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"Deep-sea bivalvian highways": An ethological interpretation of branched *Protovirgularia* of the Palaeogene Muroto-Hanto Group, southwestern Japan

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ABSTRACT

Well-preserved specimens of the trace fossil *Protovirgularia* occur in deep sea trough fills of the Palaeogene accretionary complex of the Muroto-Hanto Group in southwestern Japan. The trace fossil, occurring characteristically on the sole of sandstones of turbidite systems, is interpreted as an interstratal trail of a protobranch bivalve having a cleft foot. Among the Muroto-Hanto *Protovirgularia*, many specimens of branched variants have been found. Based on the morphological analyses, coupled with knowledge of the behaviour of the modern intertidal molluscs, the branched specimens are interpreted to have formed as the result of interstratal trail-following behaviour of the infaunal protobranchs. The animals probably followed trails of other individuals in order to save energy for locomotion. The incipient *Protovirgularia* was thus interpreted to have functioned as a "highway" for the infaunal mollusc. This is probably the first report of a trail-following behaviour of infaunal invertebrates.

1. Introduction

Trace fossils, fossilised records of animal behaviour (Seilacher, 1967), have long been used to reconstruct the ethology of benthic animals (cf. Seilacher, 2007). Such a role of trace fossils has attracted much attention in order to study the behaviour of infaunal animals (e.g., Bromley et al., 2007; Gingras et al., 2008), especially, in the cases of those living in deep-sea environments (Goldring, 1995), of which behaviour is commonly difficult to observe directly without using a highly expensive submersible. This is because ichnological studies of onshore rock records of deep-sea origin may conveniently provide us ecological insights of those animals.

From the Palaeogene deep-sea deposits of the Muroto-Hanto Group, southwestern Japan, many well-preserved specimens of the trace fossil *Protovirgularia* are found. The trace fossil is a somewhat straight interstratal trail characteristically found as a convex hypor-elief on a turbiditic sandstone. It has a median ridge or furrow and a series of bilaterally arranged, chevron-like protuberances. It is interpreted as a locomotion trace of a cleft-footed mollusc, such as the scaphopods or protobranchs (Seilacher and Seilacher, 1994; Ekdale and Bromley, 2001).

Protovirgularia has commonly been known as an unbranched burrow (cf., Uchman, 1998), except for a few examples of branched specimens reported by Mángano et al. (2002). Many specimens showing branching however are found in the Muroto-Hanto Group. Based on detailed analyses of their morphology and modes of occurrence, together with the knowledge of ethology of modern intertidal molluscs, the branched variants are interpreted to have formed through a particular interindividual behaviour of the proto-branchs, known as trail-following.

This paper describes morphologies and modes of occurrence of the trace fossils, and discusses their palaeoecological implications, on the basis of knowledge of interindividual behaviour of living molluscs.

2. Geological setting

The Muroto-Hanto Group, a Palaeogene accretionary complex, originally deposited in an oceanic trough of Palaeogene age (Katto and Taira, 1978; Taira et al., 1980, 1988, 1992), is widely distributed in the middle to southern part of the Muroto Peninsula, southwestern Japan (Fig. 1). The group, containing abundant specimens of *Protovirgularia*, crops out in some parts of the coastal areas. Observations were made in the coasts of the Hane and Gyodo points (Fig. 1), where the Naharigawa and Muroto formations of the group were well exposed, respectively.

2.1. Hane Point (Naharigawa Formation)

The middle to upper Eocene Naharigawa Formation (Taira et al., 1980) exposed at Hane Point is composed mainly of thickly bedded

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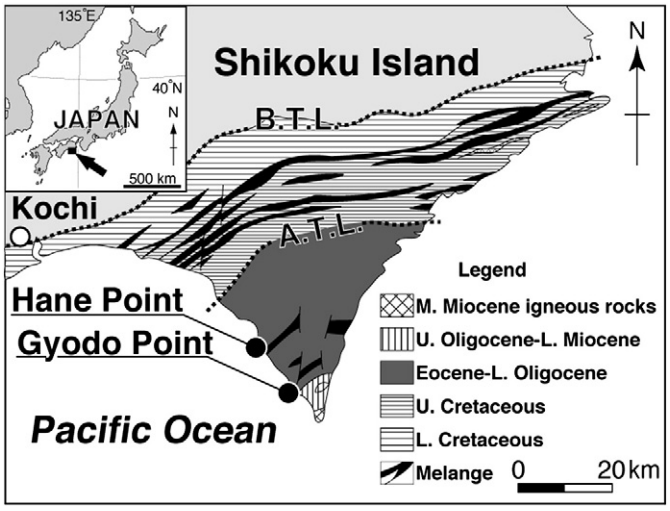

Fig. 1. Geological sketch map covering the study points in Shikoku Island situated in the southwestern part of the Japanese mainland. Modified after Taira et al. (1992). B.T.L. is the Butsuzo Tectonic Line that shows the northern boundary of the Cretaceous to Palaeogene accretionary complexes of the Shimanto Belt. A.T.L. is the Aki Tectonic Line that divides the Cretaceous and Palaeogene–Neogene accretionary complexes within the belt.

coarse-grained sandstones with intercalated thin layers of mudstones, and thinly alternating beds of fine-grained sandstones and mudstones (Fig. 2). Most of the beds were considered as turbiditic in origin (Muto, 1995).

