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Original article

First report of the ichnogenus *Phymatoderma* from the Hayama Group (Miocene, Japan): Paleobiological and paleoecological implications☆

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ABSTRACT

The trace fossil *Phymatoderma* cf. *granulata* is described for the first time from the deep-marine deposits of the Hayama Group (Miocene) of Japan. This ichnotaxon is a burrow system composed of horizontal, straight to slightly curved tunnels ranging from 7.7 to 20.4 mm in diameter (mean = 14.98 mm), occasionally representing branching. Each tunnel is filled with ellipsoidal pellets with aspect ratios generally ranging from 1.4 to 2.4. Based on the comparison between the Hayama specimens and other *Phymatoderma* specimens from tectonically and paleoenvironmentally similar settings, a deep-sea echiuran worm is suggested as the possible trace-maker. Morphometric analysis demonstrates that the pellet aspect ratios do not show any correlation with the tunnel diameter, suggesting that there was not a significant change in digestive and/or excretory systems from the smaller to the larger trace-producing animals. In addition, microscopic analysis of the pelletal infill of *P.* cf. *granulata* revealed that the trace-maker actually fed on freshly deposited organic detritus and microorganisms, such as planktic foraminifera and radiolaria.

1. Introduction

The ichnogenus *Phymatoderma* Brongniart, 1849 is a morphologically distinctive, horizontal to subhorizontal burrow system comprising clusters of radiating tunnels filled with ellipsoidal pellets (Fu, 1991; Seilacher, 2007; Miller, 2011). Owing to the pelletal infill that has been interpreted as fecal pellets, *Phymatoderma* has been regarded as a product of a deposit feeder (Seilacher, 2007). Although Miller and his co-authors demonstrated that the *Phymatoderma*-producer was engaged in both surface and subsurface deposit-feeding activities (Miller and Aalto, 1998; Miller and Vokes, 1998), surface deposit-feeding behavior was more common in many cases (e.g., Izumi, 2012).

As pointed out by Miller and Vokes (1998), because of the morphological similarity with other ichnogenera such as *Chondrites* and *Zonarites*, *Phymatoderma* has generally been misidentified as "*Zonarites*", "large *Chondrites*", or "pellet-filled *Chondrites*" during the 1950s up to the 1990s (Simpson, 1957; Sellwood, 1970; Brenner and Seilacher, 1978; Savrda and Bottjer, 1989; Kotake, 1991). However, since Fu (1991) has successfully rectified the complicated ichnotaxonomic situation by re-describing *Phymatoderma*, and summarized the morphological difference between *Phymatoderma* and superficially similar ichnogenera, *Phymatoderma* has been correctly identified and recognized by geologists from many localities of various ages and environments (Miller and Aalto, 1998; Miller and Vokes, 1998; Leszczyński, 2004; Olivero et al., 2004; Ponce et al., 2007, 2008; Seilacher, 2007; Uchman and Gaździcki, 2010; Izumi, 2012, 2013, in press; Lima and Netto, 2012; Izumi et al., 2014; Izumi and Uchman, 2015; Izumi and Yoshizawa, in press). The current ichnotaxonomy of *Phymatoderma* was recently summarized by Miller (2011).

Although recent studies have especially focused on paleoecological interpretations of the trace-maker of *Phymatoderma* such as diet, mode of feeding, and interactions with other ichnogenera (Olivero et al., 2004; Miller, 2011; Izumi, 2012, 2013, in press; Izumi et al., 2014), the trace-maker itself could not be identified by these previous studies. However, in a very recent study by Izumi and Yoshizawa (in press), *Phymatoderma* and associated star-shaped horizontal trace fossil have been discovered from the Mio-Pliocene deep-marine Misaki Formation of Japan, leading these authors to conclude that the fecal pellets of *Phymatoderma* were excreted by an echiuran worm. Therefore, because the most likely trace-maker is now proposed (Izumi and Yoshizawa, in press), new discoveries of *Phymatoderma* and further paleoecological studies become increasingly important.

In this context, the present paper is the first report on the occurrence of *Phymatoderma* from the Miocene deep-marine Hayama Group, Miura Peninsula, central Japan. In addition to an

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in-depth systematic description of the newly-described specimens, paleobiological and paleoecological interpretations are discussed based on their morphometrical and microscopic analyses.

2. Geological and tectonic settings of the Miura Peninsula

The Miocene to Pleistocene sedimentary sequence in the Miura Peninsula, central Japan (Fig. 1), is characterized by a thick accumulation of alternating clastics and hemipelagic rocks with abundant synsedimentary deformation structures associated with tight folding and faulting, which are interpreted to have been formed in a convergent tectonic setting (Ogawa et al., 1985; Saito, 1992). In particular, the sedimentary sequence was controlled by the tectonics around the collision zone of the Izu-Bonin arc (i.e., subduction of the Philippine Sea Plate; Ogawa et al., 1985; Fig. 2). The distribution of this sedimentary sequence is separated by the Hayama-Mineoka uplift zone, which is located at the middle part of the Miura Peninsula (Fig. 1(A)) into the southern and northern areas (Kanamatsu et al., 2001; Hirata, 2012). The Hayama-Mineoka uplift zone is mainly composed of the Mineoka Group (Eocene–Oligocene ophiolitic rocks; Takahashi et al., 2012) and the Hayama Group (Miocene siliciclastic rocks; Ebiko and Shibata, 2012), but the Mineoka Group crops out only in the Boso Peninsula (Takahashi et al., 2012). The paleoenvironment of the Hayama-Mineoka uplift zone has been interpreted as an ancient trench-slope break (Kanamatsu et al., 2001; Fig. 2). The sedimentary sequence in the southern and northern parts of the Miura Peninsula is generally subdivided into the Miura Group (Middle Miocene–Pliocene), and the Pleistocene Kazusa Group and Miyata Formation (Fig. 1).

