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Star-shaped trace fossil and *Phymatoderma* from Neogene deep-sea deposits in central Japan: probable echiuran feeding and fecal traces

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Abstract.—A co-occurrence of the ichnogenus *Phymatoderma* and a star-shaped horizontal trace fossil was discovered from Neogene deep-marine deposits (Misaki Formation, central Japan), and is described herein for the first time. *Phymatoderma* consists of a straight to slightly curved tunnel that shows first- or second-order branches. The tunnels are 5.30–27.25 mm in diameter and are filled with ellipsoidal pellets. The relatively well-preserved star-shaped trace fossil is a large horizontal structure (~18 cm × 19 cm) that consists of at least 10 spokes with diameters ranging from 11.49–20.96 mm. As compared to modern analogous surface-feeding traces produced by abyssal echiuran worms and their burrow morphology, it is highly likely that the star-shaped trace fossil and *Phymatoderma* found from the Misaki Formation are feeding and fecal traces of ancient deep-sea echiurans, respectively. Difference in preservation potential between surface and subsurface traces may result in rare occurrence of star-shaped trace fossils as compared to *Phymatoderma*. Microscopic observation of the pelletal infill of *Phymatoderma* also reveals that the trace-maker fed on organic debris and microorganisms such as diatoms and radiolaria.

Introduction

Trace fossils generally provide meaningful information about the paleoenvironment in which the trace-producing animals lived, and they also shed light on the paleoecology of these organisms (e.g., Bromley, 1996; Buatois and Mángano, 2011). On the other hand, the paleobiology of trace fossils is much less understood because, in most cases, it is difficult to identify the trace-maker. However, for some ichnogenera (e.g., *Macaronichnus*, *Rosselia*, *Schaubcylindrichnus*, *Tasselia*), possible trace-makers can be identified by detailed observations of fossil specimens combined with the investigation of modern analogous or counterpart traces (Clifton and Thompson, 1978; Nara, 1995, 2006; Seike, 2007, 2008; Olivero and López Cabrera, 2010; Seike et al., 2011), thus making it possible to increase our understanding of the paleobiology of trace fossils. Herein, we describe the ichnogenus *Phymatoderma* and a star-shaped horizontal trace fossils from the same lithologic unit (Neogene Misaki Formation, central Japan), and compare these trace fossils to modern analogous biogenic structures to identify the trace-maker.

Phymatoderma is composed of distinctive, sub-horizontal burrow systems comprising clusters of radiating tunnels that are filled with pellets (Fu, 1991; Seilacher, 2007; Miller, 2011). *Phymatoderma* has been regarded as a product of a deposit-feeding worm-like animal because of the presence of the pelletal infill, which is generally interpreted as fecal origin (Seilacher, 2007). In addition, sedimentologic and geochemical studies have revealed that the *Phymatoderma* producer ingested surface sediments and subsequently excreted fecal pellets into the subsurface burrow (Miller and Aalto, 1998; Miller and Vokes, 1998; Izumi, 2012). Despite such understanding of the paleoecology, the actual *Phymatoderma*-producing animal has not yet been identified (Miller, 2011).

Kotake (1990, 1991) described the fecal pellet-filled 'giant *Chondrites*' from the Pliocene deep-marine Shiramazu Formation, central Japan, and suggested an abyssal echiuran worm as a possible trace-maker of 'giant *Chondrites*' based on indirect, circumstantial evidence. Subsequently, the pellet-filled 'giant *Chondrites*' was reinterpreted as *Phymatoderma* (Izumi, 2013). Although the conclusion of Kotake (1990) about the possible trace-maker is highly probable, there is no direct trace-fossil evidence that clearly indicates echiuran activities. In this context, newly found star-shaped trace fossils from the deep-sea Misaki Formation may represent significant specimens that substantiate abyssal echiuran feeding activities, which have been demonstrated by sea-floor photography (Ohta, 1984; Herring, 2002), and support Kotake's (1990) hypothesis. Therefore, in the present study, *Phymatoderma* and the star-shaped trace fossils found from the Misaki Formation are described and discussed in detail.

Geologic setting and depositional environment

Miocene–Pliocene marine deposits ascribed to the Misaki Formation are exposed in the southern part of the Miura Peninsula, central Japan (Fig. 1). The Misaki Formation, which is unconformably overlain by the Pliocene Hatsuse Formation

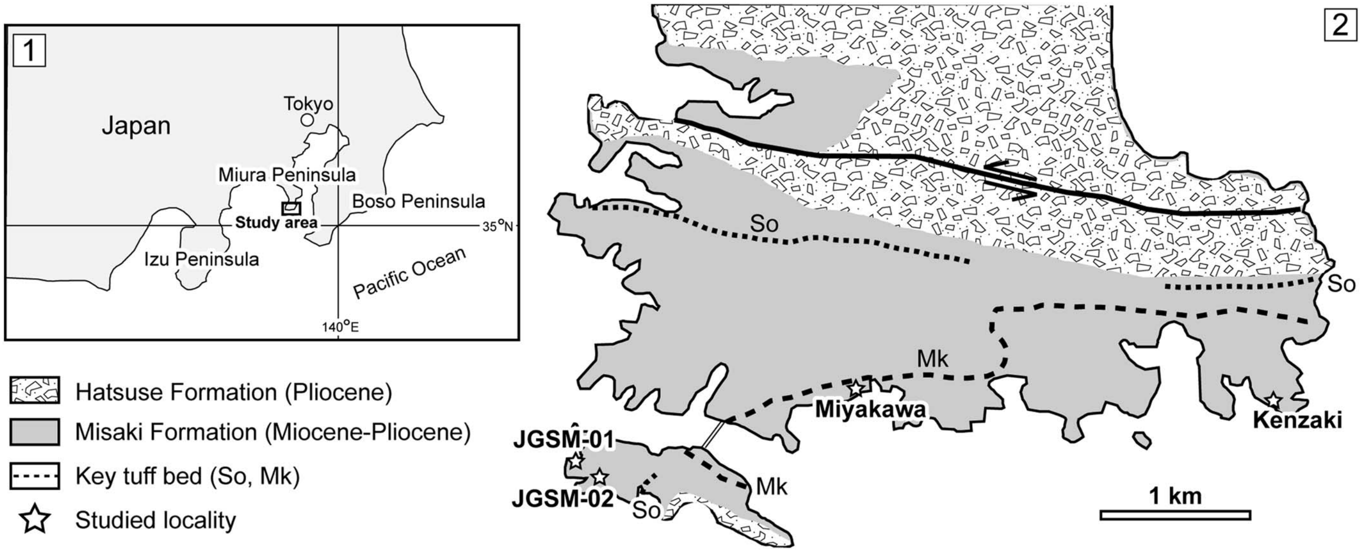

Figure 1. (**1**) Map of Japan showing the study area (southern part of the Miura Peninsula, central Japan). (**2**) Simplified geologic map of the southern part of the Miura Peninsula showing detailed localities of the four study sites (white stars). Modified from Yamamoto et al. (2009). GPS coordinates of each locality — JGSM-01: 35°08'09.7"N, 139°36'40.7"E; JGSM-02: 35°08'01.1"N, 139°36'43.5"E; Miyakawa: 35°08'28.2"N, 139°38'10.9"E; Kenzaki: 35°08'26.7"N, 139°40'32.6"E.

