedly interpreted as trace fossils. For example, sinusoidal synaeresis cracks were referred to as *Cochlichnus* (e.g., Kulkarni and Borkar, 1996), while elephant skin structures and wrinkle marks have been confused with *Protopaleodictyon* (e.g., Durand and Aceñolaza, 1990) and *Squamodictyon* (Durand et al., 1994) (see Chakrabarti, 2001 and Buatois and Mángano, 2003a, for reinterpretations).

Vertical burrows in shallow-marine Ediacaran deposits, typically assigned to *Skolithos* or, less commonly, to *Arenicolites* and *Monocraterion,* are doubtful (cf. Jensen, 2003). Supposedly vertical burrows described by Banks (1970) from Finnmark were subsequently reinterpreted as dewatering pillars (Farmer et al., 1992). Structures from Namibia assigned to *Skolithos* by Crimes and Germs (1982) have been subsequently considered as body fossils (Crimes and Fedonkin, 1996). Specimens from the Carolina slate belt, assigned by Gibson (1989) to *Monocraterion?* isp. are in all probability inorganic, most likely soft-sediment deformation structures. The origin of *Skolithos declinatus* Fedonkin from the White Sea (Fedonkin, 1985) is still uncertain. In short, no undoubted examples of vertical burrows have been documented from the Ediacaran.

### 2.2. Xenophyophorean protozoa

Xenophyophorea is a group of giant rhizopods having flexible, agglutinated chambers. Today they are restricted to abyssal depths (Tendal, 1972). It has been suggested that Ediacaran representatives still inhabited shallow seas and were embedded in biomats (Seilacher et al., 2003). This life style highly increased their fossilization potential. On the other hand, these structures may be easily mistaken for trace fossils, because in producing their chamber walls, these protists actively moved sand grains into the underlying mud layer just as a tracemaker would do (Fig. 1). Thus, the tightly packed chambers of *Palaeopascichnus delicatus* Palij, *P. sinuosus* Fedonkin and *Yelovichnus gracili*s Fedonkin were originally interpreted as meandering traces (Glaessner, 1969; Fedonkin, 1985; Crimes and Fedonkin, 1994), while chains of globular chambers (*Neonereites renarius* Fedonkin, *N. biserialis* Seilacher and *Intrites punctatus* Fedonkin) have been compared to backstuffed burrows. More recently, however, they have been regarded as body fossils (Haines, 2000; Gehling et al., 2000; Seilacher et al., 2003; Jensen, 2003), because both kinds do branch, which would be impossible in trace fossils of seemingly similar morphologies. Re-examination of some of the supposedly meandering trails (e.g., *Palaeopascichnus*) also fails to reveal the presence of actual meanders.

In the same vein, Jensen (2003) questioned the trace fossil interpretation of *Harlaniella podolica* Sokolov (see also Palij, 1976). *Harlaniella confusa* Signor described by Signor (1994) is most likely also a body fossil. A third morphotype of Ediacaran xenophyophoreans consists of an agglomerate of chambers, from which agglutinated tubules radiate into the surrounding sediment. Forms corresponding to this group