The Hayama Group crops out in the middle part of the Miura Peninsula (Fig. 1). In terms of lithology, the group is composed mainly of coarse-grained, poorly sorted sandstones, white- to pale

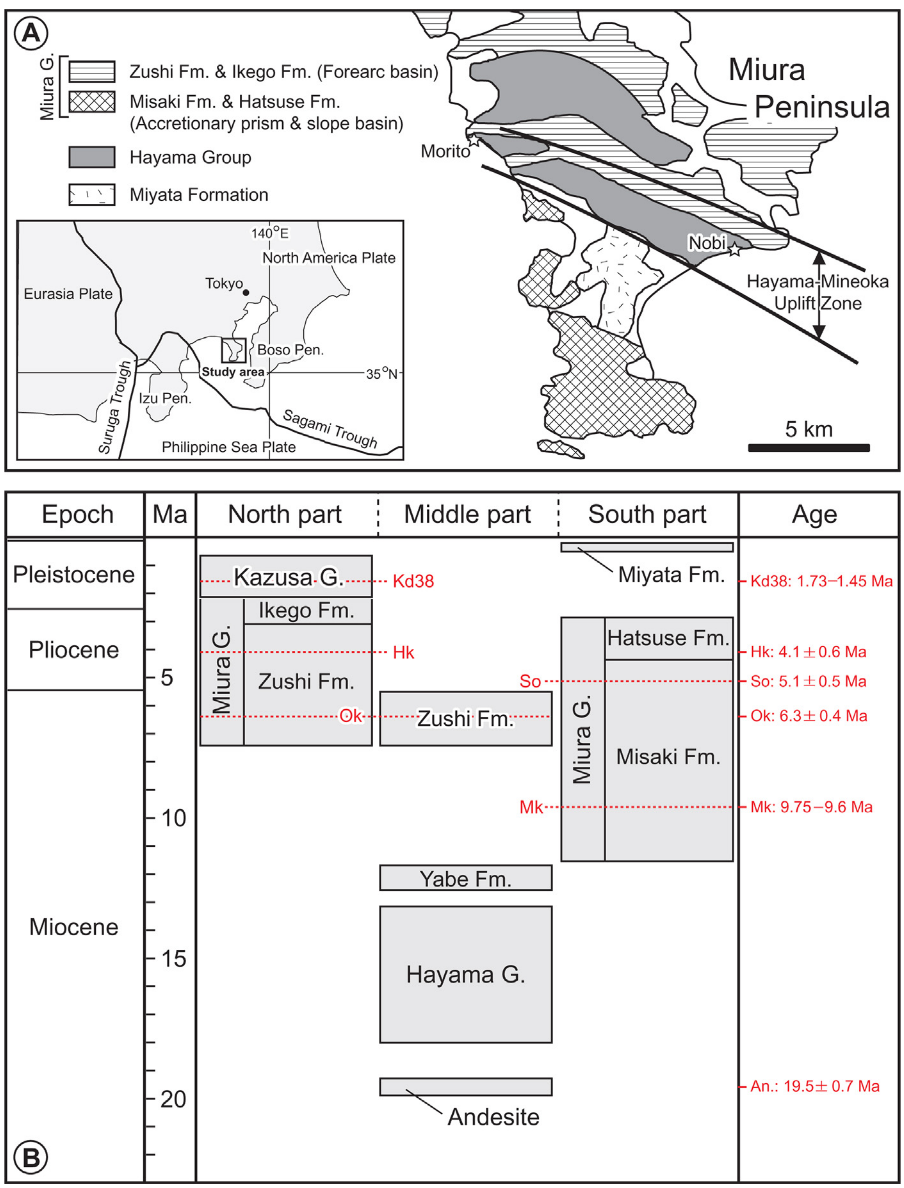

Fig. 1. Geology and stratigraphy of the Miura Peninsula, central Japan. **A**. Simplified geological map of the Miura Peninsula (modified from Kanamatsu and Herrero-Bervea, 2006 and Yamamoto et al., 2009). Plate boundaries are drawn based on Taira (2001). Sampled localities are indicated by open stars. GPS coordinates of each locality: Nobi: 35°12′36.5″N, 139°41′59.1″E; Morito: 36°16′18.9″N, 139°34′12.5″E. **B**. Simplified lithostratigraphy of the Miura Peninsula (slightly modified from Hirata, 2012, and Shibata, 2012). Ages of tuff key beds and igneous rocks are based on: Andesite: Imanaga and Yamashita (1999); Mk tuff: Yoshida et al. (1984); Ok tuff: Kasuya (1987); So tuff: Kasuya (1987); Hk tuff: Saito et al. (1997); Kd38 tuff: Fujioka et al. (2003).