(Fig. 1.2), generally consists of fine-grained, light grayish-yellow siltstone and basaltic, lapilli-dominant volcaniclastic beds of pebble-to-sand size, which are known as scoria beds, with tuff intercalations (Lee and Ogawa, 1998). The fine-grained, light-colored siltstone is massive and forms a background that has been interpreted as hemipelagite deposits (Soh et al., 1989). The beds of volcaniclastic sandstone and conglomerate may reach a maximum thickness of several tens of centimeters, and occur as turbidite, bottom current, and fall deposits (Stow et al., 1998). The Hatsuse Formation is composed of scoriaceous lapilli and pumiceous beds of calc-alkaline composition (Taniguchi et al., 1991).

In the Misaki Formation, there are a few important and well-known key tuff marker beds (Fig. 1.2). Based on the age determination of the Mk and So key tuff beds combined with calcareous nannofossil age data, the depositional age of the Misaki Formation is approximately 9.75–4.50 Ma (Yoshida et al., 1984; Kanie and Hattori, 1991; Kanie et al., 1991). The Hatsuse Formation is assigned to stage CN10c (5.0–4.8 Ma; Berggren et al., 1995).

According to the benthic foraminiferal assemblage, the depositional setting of the Misaki Formation is interpreted to be a middle abyssal to abyssal environment with a water depth of 2000–3000 m (Akimoto et al., 1991; Kitazato, 1997). In contrast, a much shallower environment, with a water depth of less than 200 m, has been estimated for the Hatsuse Formation (Kodama et al., 1980).

Materials and methods

Trace fossils from the Misaki Formation exposed along the southern part of the Miura Peninsula were investigated at four localities (JGSM-01, JGSM-02, Miyakawa, and Kenzaki; Fig. 1.2). Various types of trace fossils, such as *Chondrites*, *Ophiomorpha*, *Planolites*, *Phycosiphon*, *Scolicia*, and *Zoophycos*, were recognized, and some have been reported in previous studies (Lee and Ogawa, 1998). In the present study, *Phymatoderma* and star-shaped horizontal trace fossils were found for the first time from the Misaki Formation, and are described and discussed in detail.

Observations and measurements of the morphometric parameters of *Phymatoderma* and star-shaped trace fossils were primarily carried out in the field; however, some parameters of the star-shaped trace fossils were measured using the image-processing program ImageJ. In the laboratory, thin-section and SEM observations of the pelletal infill of *Phymatoderma* were performed to reveal the actual food source for the trace-maker. For SEM analysis, we used a field emission scanning electron microscope (FE-SEM; JSM-7000F, JEOL) at the Department of Earth and Planetary Science, Graduate School of Science, The University of Tokyo. In the preparation of material for microscopic analysis, small chips of *Phymatoderma*-bearing rocks were cut and attached to glass slides (28 × 48 mm), and were then polished with a graded series of carborundum.

Repository and institutional abbreviation.—Trace-fossil specimens, including thin sections and polished sections, are housed at The University Museum, The University of Tokyo, Tokyo, Japan (UMUT-CW). Specimen list is available in the Supplemental Data.

Systematic ichnology

Ichnogenus *Phymatoderma* Brongniart, 1849
Phymatoderma isp.
Figures 2–5

Specimens.—Approximately 80 specimens studied in the field in JGSM-01, Miyakawa, and Kenzaki, twelve specimens collected (UMUT-CW31690, 31692, 31693, 31697–31705), two thin sections (UMUT-CW31694, 31695) and two polished sections (UMUT-CW31691, 31696).

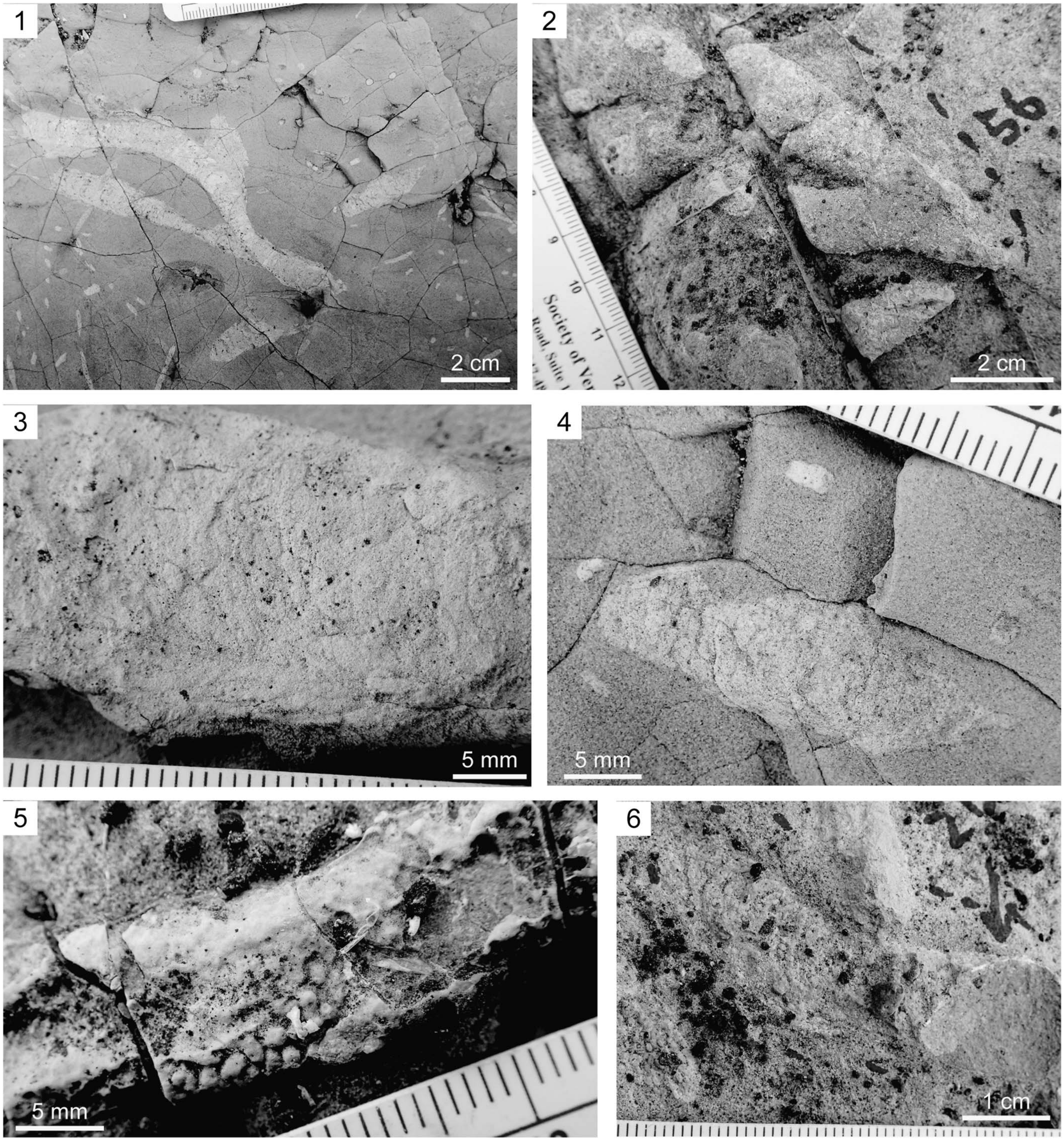

Figure 2. Field photographs of *Phymatoderma* from the Misaki Formation (all views nearly parallel to the bedding plane). (**1**) Overall view of *Phymatoderma* showing partly overlapped second-order branched tunnels; note the co-occurrence of *Chondrites* with much smaller diameters; JGSM-01 section. (**2**) Magnified photograph of *Phymatoderma* emphasizing the first-order branching; Kenzaki section. (**3**) Magnified view of the tunnel pelletal infill; Miyakawa section. (**4**) Magnified photograph of the tunnel showing well-preserved pelletal infill; JGSM-01 section. (**5**) Magnified view of the tunnel and pellets with three-dimensional preservation; Kenzaki section. (**6**) Magnified photograph showing meniscate structures; Kenzaki section.

