

学位論文（要約）

Phanerozoic Megatrends in Marine Benthic Ecosystems:

Ichnologic Evidence

(顕生代における海洋底生生態系の大規模変遷：生痕化石からの証拠)

平成 26 年 12 月 博士（理学）申請

東京大学大学院理学系研究科

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## Abstract

ORGANIC MATTER produced by phytoplankton is a key agent to connect benthos to marine surface zone. In particular, marine benthic animals (especially abyssal benthos) rely heavily on phytodetritus for their growth and reproduction. Phytoplanktons have diversified through geologic time, especially since the Mesozoic, body-fossil evidence suggests that marine benthos have changed their diversity, habitat and ecology in response to the Mesozoic phytoplanktonic diversification. However, existing data (i.e., body-fossil evidence) are mainly concentrated on benthos with skeleton, and much fewer researches have focused on soft-bodied benthos (i.e., benthos without skeleton). Considering that the most marine benthos are soft-bodied, it is essential to enhance ichnologic studies in order to uncover the full scope of the benthic response to the Mesozoic phytoplanktonic diversification. For this purpose, the present study focused on a specific ichnogenus, and investigated its changes through geologic time.

The present study systematically describes the specimens of the ichnogenus *Phymatoderma*, which is composed of fecal pellets excreted by a deposit feeder, from eleven localities (Permian–Quaternary), and examines morphometric, geochemical, and microscopic features of these specimens, in order to clarify the trends and patterns of soft-bodied benthos in response to the phytoplanktonic evolution/diversification during the Mesozoic and subsequent sea-floor eutrophication.

First, the present study has revealed, for the first time, that *Phymatoderma* is likely a fecal trace produced by an echiuran worm that ingested the sea-floor sediments, based on carbon-isotope analysis and the discovery of the fossil counterpart of a modern star-shaped feeding trace produced by an echiuran worm, effectively making the data and interpretations presented in this thesis reasonably reliable.

The obtained data from morphometric, geochemical, and microscopic analysis were then considered chronologically, along with the existing data on marine-plankton diversity. As a result, several megatrends in *Phymatoderma* have been recognized; namely, 1) deep-seaward migration during the mid-Mesozoic, 2) diversification of ingested diets, 3) increased efficiency in deposit-feeding strategy since the Cretaceous, 4) size increase since the Late Cretaceous, 5) increased frequency in reburrowed *Phymatoderma* specimens (i.e., evidence of coprophagy by small benthos) during the Cenozoic. Previous studies have already demonstrated a similar pattern to the first megatrend (i.e., deep-seaward migration) using both body- and trace-fossil evidence, which was further confirmed by the present study. Other megatrends have been revealed for the first time, which are also supported by the systematic compilation of published

data on the other deposit-feeding ichnogenera. All the recognized megatrends in marine soft-bodied benthos appear to have been synchronized with the Mesozoic phytoplankton diversification and subsequent sea-floor eutrophication, and with the associated increase in benthic-food competition; therefore, the five megatrends, which generally occurred since the mid-Mesozoic, might represent the benthic response to the coeval phytoplankton diversification and its associated biological/environmental changes.

The present study provides a comprehensive and reliable trace-fossil evidence for the benthic response to the Mesozoic phytoplanktonic diversification and associated environmental changes.

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## CHAPTER 1

### General Introduction: Phanerozoic marine benthic ecosystems

#### 1.1. Modern marine ecosystems: Organic matter and benthic life

*“THE OCEAN is aphotic and therefore aphotosynthetic below the upper few tens to hundreds of meters, yet there is animal and microbial life throughout, including down to the greatest depths. Except for communities around hydrothermal vents, which produce organic matter by bacterial chemosynthesis, the organic matter required to maintain deep-water pelagic and benthic ecosystems must ultimately derive from the photosynthetic system in the epipelagic”* (Turner, 2002). As clearly summarized by Turner (2002), marine benthic animals are sustained by photosynthetically produced organic matter. In particular, for marine benthos that live below the photic zone, a ‘rain’ of organic detritus from overlying epipelagic water is essentially important.

