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Bioturbation structures of polychaetes in modern shallow marine environments and their analogues to *Chondrites* group traces

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Abstract

The present interdisciplinary study comprising actuopalaeontology, marine biology and marine chemistry reveals particular polychaete species as trace-makers of distinct branched burrow systems in modern intertidal and shallow subtidal deposits. In this way, the study concerns one of the most enigmatic trace fossils in earth history, the cosmopolitan ichnogenus *Chondrites*. Bioturbate structures of this type are frequently found and described in the fossil record, as well as in deep sea cores from modern environments. So far, they have generally been ascribed to unknown producers living as endobenthic, chemosymbiontic organisms in anoxic sediments, mostly in deep sea environments.

Scoloplos armiger, occurring in the German Wadden Sea in the lower parts of tidal flats, produces burrow structures that conform with numerous trace fossils of the ichnogenus *Chondrites*. *Heteromastus filiformis*, typical of the upper parts of tidal flats, produces burrows resembling trace fossils of the extended *Chondrites* group, namely the ichnogenus *Pilichnus*. Burrows of this trace fossil type were also found in subtidal muddy sediments near a barrier island at the coast of Georgia, U.S.A., originating from *Capitella* cf. *aciculata*.

Pathways for detection of the modern traces, chemical properties of the sediments, life modes of the respective organisms and their environmental implications are briefly discussed. The results contribute to a more precise and differentiated interpretation of palaeoecologic and palaeooceanographic data.

Keywords: Palaeoecology; Bioturbation; Burrow systems; *Chondrites*; Polychaetes; Recent

1. Background of the investigation

The taxon '*Chondrites*' was originally established by von Sternberg, 1833 as a genus of fossil algae because of their multi-branched, bushy appearance. Later, Fuchs (1885, 1909) regarded them as trace fossils originating from intrasedimentarily crawling animals. The group to which he assigned them includes a variety of shapes and sizes.

These varieties in burrow configuration range from simply bushy, to regular or irregular branching, thus constituting the diversified *Chondrites* group. The general pattern of *Chondrites* structures has led to the palaeoecological interpretation of these trace fossils as intrasedimentary feeding-burrows (Richter, 1931; Simpson, 1957). In the ethological classification of Seilacher

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(1953) they are grouped into the 'fodinichnia', which implies a mining-like feeding procedure of their producers below the sediment surface. This also includes a phobotactic arrangement of the burrows or partial burrow branches, respectively (Richter, 1927, 1931). This means the producer avoids crossing an open burrow of its own construction. However, where structures are produced by different individuals at different times they certainly intersect each other (Ekdale and Bromley, 1991). In this way, a dense *Chondrites* ichnofabric can be built up. Some authors report meniscate burrow infills (Wetzel, 1979; Fu, 1991). Considering the occurrence of *Chondrites* trace fossils mostly in black fine-grained sediments, as well as in the deepest intrasedimentary position of trace fossil tier sequences, Bromley and Ekdale (1984: 872) regard *Chondrites* as 'a trace fossil indicator of anoxia in sediments'. Also, they stress that in modern environments *Chondrites* is only found in deep-sea deposits. The same had already been stated by Ekdale and Berger (1978) and Wetzel (1979, 1981, 1983a,b). According to Seilacher (1990) and Fu (1991) *Chondrites* represents the burrow of a chemosymbiontic trace-maker. This view was seconded by Bromley (1996).

Up to now, all authors surveyed, e.g. Wetzel (1979), Bromley and Ekdale (1984), Fu (1991), Bromley (1996), Uchman (1999), Rodríguez-Tovar and Uchman (2004), emphasize that *Chondrites* originates from an unknown producer. Swinbanks and Shirayama (1984) assume abyssal endobenthic nematodes as producers of *Chondrites* traces. On the other hand, Bromley (1996) devotes special attention to a small-sized order of the Pogonophora, i.e. the Perviata. These animals which live deeply in the sediment, some species even down to 1.5 m, have a chemosymbiotic mode of life. They occur in anoxic muddy sediments in the deep sea (Southward, 1979), as well as in shallow waters of Norwegian fjords (Southward et al., 1986). Bromley (1996) expresses the hope that bioturbation structures of Pogonophora can be found eventually that resemble *Chondrites* and, thus, reveal possible producers of these lebensspuren types. Another example of chemosymbiosis related to the formation of burrows is provided by bivalves of the genus *Thyasira*. These organisms produce vertical to steeply inclined burrows with their foot while taking up H_2S from deeper sediment layers (Dando and Southward, 1986; Seilacher, 1990). In the fossil record, however, such a trace fossil would be expected to be connected with a body fossil, namely the shell of the bivalve (Pervesler and Zuschin, 2004: Fig. 3).

In summary, a complex system of morphologic properties and ecologic aspects including the phobotactic mining-model, muddy and deep-sea environments, as well as anoxia and chemosymbiosis, have been attributed to this trace fossil. Thus, the scope of research for the detection of *Chondrites* trace-makers has been narrowed considerably. However, Bromley and Ekdale (1984) concede a wide variety of rock types, i.e. depositional environments, and do not claim anoxic conditions in the sediment as an exclusive prerequisite. They also consider an extended bathymetric range, including very shallow environments.

2. Regional setting

The study area comprises the intertidal area of the southern part of the German Wadden Sea. Observations on *Scoloplos armiger* and *Heteromastus filiformis* were carried out on tidal flats surrounding the outer Jade Bay, as well as on backbarrier tidal flats of the East Frisian Islands. The tidal flat system of the German Wadden Sea is characterized by exposed to semi-sheltered hydrodynamic conditions. This results in a conspicuous zonation of sediments as well as of benthic habitats and faunal associations. The tidal range of this area increases from 2.5 m in the western part to 3.9 m in the innermost part of the Jade Bay. The salinity shows seasonal variations from 26 to 34 PSU.

The example of *Capitella* burrows was taken from box core analyses of a former study at Sapelo Island in the coastal area of Georgia (U.S.A.). There, *Capitella* cf. *aciculata* was observed in the shallow upper offshore area 1 to 8 km away from the shore line, corresponding to water depths of 2 to 10 m below Mean Low Water Line.

3. Materials and methods

3.1. Box-coring

The investigations were carried out with box cores of recent marine sediments. The samples from intertidal environments were taken with hand-operated coring boxes of 25 or 35 cm height, those from subtidal environments with a ship-operated box corer penetrating up to 45 cm into the sea floor. The undisturbed, partly desiccated sediment cores were dissected in the laboratory in order to describe the entire design of specific burrow structures. Additionally, relief casts were prepared with ARALDIT® resin: the cores were dried in an oven, partially impregnated with the resin on one vertical side, and then kept at a temperature of 120 °C for 24–36 h. Subsequently, the non-impregnated major part of the core was washed away, allowing all impregnated physical and biogenic sedimentary structures to be viewed.