Description.—A burrow system composed of horizontal to subhorizontal, straight to slightly curved tunnels with an ellipsoidal cross-section. The tunnels are mostly parallel to the bedding planes, representing first-order, and less commonly second-order branches (Fig. 2.1, 2.2), which overlap in some cases (Fig. 2.1). Although rare, in the vertical cross-sectional view, the tunnels extend slightly upward in direction (Fig. 3). Each tunnel is stuffed with ellipsoidal pellets, which generally show white to light-gray color with minor amounts of black scoria grains (Figs. 2.3–2.5, 3). In some specimens, the tunnels were

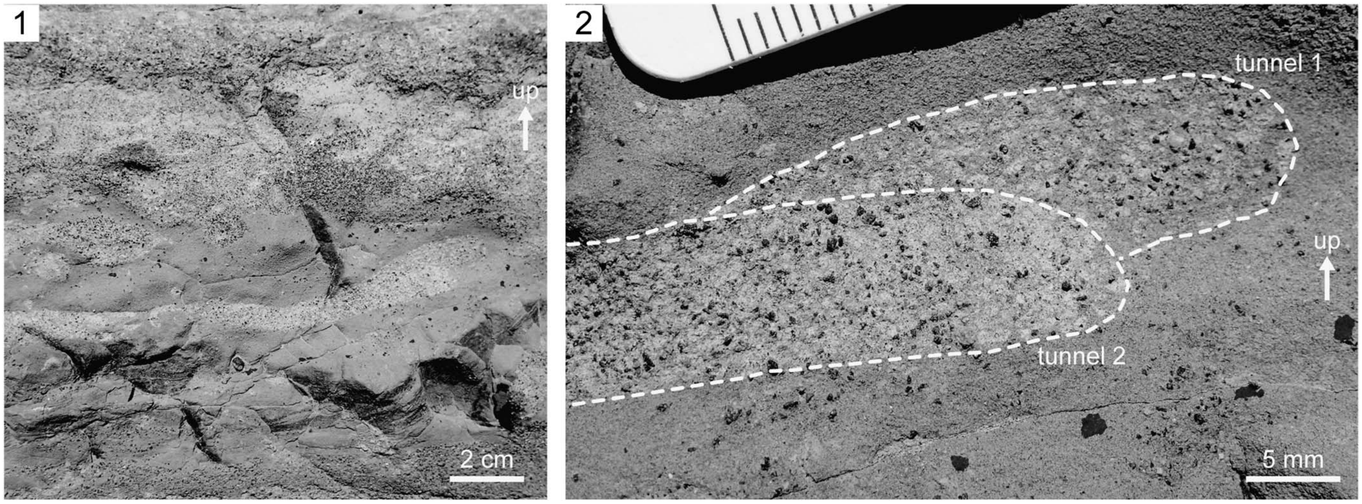

Figure 3. Field photographs of *Phymatoderma* tunnels extending in a slightly upward direction; vertical cross-sectional view; JGSM-01 section. (**1**) Overall view. (**2**) Close-up photograph of the tunnels displaying an upward direction; pellets are relatively well preserved and consist of white-colored sediments with minor amounts of black scoria grains; note the partial overlap of tunnel 1 and tunnel 2; dotted lines represent the contour of the tunnels.

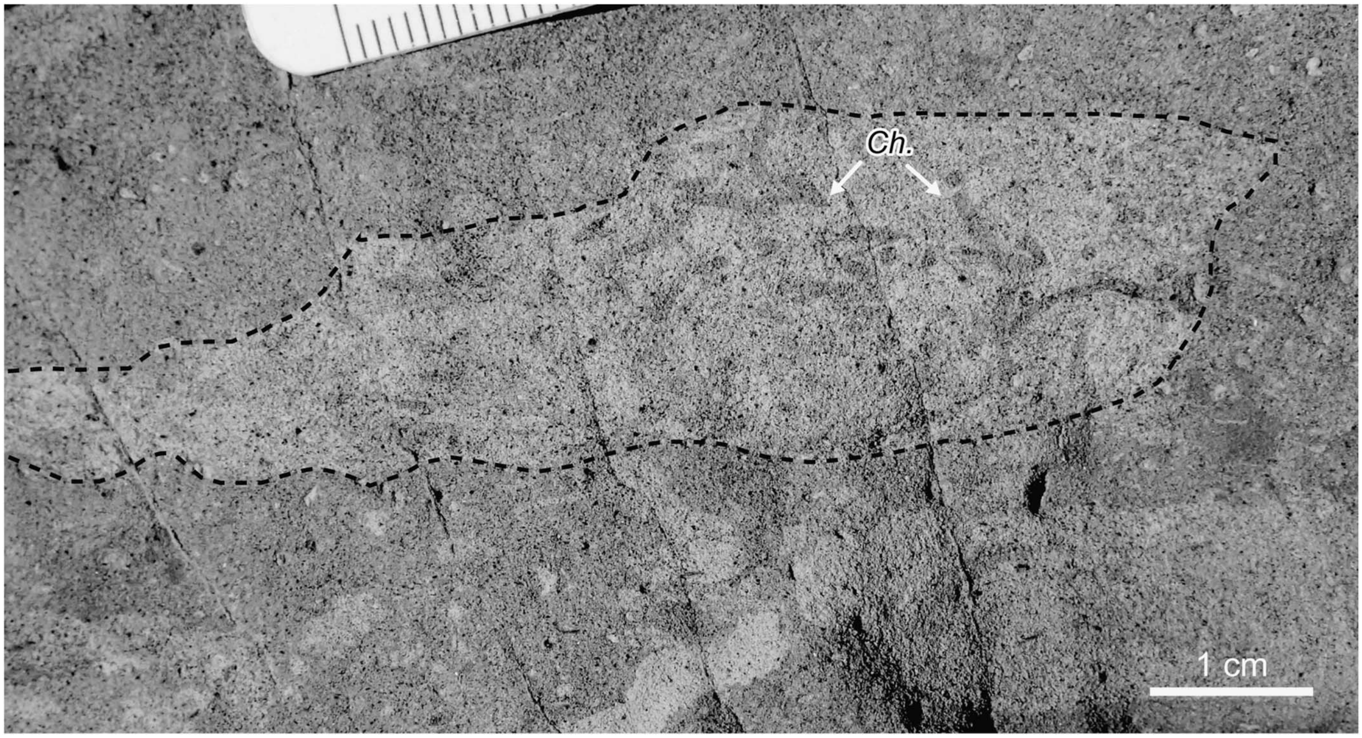

Figure 4. Field photograph of the composite *Phymatoderma*, which was reburrowed with *Chondrites* (white arrows); vertical cross-sectional view; Miyakawa section; dotted line represents the contour of the tunnel.