Traditionally, zooplankton fecal pellets have long been thought to be a dominant agent of organic-matter flux in marine ecosystem (e.g., Turner and Ferrante, 1979). However, depending on marine waters, much of the zooplankton fecal pellets are reprocessed by microbial decomposition or coprophagy (Turner, 2002), resulting in a minor contribution to total particulate organic carbon flux (e.g., Asper, 1987; Pilskaln and Honjo, 1987; Taylor, 1989; Ayukai and Hattori, 1992). Instead, substantial portions of the vertical flux are from marine snow (i.e., organic aggregates > 500  $\mu\text{m}$  in size; Alldredge and Silver, 1988) or sinking phytoplankton blooms, which descend directly to the sea floor (Turner, 2002). In particular, sinking phytoplankton blooms are highly important because widespread and abundant phytodetrital aggregates have been photographed on the sea floor in various water depths (i.e., 450–2400 m) after the spring bloom (e.g., Hecker, 1990; Smith et al., 2002; Wetzel, 2008).

It is well known that such phytodetrital material is actually utilized as food by a wide variety of benthic organisms (e.g., Billett et al., 1983; Thiel et al., 1988; Gooday, 1988). The episodic deposition of phytodetritus has also been linked to both seasonal growth pattern and to reproduction pattern (Tyler, 1986, 1988) as well as to regional variability in benthic biomass (Thurston et al., 1994). In addition, deposited phytodetritus enhances microbial and macrobenthic activities (e.g., Gooday and Turley, 1990). Especially, abyssal benthic animals rely heavily on phytodetritus because of aphotic environment and large water depth (Hüneke and Henrich, 2011). A considerable portion of the organic particles is oxidized during settling (e.g., Suess, 1980; Tyson, 2001); thus, phytodetrital input available for the benthic organisms dramatically decreases depending on the water depth. Furthermore, the amount and frequency of

terrigenous organic-matter input must decrease with increasing distance from the shore or with water depth (Kotake, 2014). Due to such oligotrophic condition at the deep-sea floor, episodic input of organic matter mainly derived from phytoplankton blooms or marine snow can be critical for sustaining abyssal benthic communities (Smith et al., 1992). Such a linkage between organic matter produced in the epipelagic and benthic ecosystem, especially at the deep-sea floor, has well been known as ‘benthic-pelagic coupling’ or ‘benthic-pelagic coupling’ (e.g., Graf, 1989; Ritzrau et al., 2001).

## **1.2. Phytoplankton through geologic time**

In the modern ocean, calcareous planktons (mainly coccolithophores), dinoflagellates and diatoms are the most important phytoplankton groups (e.g., Falkowski et al., 2004). However, such groups have been dominant not throughout the Phanerozoic, but only since the Mesozoic (e.g., Lipps, 1970; Stover et al., 1996; Spencer-Cervato, 1999; Brown et al., 2004; Falkowski et al., 2004; Falkowski and Knoll, 2007; Katz et al., 2007; see Fig. 1-1). In the Paleozoic ocean, such phytoplankton groups as prasinophytes and chlorophytes were dominant instead, a fact which has been inferred from the abundant occurrence of acritarchs (e.g., Armstrong and Brasier, 2005; see Fig. 1-1). Calcareous nannofossils and dinoflagellates first appeared in the Upper Triassic strata, and their species diversity increased during the Cretaceous (e.g., Stover et al., 1996; Brown et al., 2004; Falkowski et al., 2004). Diatoms first appeared in the mid-Cretaceous strata and subsequently diversified during the Paleogene (Spencer-Cervato, 1999; Falkowski et al., 2004; Delwiche, 2007).

