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Paleoecology of a marine endobenthic organism in response to beach morphodynamics: Trace fossil *Macaronichnus segregatis* in Holocene and Pleistocene sandy beach deposits

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HIGHLIGHTS

- We describe two occurrence modes of *Macaronichnus segregatis* from ancient beach deposits.
- One mode reflects the burrowing pattern of the producer under fair weather conditions.
- The other represents the burrowing pattern of the producer under storm conditions.
- We defined the relationship between a trace fossil and beach morphodynamics in ancient settings.

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ABSTRACT

Trace fossils made by ancient animals provide information on the ecology of their producers. Insights from their modern analogues also help us to understand the paleoecology of trace fossils. The arrangement of the trace fossil *Macaronichnus segregatis*, a probable feeding trace of an opheliid polychaete occurring in ancient beach deposits, was investigated to verify whether findings from modern beaches can be used to interpret geological records. The mode of occurrence of this trace fossil on horizontal sections of sediment was analyzed in Holocene and Pleistocene beach deposits. Two modes of the trace fossil arrangement were identified, as in a modern example. One mode shows a weak preferred orientation, whereas the other shows a strong preferred orientation. According to data from modern beaches, the weak preferred arrangement of the trace fossil corresponds to the pattern of subsurface burrowing under fair weather conditions. In contrast, the preferred orientation of the trace fossil indicates that it was formed under storm conditions. These interpretations are also supported by sedimentological evidence of the trace-fossil-bearing strata. The preferred orientation mode occurs just below an erosional surface, which was possibly created by a strong storm event. The results indicate that the trace fossil *M. segregatis* represents the behavior of its producer in response to beach morphodynamics, or the dynamic migration of a beach face on an ancient sandy beach.

1. Introduction

Trace fossils, such as burrows, trails, borings, and footprints, made by ancient animals provide information on the activities of their producers (e.g., Seilacher, 1967, 2007). However, improving our understanding of trace fossils requires the analysis of their modern analogues (Bromley, 1996). Many studies have examined modern traces of endobenthic marine invertebrates, and have revealed interesting infaunal modes of life that are usually difficult to observe directly (e.g., Hayasaka, 1935; Curran and White, 1991; Dworschak and Rodrigues, 1997; Seike and Nara, 2007; Gingras et al., 2008; Nara et al., 2008; Seike and Nara, 2008; Wetzel, 2008; Seike et al., 2011, 2012 and Seike and Curran, 2014).

The opheliid polychaete *Thoracophelia* (formerly called *Euzonus*) inhabits subsurface sediments of the intertidal environment on sandy beaches worldwide (e.g., McConnaughey and Fox, 1949;

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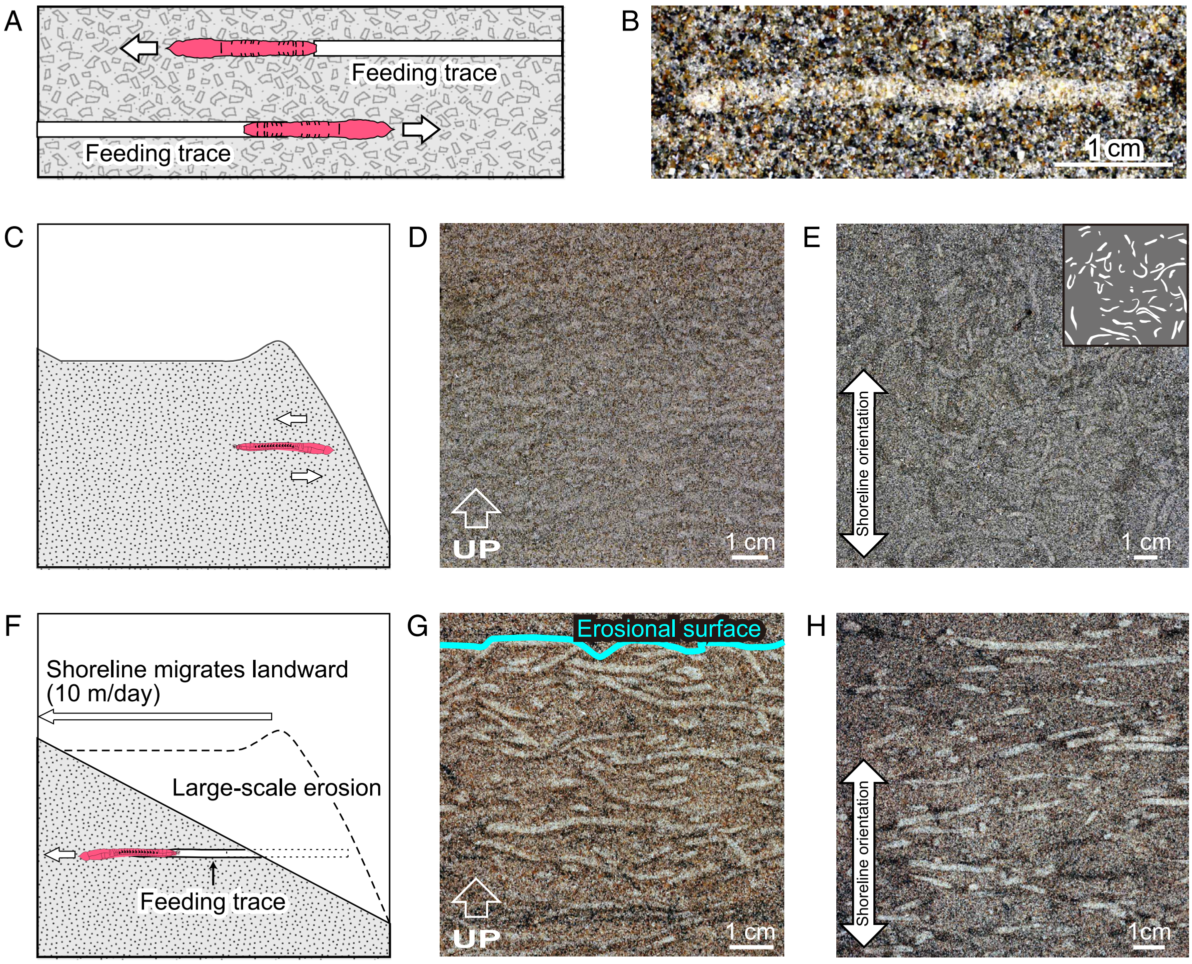