reburrowed with *Chondrites* (Fig. 4). The tunnels are highly compressed in most cases; however, three-dimensional preservation is evident in some tunnels and pellets at Kenzaki section (Fig. 2.5). The tunnel diameters, which were measured nearly parallel to the bedding plane, range from 5.30–27.25 mm, with a mean value of 13.97 mm (n = 76; Fig. 5). The branching angle is basically constant in a single specimen (ca. 25–40°; Fig. 2.1, 2.2). Both the tunnels and pellets have no linings. In some specimens, pellets are organized in meniscate structures (Fig. 2.6). However, in other tunnels, such meniscate structures are either nonvisible or only weakly visible (Fig. 2.3).

Remarks.—Although these trace fossils might be ascribed to *Phymatoderma granulata* von Schloteim, 1822 or *Phymatoderma melvillensis* Uchman and Gaździcki, 2010, the exact classification is difficult. Tunnels filled with pelleted sediments that show local meniscate structure is a diagnostic feature of *P. melvillensis* (Uchman and Gaździcki, 2010), which can also be recognized for the present specimens (Fig. 2.6). On the other hand, Miller and Vokes (1998) recognized withdrawal structures within the tunnels of *P. granulata*. However, the occasional occurrence of the primary successive branches in the specimens examined (Fig. 2.1) has never been observed in

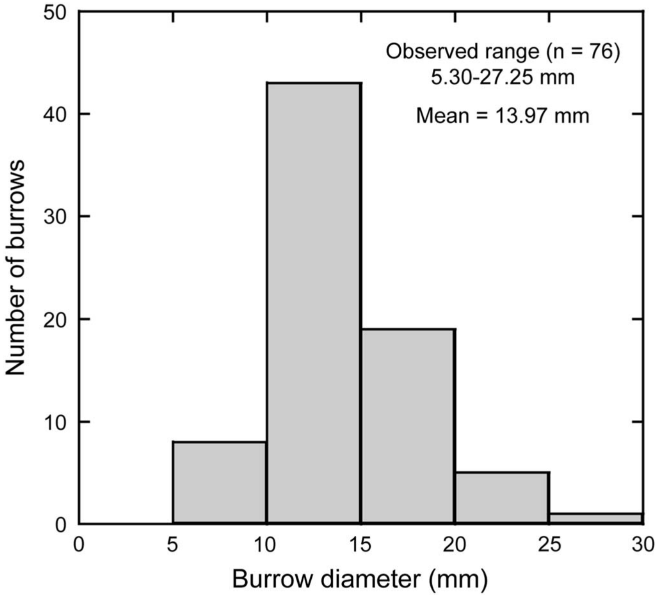

Figure 5. Size distribution of *Phymatoderma* from the Misaki Formation.

P. melvillensis (Uchman and Gaździcki, 2010; Mazumdar et al., 2011; Izumi and Uchman, 2015); instead, these features are commonly recognized in *P. granulata* (Izumi, 2012). Therefore, specimens with preserved better branching patterns are required to resolve the current ambiguous classification.

Indeterminate star-shaped trace fossil
Figure 6

Specimens.—Two specimens studied in the field in JGSM-02.

Description.—The nearly complete specimen (specimen 1; Fig. 6) is a relatively large star-shaped (i.e., rosetted) horizontal trace fossil, which consists of a set of many spokes radiating from the center (Fig. 6.2). The specimens occur horizontally in the bedding plane (top surface) of the black scoriaceous conglomerate (Fig. 7). The overall size of specimen 1 is 18 × 19 cm (Fig. 6.3). Some spokes show sharp contours; however, other spokes amalgamate with contiguous spokes, which leads to ambiguous contours (Fig. 6.3). In some cases, several spokes overlap near the center, resulting in branched morphology (Fig. 6.2, 6.3). Spokes are filled with light-gray to yellowish, fine-grained sediments and covered with scarce black, coarse scoria grains (Fig. 6.2). Infilling fine-grained sediments are homogenous (Fig. 6.2). Lithologic composition and color of the main infill of the spokes are remarkably different from the surrounding host scoriaceous conglomerate, and instead resemble and reflect the underlying fine-grained hemipelagite (Figs. 6.1, 7). The exact number of spokes cannot be determined because of the overlapping and/or amalgamation of the spokes, but at least ten spokes can be clearly recognized in specimen 1 (Fig. 6.3). At least three spokes are preserved in the case of the incomplete specimen (specimen 2; Fig. 6.3). The spoke diameters, which were measured nearly parallel to the bedding plane, range from 11.49–20.96 mm for specimen 1 (mean value = 15.94 mm; n = 10) and 12.40–16.20 mm for specimen 2 (mean value = 13.77 mm; n = 3). Morphometric parameters are also summarized in Table 1.

Remarks.—The ichnogenus *Dactyloidites* Hall, 1866 has a similar rosetted morphology (Fürsich and Bromley, 1985; Gibert et al., 1995; Uchman and Pervesler, 2007). The diagnostic feature of *Dactyloidites* is the vertical radial spreite structure having a central shaft (Fürsich and Bromley, 1985), although spreite are occasional (Wilmsen and Niebhur, 2014). However, the present specimens are clearly horizontal surface traces that lack vertical shafts and spreiten structures (Fig. 6), thus they are not ascribed to *Dactyloidites*. Alternatively, the present specimens may also be similar to the ichnogenus *Glockerichnus* Pickerill, 1982, which is a star-shaped sole trail with numerous ribs radiating from the center. However, the rare occurrence of the star-shaped trace fossil from the Misaki Formation prevents accurate classification.

Microscopic observation of the pelletal infill of *Phymatoderma*

Dark-brown to black amorphous organic debris of various sizes are recognized in thin sections and are abundant within the pelletal infill of *Phymatoderma* (Fig. 8.1), along with inorganic mineral particles that are the main component. SEM observations revealed the presence of various types of microfossils (e.g., diatoms, radiolaria) in the pelletal infill (Fig. 8.2–8.6). In most cases, the diatom tests within the pellets were mostly discrete test fragments (Fig. 8.2). Although much less common, relatively well-preserved diatoms such as *Stephanopyxsis* sp. (Fig. 8.3) and *Paralia* sp. (Fig. 8.4) were occasionally observed. The preservation of radiolaria was generally better than that of diatoms (Fig. 8.5, 8.6).