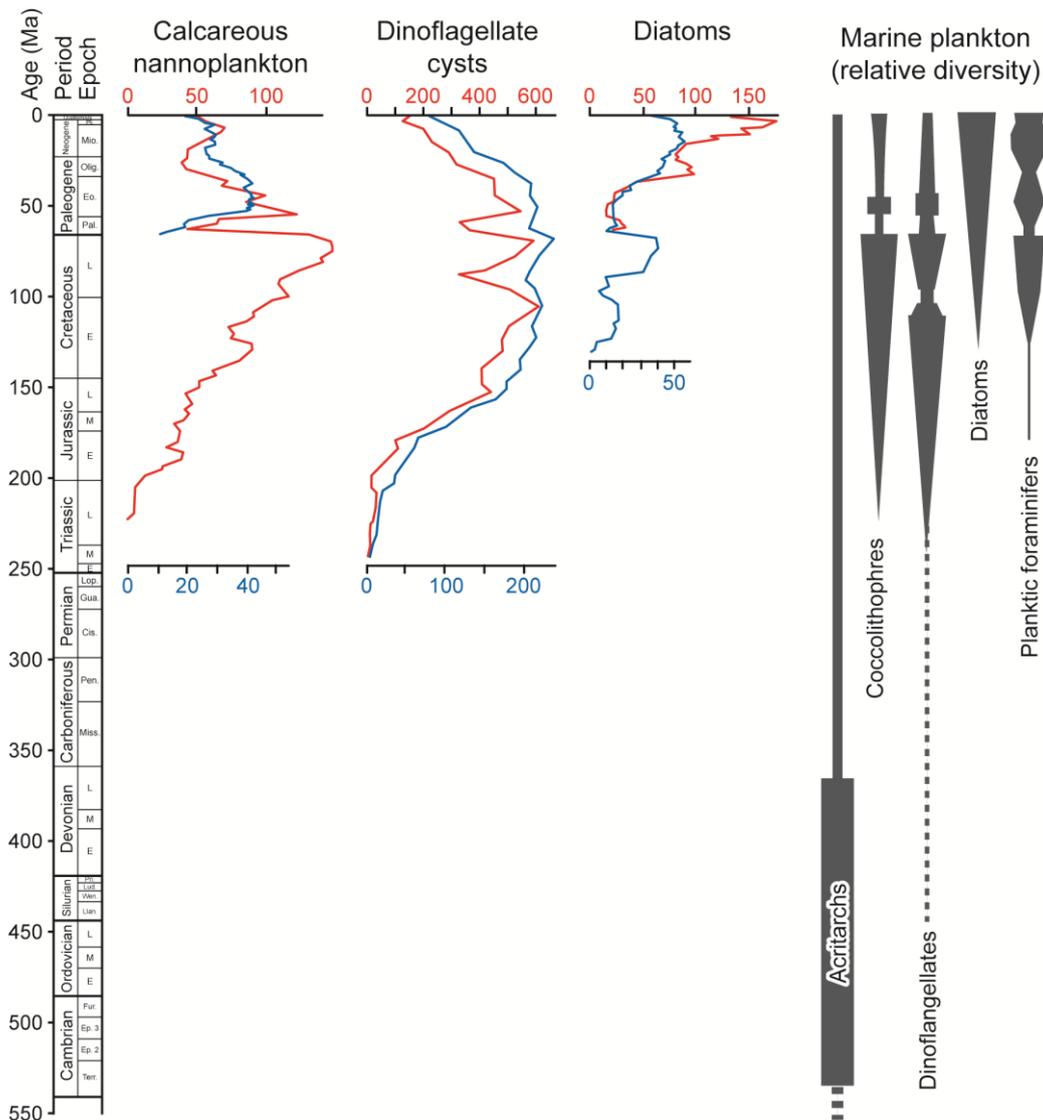


Fig. 1-1. Important marine plankton groups through geologic time. Line graphs: Major phytoplankton species (red line) and genus (blue) diversities, which are slightly modified from Falkowski et al. (2004). Solid bars: Relative diversities of major phytoplankton groups (including acritarchs) and planktic foraminifera (modified from Martin and Quigg, 2012). Note the explosive diversification since the Mesozoic. Terr.: Terreneuvian, Llan.: Llandovery, Wen.: Wenlock, Lud.: Ludlow, Pri.: Pridoli, Miss.: Mississippian, Pen.: Pennsylvanian, Cis.: Cisuralian, Gua.: Guadalupian, Lop.: Lopingian, Pal.: Paleocene, Eo.: Eocene, Olig.: Oligocene, Mio.: Miocene, Pli.: Pliocene, E: Early, M: Middle, L: Late.