Fig. 1. Subsurface ecology and feeding trace of the opheliid polychaete *Thoracophelia* (after Clifton and Thompson, 1978 and Seike, 2008). (A) Formative process of the feeding trace by the worm. (B) Feeding traces of *Thoracophelia* (modern *Macaronichnus segregatis*) on a horizontally sectioned sediment surface. The axis of the feeding trace represents the orientation of the subsurface movement of the worm, although its direction is unclear. (C) Subsurface ecology of a *Thoracophelia* worm under fair weather conditions: the worm burrows horizontally in various directions. (D) Modern *M. segregatis* on a vertically sectioned sediment surface (seaward is to the right) under fair weather conditions. The traces have a spotted appearance on the surface perpendicular to the shoreline (Mode 1). (E) Modern *M. segregatis* traces on a horizontally sectioned sediment surface (seaward is to the right) under fair weather conditions. Note that the traces show weak preferred orientations (Mode 1). (F) Subsurface ecology of a *Thoracophelia* worm under storm conditions: the worm moves preferentially landward. (G) Modern *M. segregatis* on a vertically sectioned sediment surface (seaward is to the right) under storm conditions. Note that the trace occurs just beneath an erosional surface and has an elongate shape on the section of the sediment perpendicular to the shoreline (Mode 2). (H) Modern *M. segregatis* on a horizontally sectioned sediment surface (seaward is to the right) under storm conditions. Note that the traces show a strong preferred orientation (Mode 2). All sediment peel specimens are housed at the University Museum, the University of Tokyo, Japan (UMUT-RR30729–30852).

McLachlan and Jaramillo, 1995 and Dugan et al., 2013). The *Thoracophelia* worms are known to produce a feeding trace (Fig. 1) created by their burrowing locomotion (Pemberton et al., 2001; Gingras et al., 2002; Nara and Seike, 2004; Seike, 2007, 2008, 2009; Dafoe et al., 2008a,b). The feeding trace is represented by a horizontal nonbranching burrow, 3–5 mm in diameter, which is characterized by mineralogical segregation between the core (light-colored sand grains) and surrounding mantle (dark-colored sand grains). Therefore, the feeding trace of *Thoracophelia* allows us to infer its subsurface behavior in detail (Seike, 2007, 2008, 2009).

The habitat of the *Thoracophelia* worms is sandy beaches facing an open ocean, one of the most dynamic and changing topographies. Under fair weather conditions, the beach face (shoreline) progrades seaward in response to gentle ocean waves, which usually cause onshore sediment transportation. In contrast, under storm conditions the beach face retreats landward under the action of large waves that transport coastal sediments offshore. Therefore, the beach topography changes dynamically in response to wave conditions, in a process known as beach morphodynamics (Short, 1999). Consequently, *Thoracophelia* worms have a unique ecology and have adapted to these beach morphodynamics.

Seike (2008) determined the subsurface ecology of *Thoracophelia* by analyzing its feeding trace (Fig. 1). The worm burrows almost horizontally, but in various directions (azimuths), under fair weather conditions (relatively stable beach topography). Under these conditions, a group of feeding traces has a spotty appearance on a vertically sectioned sediment surface perpendicular to the shoreline (Fig. 1(D)), and shows a relatively random orientation on a horizontally sectioned sediment surface (Fig. 1(E)). Here, we define this trace occurrence as Mode 1. In contrast, the worm moves preferentially landward under storm conditions (heavy erosion of the beach face) to avoid exhumation (Fig. 1(F)), and creates feeding burrows with elongate shapes on vertical sections of sediment, perpendicular to the shoreline (Fig. 1(G)). On the horizontally sectioned sediment surface, the traces show distinct preferred orientations (Fig. 1(H)). Here, we define this mode of trace occurrence as Mode 2. This plasticity in their subsurface movement pattern protects the *Thoracophelia* worms from excessive burial and washing out as a result of beach morphodynamics (Seike, 2008).

Biogenic sedimentary structures that are comparable to the feeding traces of *Thoracophelia* have been identified in ancient beach deposits, as the trace fossil *Macaronichnus segregatis* Clifton