Discussion

Comparison with modern analogues and likely trace-maker.—To identify the animal that most likely produced the specific trace fossils, it is useful to compare them to modern analogous traces. The relatively large star-shaped horizontal trace fossil is closely similar to surface-feeding traces produced by echiuran worms, which have been recognized on modern deep-sea floor (Ohta, 1984; Herring, 2002). Among the modern analogous star-shaped surface feeding traces, Type IV traces described by Ohta (1984), whose possible producers are echiuran worms, are most similar to the present fossil specimens (Figs. 6, 9; see also Ohta, 1984, fig. 4).

Not only are overall morphologic similarities between the fossil specimens and modern analogues evident (Figs. 6, 9), but dimension and the number of spokes are also similar (discussed below; Table 2). Namely, lengths of spokes of modern type IV star-shaped traces range from 86–152 mm (Ohta, 1984, table 1). Although Ohta (1984) did not describe the overall size of the type IV traces, the overall size ranges from ~17.2 cm-radius (= 86 mm × 2) to 30.4 cm radius (= 152 mm × 2). The star-shaped trace fossil from the Misaki Formation (specimen 1) is ~18 cm × 19 cm (Fig. 6.3), which is probably within the range of Ohta's (1984) type IV traces. In addition, the spoke diameters of both modern and fossil specimens are also very similar (Table 2). In the case of fossil specimen 1 from the Misaki Formation, the spokes are 11.49–20.96 mm in diameter

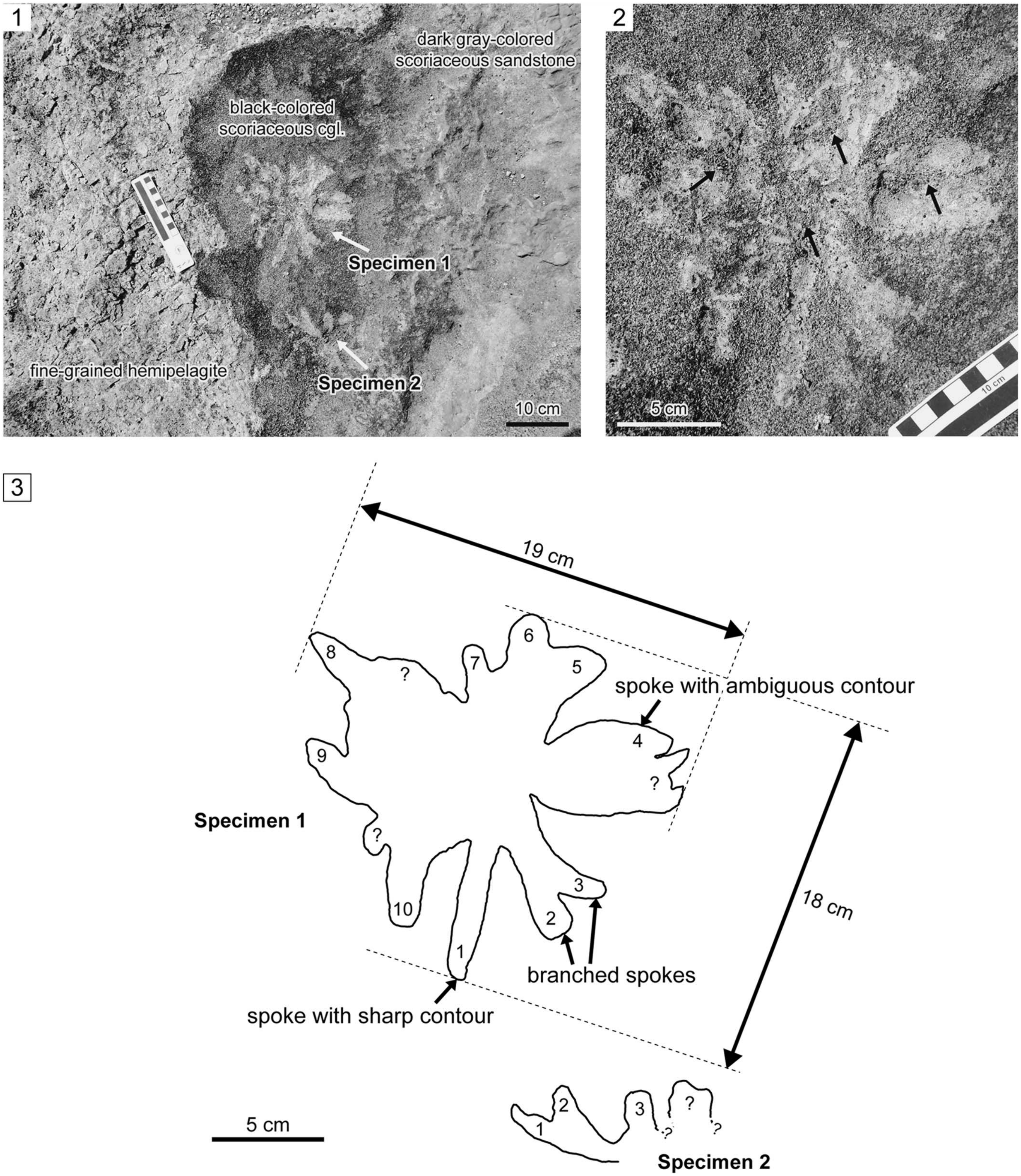

Figure 6. Star-shaped horizontal trace fossils from the Misaki Formation; view parallel to the bedding plane; JGSM-02 section. (**1**) General view of the two specimens. (**2**) Magnified view of the relatively well-preserved specimen (specimen 1); note that the spokes are mainly filled with light-gray to yellowish, fine-grained sediments (hemipelagite), with minor amounts of coarser scoria grains (arrows), which might have been derived from the overlying scoriaceous sandstone. (**3**) Sketch of specimen contours; each obvious spoke is numbered serially.

(Table 1), which is also within the range of the recorded spoke diameters of the modern type IV traces (10.70–26.50 mm; Ohta, 1984). Both fossil and modern star-shaped traces also have a comparable number of observed spokes (Table 2). At least 10 spokes can be distinguished in fossil specimen 1 (Fig. 6.3), and Ohta (1984) observed 12–20 spokes in the type IV traces. Type IV traces have smaller numbers of spokes than other types of modern deep-sea star-shaped traces (type II, III; Ohta, 1984), but are quite similar to fossil specimen 1. Lastly, bathymetry of both modern and fossil traces is quite similar (Table 2), which occur in deep-water settings with water depth of more than 2000 m (Ohta, 1984; Akimoto et al., 1991; Kitazato, 1997). These lines of evidence suggest that the star-shaped horizontal trace fossils from the Misaki Formation are the feeding traces produced by surface deposit-feeding activity of echiuran worms (Fig. 10).