These lines of evidence may indicate that the phytoplankton assemblage dramatically changed during the mid-Mesozoic and thus, quality of the components of the biological pump changed significantly, as described below. First, phytoplanktons were different in terms of the presence of mineralized test between the Paleozoic and

Meso-Cenozoic oceans. Acritarchs are organic microfossils without mineralized tests (Armstrong and Brasier, 2005), while the Meso-Cenozoic phytoplanktons (coccolithophores and diatoms in particular) are equipped with mineralized tests. Due to their large specific gravity, phytoplanktons with mineralized tests sink far more rapidly than soft-bodied phytoplanktons. In addition, although not a phytoplankton, planktic foraminifera also appeared and diversified since the Mesozoic; they first appeared in the Middle Jurassic and became widespread at the end of the Early Cretaceous, and further diversified during the Late Cretaceous (e.g., Tappan and Loeblich, 1988; Kuypers and Pancost, 2002; Falkowski et al., 2004; Hay, 2004). The Mesozoic diversification of planktic foraminifera, which have a calcareous test, might also have contributed to the significant increase in the sinking rates for phytodetritus and zooplankton fecal pellets. Furthermore, there is another important difference in phytoplanktons between the Paleozoic and Meso-Cenozoic, related to the seasonal blooms. Considering the chronological patterns of phytoplanktons as mentioned above, phytoplankton blooms may have been common since the Mesozoic because in the modern ocean coccolithophores, dinoflagellates and diatoms cause episodic blooms (e.g., Furnas, 1990).

Because phytoplankton blooms are one of the most important components of the biological pump (Turner, 2002), it would be reasonable to assume that sea-floor sediments had become more eutrophic since the Mesozoic than in the Paleozoic. This interpretation has been supported by various pieces of evidence (e.g., Bambach, 1993; Martin, 1996, 2003; Allmon and Martin, 2014). In other words, geologic, biotic, and paleoenvironmental evidence suggest that “trophic resources” (sensu stricto Allmon and Martin, 2014; sources of metabolic energy such as nutrients and food) within marine realm has been generally increased over the Phanerozoic, although the increase has been irregular (Allmon and Martin, 2014).

### **1.3. Benthic responses to the phytoplankton evolution and diversification during the Mesozoic**

During the Mesozoic, especially since the mid-Mesozoic, various groups of benthic animals changed their diversity, ecology and habitat, a change which appears to have been synchronized with the contemporary evolution and diversification of phytoplankton such as coccolithophores, dinoflagellates and diatoms (see section 1.2). In general, such changes of benthos have been interpreted as benthic responses to the Mesozoic phytoplankton diversification (e.g., Falkowski et al., 2004) and resulting eutrophication of sea-floor sediments (see section 1.2). In the next few paragraphs,

several examples of the Mesozoic benthic changes are described.