The thickly bedded sandstones having groove-casted bottoms show overall normal grading, distinct amalgamations, and contain numerous water-escape structures or muddy rip-up clasts. These sandstones characteristically show overall fining-up facies successions.

On the other hand, sandstones of the thin alternations show parallel lamination, which may pass up into current ripple, or climbing current ripple cross-laminations. Palaeocurrent data obtained from the sandstones and the alternations are almost concordant within each unit. However, flow directions of the thick sandstones systematically deviate about 90° from those of the alternations (Fig. 2).

Taking these into consideration, the sediments are interpreted to have been deposited in a deep-sea channel-levee system (cf., Walker, 1985; Posamentier and Walker, 2006), developed in the oceanic trough in Palaeogene times. The overflowing currents that deposited the thin alternations on the levees were probably deflected from the main flow in the channel where the thicker sandstones were deposited.

Most specimens of *Protovirgularia* treated here occur on soles of the sandstones of probable levee deposits (Fig. 2). The thick sandstone

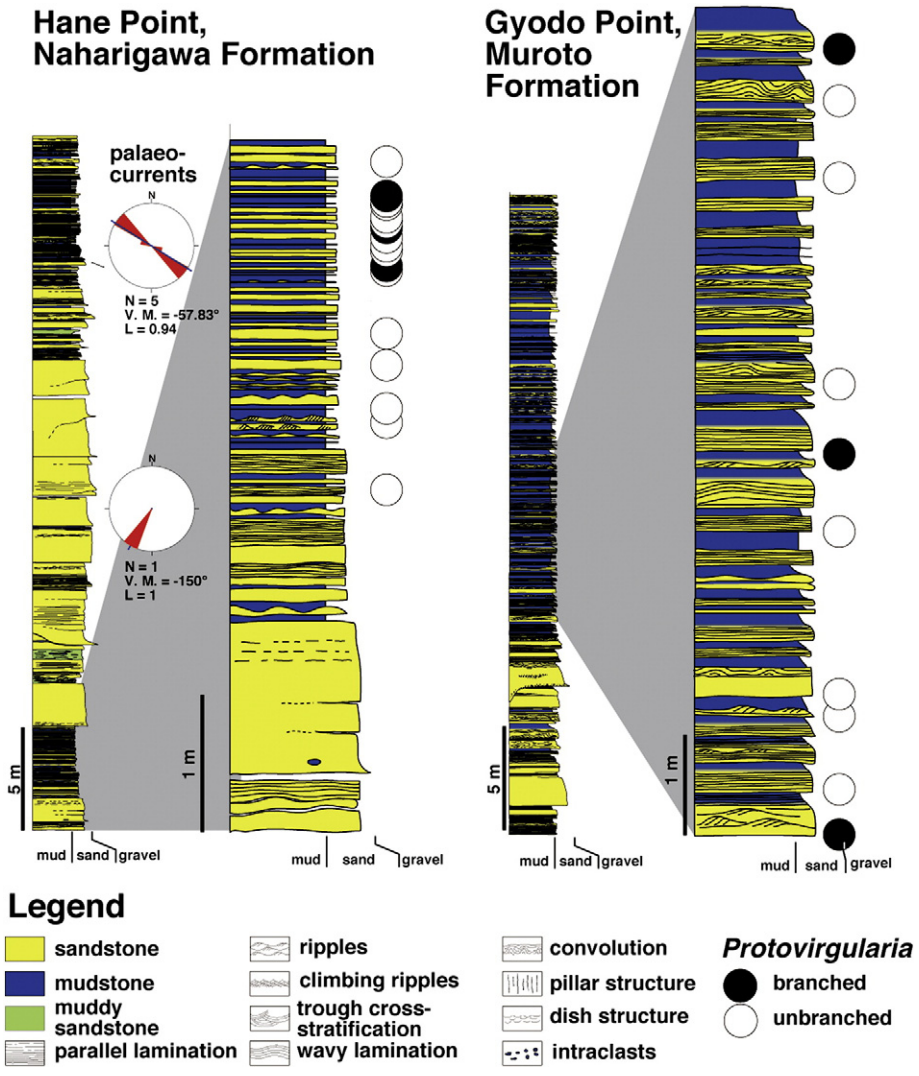

Fig. 2. Columnar sections of selected parts of the Naharigawa and Muroto formations, exposed in the Hane and Gyodo points, respectively. White and black circles represent horizons of unbranched and branched *Protovirgularia* occurrences, respectively. The trace fossils characteristically occur in the thinly alternating beds sandstone and mudstone of deep-sea levee.