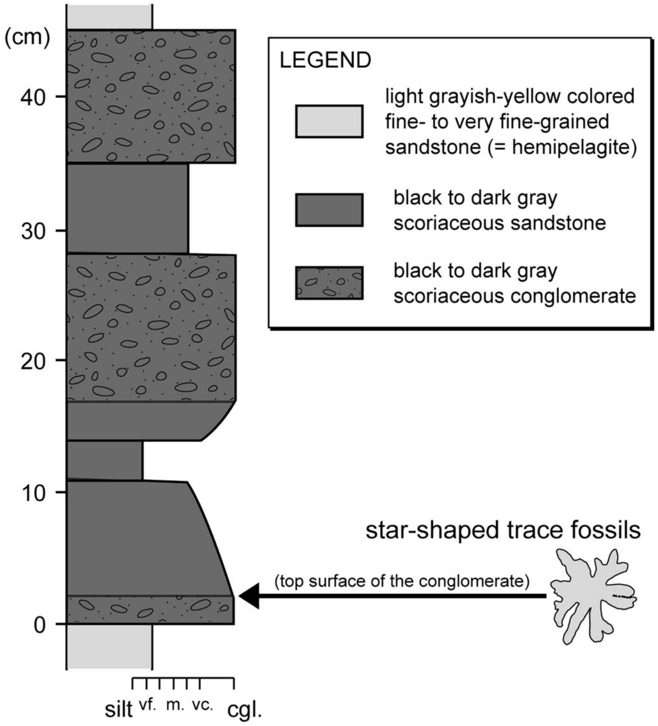

Figure 7. Lithologic column near the occurrence horizon of the star-shaped trace fossils. Note that the star-shaped trace fossils occur horizontally in the bedding plane (top surface) of the black scoriaceous conglomerate, which is indicated by an arrow.

The pellets of *Phymatoderma* have been interpreted as fecal pellets that were excreted by a surface deposit-feeding producer and were stuffed within the burrow (Miller and Aalto, 1998; Miller and Vokes, 1998; Izumi, 2012). Considering that both *Phymatoderma* and star-shaped trace fossils occur in the same lithologic unit (Misaki Formation), it is reasonable to presume that *Phymatoderma* from the Misaki Formation represents the fecal pellets excreted by deposit-feeding echiuran worms (Fig. 10). Abyssal echiuran worms typically produce L-shaped burrows (de Vaugelas, 1989), and the fecal pellets resulting from deposit-feeding activity on the sediment surface may be excreted and retained in the burrow (Ohta, 1984). Such a mode of excretion (e.g., fecal pellets stuffed within the burrow) has been known also for the shallow-water echiuran worm *Echiurus* (see Elders, 1975); thus, this may be considered a common excretion mode of echiurans. Some of the subsurface fecal pellets excreted by ancient deep-sea echiuran worms might have been preserved in *Phymatoderma*, as illustrated in Figure 10. Vertical cross-sectional views of *Phymatoderma* from the Misaki Formation occasionally show upward branching (Fig. 3), which implies that the trace-maker of *Phymatoderma* produced J-shaped burrow in some cases (Fig. 10). J-shaped burrows made by echiuran worms have been observed in *Maxmuelleria lankesteri* (see Nickell et al., 1994, fig. 2c), although this species lives in the muddy sediments of shallow-marine environments (Nickel et al., 1994). In addition, it is worthwhile to compare the sizes of *Phymatoderma* from the Misaki Formation with those of the central holes of Ohta's (1984) type IV traces, because the tunnel diameter of *Phymatoderma* and the central hole of the echiuran feeding trace might roughly correspond to the body width of the producers. Because of the lack of the original description by Ohta (1984), the widths and lengths of the central holes of type IV traces (Ohta, 1984, fig. 4) were measured using an image-processing program (Image J). As a result, the width and length of the central hole range from 15.16–21.95 mm and 25.75–26.73 mm, respectively (Table 2), which are within the range of the tunnel diameter of *Phymatoderma* (5.30–27.25 mm; Fig. 5). This similarity in size may also support our interpretation that both star-shaped trace fossils and

Table 1. Morphometric parameters of the studied star-shaped horizontal trace fossils from the Misaki Formation; SD = standard deviation; mm = millimeters.

Locality	Specimen	Spoke number (Fig. 6.3)	Spoke diameter (mm)	Mean (mm)	SD (mm)
JGSM-02	1	1	14.50	15.94	2.67
		2	18.45		
		3	14.15		
		4	16.60		
		5*	20.96		
		6*	16.47		
		7*	11.49		
		8	17.20		
		9*	15.97		
		10	13.60		
	2	1	12.70	13.77	2.11
		2	12.40		
		3	16.20		