First, there is a broad correspondence between diversification patterns of phytoplankton groups and marine benthic groups of Sepkoski's (1981) evolutionary Faunas III (e.g., gastropods, bivalves). In particular, explosive diversification of marine benthic groups of Sepkoski's (1981) Fauna III took place since the Mesozoic, which is coincided with phytoplankton (i.e., coccolithophores, dinoflagellates and diatoms) diversification. This coincidence is suggestive of an indirect link between these primary producer and consumer groups, although it must be noted that the coincidence does not assume a direct trophic relationship between them (MacLeod, 2003). In addition, with respect to taxa containing substantial numbers of bioturbating deposit feeders, they have diversified throughout the Phanerozoic (Thayer, 1983). Particularly, the most pronounced diversification of bioturbating deposit feeders including Sepkoski's (1981) Fauna III (e.g., Mysidacea, Enteroptneusta, Tellinacea, Arenicolidae, Paguridea, Thalassinidea, Spatangoida) took place in the Mesozoic (see fig. 5A in Talyer, 1983). It is also reasonable to assume that this phenomenon was synchronized with the explosive diversification of phytoplankton during the Mesozoic (e.g., Falkowski et al., 2004). As a probable consequence of the Mesozoic diversification of the bioturbating deposit-feeding taxa, bioturbation rate by these taxa has also been significantly increased through geologic time (Thayer, 1983). Especially, the Mesozoic and Cenozoic taxa rework sediment faster and deeper than the Paleozoic taxa (Thayer, 1983). Not only deposit-feeding organisms but also suspension feeders represented the similar change during the Mesozoic, which can be documented in the depth of infaunal tiering; namely, it reached the deepest level (ca. 100 cm below sediment-water interface) of organization after the Paleozoic (e.g., Ausich and Bottjer, 1982).

More distinctive and specific example can be observed in echinoids; namely, they changed their diversity, lifestyle and habitat dramatically during the Mesozoic (e.g., MacLeod, 2003; Smith and Stockley, 2005). In terms of their lifestyle, all echinoids in the Paleozoic and Triassic were epibenthic (Smith, 1984; MacLeod, 2003). A significant change occurred in the Middle Jurassic; endobenthic echinoids first appeared in four independent orders (i.e., Holoctypoids, Pygasteroids, Cassiduloids and Disasteroids; Smith, 1984; MacLeod, 2003). The coincident appearance of the endobenthic groups in the Middle Jurassic might have been related to the eutrophication of the sea-floor sediments. It is well known that the quality and quantity of organic matter are significantly different between surface and subsurface sediments. Freshly deposited organic matter is generally decomposed within the top few centimeters of the sediments by microbial metabolisms (e.g., Druffel et al., 1992; Burdige, 2006; Sarmiento and

Gruber, 2006). As a result, organic matter in subsurface sediments contains rare labile fractions which may be utilized by marine benthos, and mainly consists of refractory fractions which cannot be separated from the mineral matrix (e.g., Littke et al., 1997; Hartnett et al., 1998; Kennedy et al., 2002; Arnarson and Keil, 2007). Therefore, for deposit-feeding marine benthos, surface sediments are much better, and benthic diversity is higher in surface sediments than in subsurface (e.g., Itoh et al., 2011). Considering chronologically, as mentioned in the section 1.2, onset of diversification of modern-type phytoplankton (i.e., coccolithophores, dinoflagellates) during the Jurassic must have caused the eutrophication of both surface and subsurface sediments, making it possible for endobenthic echinoids to obtain sufficient organic matter.

In addition, modern fauna of abyssal deposit-feeding echinoids independently migrated into the deep sea in a relatively short time-interval between approximately 75 to 55 Ma (Smith and Stockley, 2005). The onset of deep-sea colonization during the Late Cretaceous coincides with a marked increase in surface water productivity (Handoh et al., 2003), which is possibly related to diversification of marine phytoplankton (e.g., Falkowski et al., 2004). Smith and Stockley (2005) interpreted that increasing organic delivery into deep-sea environments in the Late Cretaceous made life more feasible for deposit feeders at depth; thus, it is suggested that echinoids migrated into the deep sea to exploit newly available food sources during the Late Cretaceous.

As a probable consequence of the diversification and deep-seaward migration of marine benthos during the Mesozoic (e.g., MacLeod, 2003; Smith and Stockley, 2005), benthic-food competition has been dramatically accelerated since the Cretaceous, which was suggested by the time-series analysis of the graphyglitid trace fossils (Uchman, 2004). It is reasonable to consider that the increased competition for benthic food also affected the ecology of marine benthos. One of the distinctive examples is the increased feeding efficiency, which can be recognized in benthic foraminifera. Also during the Late Cretaceous, such genera as *Uvigerina*, *Bulimina* and *Bolivina* first appeared (e.g., ). Previous study suggested that such groups can actively ingest freshly deposited particulate organic matter (Nomaki et al., 2005). The Late Cretaceous change of benthic foraminiferal assemblage is synchronized with, and thus might be related to, the significant diversification of modern-type phytoplankton (i.e., coccolithophores, dinoflagellates and diatoms; Falkowski et al., 2004).

In summary, various groups of benthic animals changed their diversity, ecology and habitat especially after the mid-Mesozoic (Fig. 1-2), which appeared to have coincided with, and therefore responded to, the evolution and diversification of marine phytoplankton and subsequent environmental/biological changes (i.e., sea-floor

eutrophication, increased competition for benthic food).

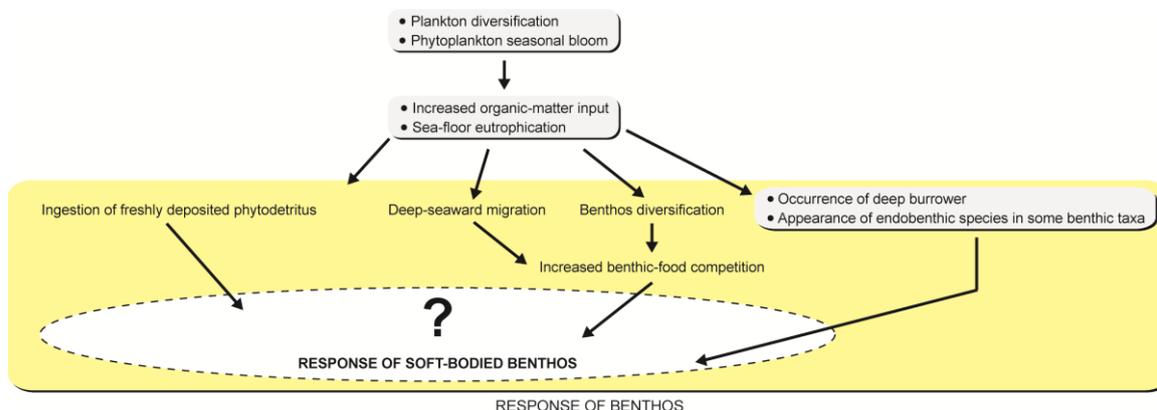


Fig. 1-2. Summary of the benthic responses to the Mesozoic phytoplankton diversification and associated environmental/biological changes. Yellow box emphasizes the benthic responses. Most previous studies focused on body fossils or conducted the experiments using the specific benthic animal with skeleton; however, such studies cannot clarify the response of soft-bodied benthos.

#### 1.4. Problems in previous studies and ichnologic approach as a solution

Despite such pronounced examples of benthic responses to the phytoplankton diversification (and subsequent sediment eutrophication) during the Mesozoic (see section 1.3), these findings have been derived mainly from body-fossil records. This is a significant problem because such body-fossil data cannot reveal any information on the response of soft-bodied benthic organisms. Considering that a considerable portion of marine organisms are occupied by such soft-bodied benthos, it is necessary also to evaluate the response of soft-bodied benthos in order to uncover the full scope of benthic responses to the Mesozoic phytoplanktonic diversification.

Trace fossils are powerful and useful tools to resolve this problem because they are ‘fossil behavior’ of ancient animals (Seilacher, 1967). Thus, trace fossils may reveal the specific behavioral ecology of their producing soft-bodied benthic organisms (e.g., Bromley, 1996; Buatois and Mángano, 2011). Although it is generally difficult or impossible to identify the producing animal of the specific trace fossil, in terms of such ichnogenera as *Macaronichnus*, *Rosselia* and *Schaubcylindrichnus*, possible trace-makers can be assumed or identify by detailed observations of fossil specimens combined with the investigation of modern analogous or counterpart traces (e.g., Clifton and Thompson, 1978; Nara, 1995, 2006; Nara and Seike, 2004; Seike, 2007, 2008, 2009; Dafoe et al., 2008a, b; Seike et al., 2011). Furthermore, there are many ichnogenera with long chronological distribution (i.e., throughout the Phanerozoic) such as *Chondrites*, *Palaeophycus* and *Planolites* (e.g., Gerard and Bromley, 2008).