*Measured in the lab using an image-processing program called ImageJ

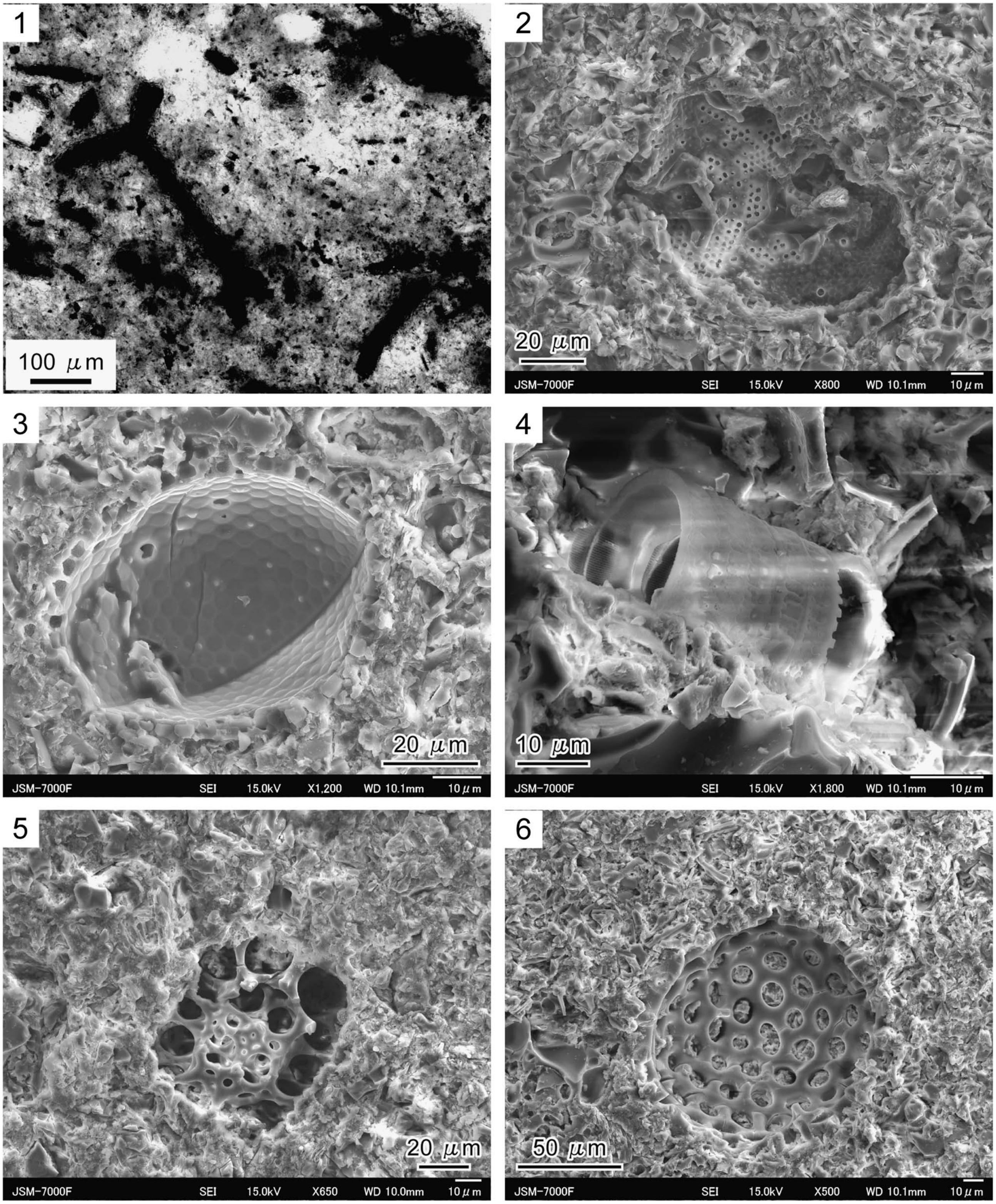

Figure 8. Photomicrographs of the pelletal infill of *Phymatoderma* from the Misaki Formation; thin-section (**1**) and SEM (**2–6**) images; samples UMUT-CW31694 and UMUT-CW31696 from Miyakawa section were used for thin-section and SEM observations, respectively. (**1**) Photomicrograph emphasizing the presence of amorphous dark-gray to black organic debris. (**2**) Fragment of diatom microfossil. (**3**) Diatom genus *Stephanopyxsis*. (**4**) Diatom genus *Paralia*. (**5**, **6**) Indeterminate radiolarian.

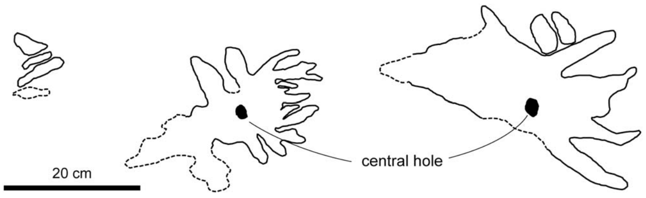

Figure 9. Sketch of modern star-shaped feeding traces produced by abyssal echiuran worms (type IV traces by Ohta, 1984, fig. 4, redrawn). Central holes are present (arrows); dotted lines represent the ambiguous contour of the traces. Note the general similarity of overall morphology between these traces and the star-shaped trace fossils from the Misaki Formation (Fig. 6).

Table 2. Comparison of the present star-shaped trace fossils with their modern analogous echiuran feeding traces; mm = millimeters; cm = centimeters.

	Star-shaped traces	
	*Fossil specimen	*Modern analogue
Overall morphology	Simple rosette	Simple rosette
Central structure	–	Hole
**Length of hole (mm)	–	25.75–26.73
***Width of hole (mm)	–	15.16–21.95
Length of spoke (mm)	–	86–152
Width of spoke (mm)	11.49–20.96	10.70–26.50
Overall size	18 × 19 cm	ca. 17.2 cm-radius to 30.4 cm-radius
Maximum number of spokes observed	>10	12–20
Water depth (m)	ca. 2000–3000	2635–5025
Remark	Fig. 6	Fig. 9; fig. 4 in Ohta (1984)

*Fossil specimen: Specimen 1 from the Misaki Formation described by this study.
*Modern analogue: type IV traces described by Ohta (1984).
**Longer axis of the central hole, which was measured using fig. 4 in Ohta (1984).
***Shorter axis of the central hole, which was measured using fig. 4 in Ohta (1984).

Phymatoderma from the Misaki Formation were feeding and fecal traces of ancient abyssal echiuran worms (Fig. 10).

On the basis of comprehensive studies of the pellet-filled *Zoophycos* from the Neogene deep-marine deposits exposed in the southern part of the Boso Peninsula, central Japan, Kotake (1990, 1992, 1995) assumed that the abyssal echiuran worm was a possible trace-maker of *Zoophycos*. Indeed, *Zoophycos* was also observed from the Misaki Formation by previous authors (Lee and Ogawa, 1998) and during our fieldwork at the Kenzaki section. However, pellets are only weakly visible or nonvisible in the Misaki *Zoophycos*. Although this study cannot exclude the possibility that *Zoophycos* was also a fecal trace made by deep-sea echiuran worms, the overall complex morphology of pellet-filled *Zoophycos* (Kotake, 1989, 1992, 1995) does not resemble the previously known echiuran burrow morphology (de Vaugelas, 1989; Nickell et al., 1994); thus, our interpretation that the deep-sea *Phymatoderma* was produced by echiuran worms (Fig. 10) seems more probable.

Chronologic comparisons.—During the Phanerozoic, the oldest known body-fossil evidence of echiuran worms is *Coprinoscolex ellogimus*, which was described from the Middle Pennsylvanian Francis Creek Shale of the Mazon Creek area, northeastern Illinois (Jones and Thompson, 1977). The oldest known record of *Phymatoderma* is *P. burkei* from the Permian Teresina Formation of Brazil (Lima and Netto, 2012). However, considering the records of '*Chondrites granulatus*' that are now interpreted as *Phymatoderma granulata* (e.g., Fu, 1991; Miller, 2011; Izumi, 2012, 2013), the oldest known *C. granulatus* was found from the Carboniferous Limestone in Bristol (Simpson, 1957). The temporal coincidence of the oldest known Phanerozoic evidence of both echiuran body fossil and *Phymatoderma* may further reinforce the possibility that *Phymatoderma* is an echiuran fecal trace fossil (Fig. 10).

Preservation potential.—The occurrence of the star-shaped trace fossil is far rarer than that of *Phymatoderma*, in the case of the Misaki Formation. This may be related to the difference in preservation potential between surface and subsurface biogenic structures. As discussed above, the star-shaped trace fossils are interpreted as surface feeding traces produced by a probable echiuran worm (Fig. 10). On the other hand, fecal pellets excreted within the subsurface burrows may be preserved in *Phymatoderma* (Fig. 10), although *Phymatoderma* generally occupies a relatively shallow tier (e.g., Miller and Vokes, 1998).

It is reasonable to assume that the deeper a trace is produced below the surface, the higher its preservation potential; thus, surface traces have a very small chance of being preserved (Wetzel, 2010). Despite the low preservation possibility of surface traces, it has been inferred that the preservation filter is switched off by non- or low-erosive event deposits (e.g., volcanic ash, distal turbidites) that prevent further bioturbation below (Wetzel, 2010). This process enables surface traces to be observed on the sediment surface, as presented by previous authors (e.g., Ekdale and Berger, 1978; Kitchell et al., 1978; Gaillard, 1991; Wetzel, 2008). In fact, the star-shaped horizontal trace fossils from the Misaki Formation can be observed just on the sediment surface (Fig. 6). The star-shaped trace fossils are overlain by volcaniclastic (scoriaceous) sandy sediments, which are interpreted to have been deposited quickly (Lee and Ogawa, 1998); and this may have prevented further erosion of surface traces by bioturbation.