Considering all of them, trace fossil, especially of which possible trace-maker has been identified, must be the most suitable material for elucidating the geologic history (i.e.,  $10^6$ – $10^8$  year-scale) of soft-bodied benthos.

### **1.5. Purpose and strategy of the current Ph. D thesis**

In accordance with such background described above, the purpose of the present study is to clarify the trends and patterns of soft-bodied benthos in response to the Mesozoic phytoplanktonic evolution/diversification and subsequent eutrophication of sea-floor sediments. Particularly, special attention is paid to whether significant changes of soft-bodied benthic ecosystem occurred after the mid-Mesozoic, as is the case with body-fossil records (see section 1.3).

Although not so frequently, researchs that investigated trends seen in specific types of trace fossil or ichnofabrics through geologic time have been published so far (e.g., Seilacher, 1986; Bottjer et al., 1988; Uchman, 2004; Knaust, 2013; Kotake, 2014), most of which clearly detected some significant changes (e.g., diversity, distribution pattern, lifestyle, occurrence pattern) during the Mesozoic, especially in the Cretaceous. Among such studies, one of the most important papers was published recently by Kotake (2014), who systematically analyzed the ichnogenus *Zoophycos* from the Devonian to Neogene marine strata. As a result, he recognized the following pronounced changes in habitat and lifestyle during the Cretaceous; 1) offshore transition (i.e., shelf to deep-sea environment) that is interpreted as trace-maker's migration to deep-sea floor, and 2) dramatic increase in whorl number of spreite that may reflect the shift from short- to long-term occupation of the same burrow. Kotake (2014) interpreted that such changes appear to be associated with the increased phytodetritus vertical input, which must have been related to an explosive diversification of phytoplanktons during the Late Jurassic to the Late Cretaceous. Kotake's (2014) paper is considerably important for the present study because he provided the clear evidence of the response of soft-bodied benthic animals (i.e., *Zoophycos*-producers) to the Mesozoic phytoplankton diversification and subsequent sea-floor eutrophication, which is exactly the purpose of this Ph. D thesis.

Despite Kotake's (2014) comprehensive findings, it must be said that there are several serious concerns that are described below. Because *Zoophycos* shows a highly complex and three-dimensional morphology, many constructional models have been proposed to account for its intricate morphology and the ethology of its trace-maker, which is appropriately summarized in Buatois and Mángano (2011). Briefly mentioned, strip-mine model (i.e., subsurface deposit feeding), detritus-feeding model (i.e., surface deposit feeding), refuse-dump model (i.e., both surface and subsurface feeding), cache

model (i.e., storing food in the case of oligotrophic condition) and gardening model (i.e., microbial housing) have been suggested so far (e.g., Simpson, 1970; Wetzel and Werner, 1981; Kotake, 1989; Bromley, 1991; Miller, 1991; Ekdale and Lewis, 1991; Wetzel, 1992; Gaillard and Olivero, 1993; Fu and Werner, 1995; Olivero and Gaillard, 1996, 2007; Bromley et al., 1999; Miller and d'Alberto, 2001; Bromley and Hanken, 2003; Löwemark and Schäffer, 2003; Knaust, 2004, 2008; Löwemark et al., 2006, 2007; Seilacher, 2007). Although the gardening model may be a generally-accepted model as it is now, each model has its own problems and difficulties (Buatois and Mángano, 2011), making it difficult to achieve consensus on the ethological interpretation of *Zoophycos*. Controversy over the ethology of the *Zoophycos*-producer prevents an accurate interpretation of the meaning of 'whorl number of spreite', which showed a dramatic increase during the Cretaceous (Kotake, 2014). In addition, despite the linkage between the *Zoophycos*-producers and phytoplankton diversification (Kotake, 2014), micropaleontological data (i.e., SEM images of phytoplankton microfossils) has not been provided in his paper.