Diets of the trace-maker.—Potential food sources for deposit feeders are fresh organic fractions such as microbes, plankton, meiofauna, microalgae and non-living organic matter in ingested sediment particles (Lopez and Levinton, 1987; Levinton, 1989; Mayer, 1989). Therefore, in the case of fossil fecal pellets excreted by deposit feeders, it is reasonable to assume that organic matter and/or microfossils preserved within the pellets were the actual diets of the producers. In particular, amorphous organic debris (phytodetritus) and various types of microfossils (coccoliths, dinoflagellates, and planktic foraminifer) have been actually observed within the pelletal infill of *Phymatoderma* (Miller and Vokes, 1998; Olivero et al., 2004; Miller, 2011; Izumi, 2013; Izumi et al., 2014). This study provides new evidence that amorphous organic debris and siliceous microfossils (e.g., diatoms and radiolaria) are preserved in the fecal pellets of *Phymatoderma* from the Neogene Misaki Formation (Fig. 8), strongly suggesting that such materials were the main dietary sources for the trace-maker (Fig. 10). Considering that calcareous nannofossils and foraminifers are recognized from the Misaki Formation (Kanie et al., 1991; Kitazato, 1997), these microorganisms might have also been fed upon by the *Phymatoderma*-producer; however, microscopic observations by this study did not detect calcareous nannofossils or foraminifers.

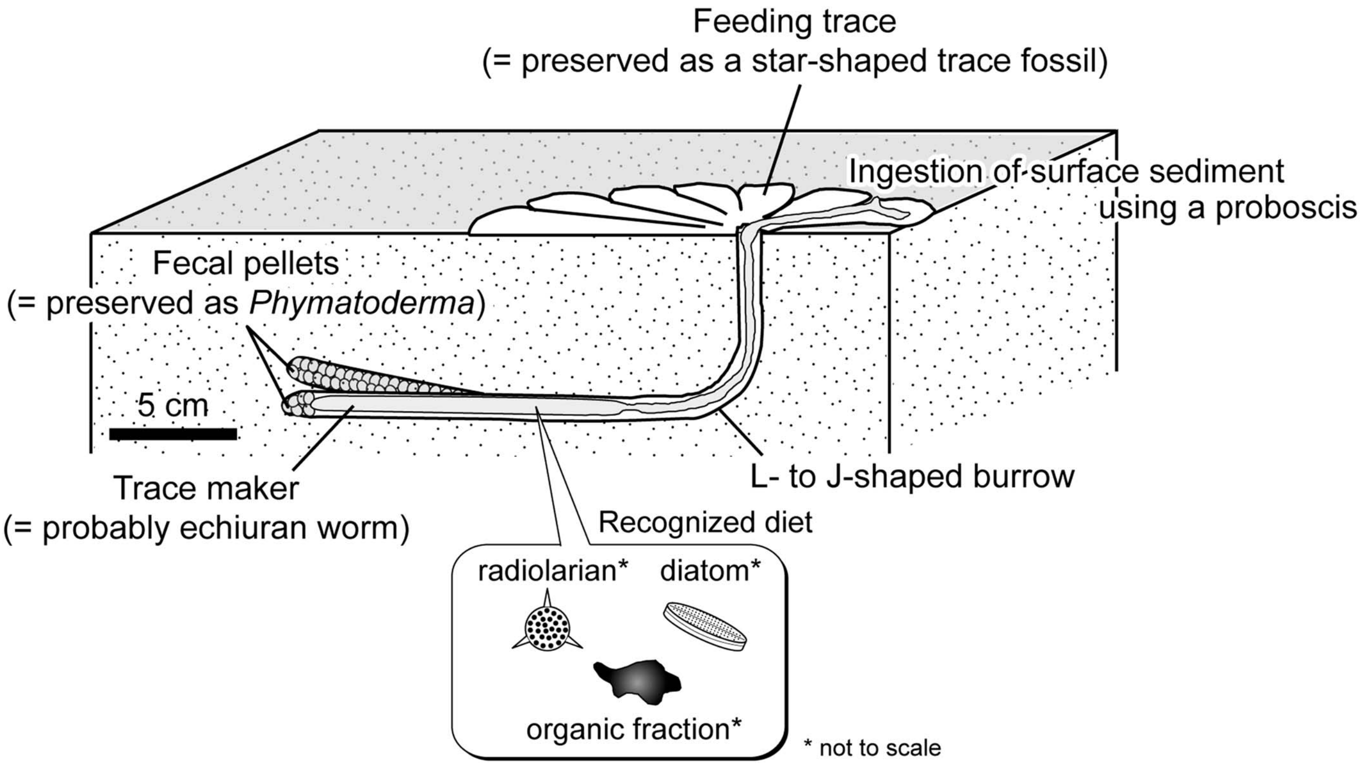

Figure 10. Schematic diagram reconstructing the formation process of *Phymatoderma* and the star-shaped trace fossils from the Misaki Formation. Both types of trace fossils were probably produced by abyssal echiuran worms. The star-shaped trace fossil may have been a surface-feeding trace produced by deposit-feeding activity, whereas *Phymatoderma* is interpreted to have been subsurface fecal pellets excreted in the L- or J-shaped burrow by the trace-maker. Echiuran feeding trace and burrow were drawn based on de Vaugelas (1989). Because the star-shaped feeding traces are surface biogenic structures, the preservation potential might be much lower than that of the subsurface fecal pellets. Microorganisms (e.g., diatom, radiolarian) and fresh organic fraction may have been the actual food source for the trace-maker.

Among such various microorganisms, diatoms might have played an extremely significant role as a dietary source for the *Phymatoderma*-producer because diatoms have relatively higher blooming rate than other blooming phytoplankton such as calcareous nannoplankton (Margalef, 1979; Furnas, 1990; Hüneke and Henrich, 2011).

In general, phytodetrital organic matter is much more important than terrigenous organic matter for deep-sea benthos because there is usually little or infrequent flux of terrestrial organic debris to the deep-sea floor, whereas sinking phytodetritus is continuously delivered through the water column to the seafloor despite seasonal fluctuation (Alldredge and Cohen, 1987; Gage and Tyler, 1991; Kepkay, 1994; Armstrong et al., 2001; Klass and Archer, 2002; Honjo et al., 2008). In addition, various oceanographic studies have revealed that episodic inputs of organic matter due to phytoplankton bloom aggregation may be critical for sustaining abyssal benthic communities including mobile megabenthos (see Turner, 2002 for review). These lines of evidence may also support our interpretation that diatoms are the most significant diet for the trace-maker.

Conclusions

Phymatoderma and the star-shaped horizontal trace fossil were discovered from the same lithologic unit (Neogene deep-marine Misaki Formation, central Japan). Compared with modern analogous surface-feeding traces and subsurface burrows produced by deep-sea echiuran worms, the star-shaped trace fossil and *Phymatoderma* found in the Misaki Formation may be interpreted as feeding and fecal traces of ancient abyssal echiurans, respectively. The difference in preservation potential between surface and subsurface traces may result in the abundant occurrence of *Phymatoderma* as compared to the relatively rare star-shaped trace fossil. Thin-section and SEM analyses of the pelletal infill of *Phymatoderma* provide evidence that the trace-maker fed on organic debris and microorganisms (diatoms and radiolaria). It may be assumed that other microorganisms, such as foraminifer and calcareous nannoplankton, were also the prey of the trace-maker, although these microfossils were not observed. Considering that the oldest known Phanerozoic echiuran body fossil and ‘*Chondrites granulatus*,’ which has been now interpreted as *Phymatoderma granulata*, have been found from Carboniferous marine strata, our interpretation that *Phymatoderma* contains echiuran fecal pellets is further reinforced.

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Accessibility of supplemental data

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