Thus, to solve these issues, it is necessary to focus on the trace fossil that reflect the specific type of ethology and that can provide the data on plankton microfossils. Additionally, it is important to pay attention to the specific trace-fossil characters that may be sensitively influenced by the eutrophication of sea-floor sediments. The present study first focuses simply on the ichnogenus that is composed of fecal pellets by deposit-feeding organisms; in particular, the ichnogenus *Phymatoderma* (see Chapter 2). This is because it is predicted that fecal pellets may contain plankton debris, which may have been actually ingested by the fecal producer (see Chapter 4). Given the Mesozoic phytoplankton diversification (e.g., Falkowski et al., 2004), it is predicted that the diet of soft-bodied benthos has also diversified since the Mesozoic (Fig. 1-3). Furthermore, if fecal pellets are analyzed appropriately, it is possible to reconstruct the feeding strategy of the trace-maker (see also Chapter 4). Therefore, considering the benthic responses to the Mesozoic phytoplankton diversification and subsequent environmental/biological changes (i.e., sea-floor eutrophication, increased benthic-food competition), which were inferred from the experimental evidence (e.g., Nomaki et al., 2005), it is also reasonable to predict that the feeding efficiency of soft-bodied benthos was better after mid-Mesozoic (Fig. 1-3).

Second, special attention is paid to the depositional setting and size of *Phymatoderma* (see Chapter 2 for systematic descriptions). With respect to depositional setting, based on the previous studies using both body- and trace-fossil specimens (e.g., Seilacher, 1986; Smith and Stockley, 2005; Kotake, 2014), deep-seaward migration

since the Cretaceous is likely detected in the case of *Phymatoderma* (Fig. 1-3). The size of trace fossils (e.g., burrow diameter) may be controlled by several environmental factors; the most important ones are oxygenation and food content (i.e., organic matter) within the substrate (e.g., Wetzel, 1991; 2010). However, in the case of the Mesozoic and Cenozoic trace fossils, oxygenation was probably less critical for the trace-makers because, during the Phanerozoic, a large oxygenation event took place around 400 Ma (i.e., Devonian) and therefore, the post-Devonian oceans remained far more oxygenated than pre-Devonian oceans (Dahl et al., 2010) except for the episodic worldwide OAEs during the Mesozoic (i.e., oceanic anoxic events; Takashima et al., 2006). As a result, at least since the Carboniferous, food content may have been the most significant environmental factor that controls the burrow size. Therefore, because a dramatic phytoplankton diversification and subsequent sea-floor eutrophication took place during the mid-Mesozoic, it is predicted that post-Cretaceous *Phymatoderma* is larger (Fig. 1-3).

Finally, the present study pays attention to the occurrence of composite *Phymatoderma* (see Chapter 5); namely, *Phymatoderma* that is secondarily reburrowed with other smaller ichnogenus (e.g., *Chondrites*, *Phycosiphon*). In that case, the pelletal infill of *Phymatoderma* was utilized by the trace-makers of *Chondrites* and *Phycosiphon* as a preferential feeding site (e.g., Wetzel, 2010), which means that *Chondrites* and *Phycosiphon* in the pelletal infill represent the coprophagous activities of their trace-makers. The eutrophication of the trace-fossil infilling sediments must have occurred since the mid-Mesozoic, which was coupled with the eutrophication of the sea-floor sediments. In addition, Uchman (2004) suggested that the benthic-food competition has been dramatically accelerated since the Cretaceous. Under high competition for benthic food, coprophagous behavior (i.e., to explore the unutilized fecal sediment as a new feeding site) probably resulted in avoidance of competition; thus, it might be an adaptive behavior. Therefore, it is predicted that the frequency of reburrowed *Phymatoderma*, which represents coprophagous activity of the trace-maker of reburrowing ichnogenus, has increased since the Cretaceous (Fig. 1-3).

Combined with the results and interpretations by the present study (Chapters 2–5) and previous studies, in Chapter 6, a new perspective on the benthic response to the Mesozoic phytoplankton diversification is proposed.

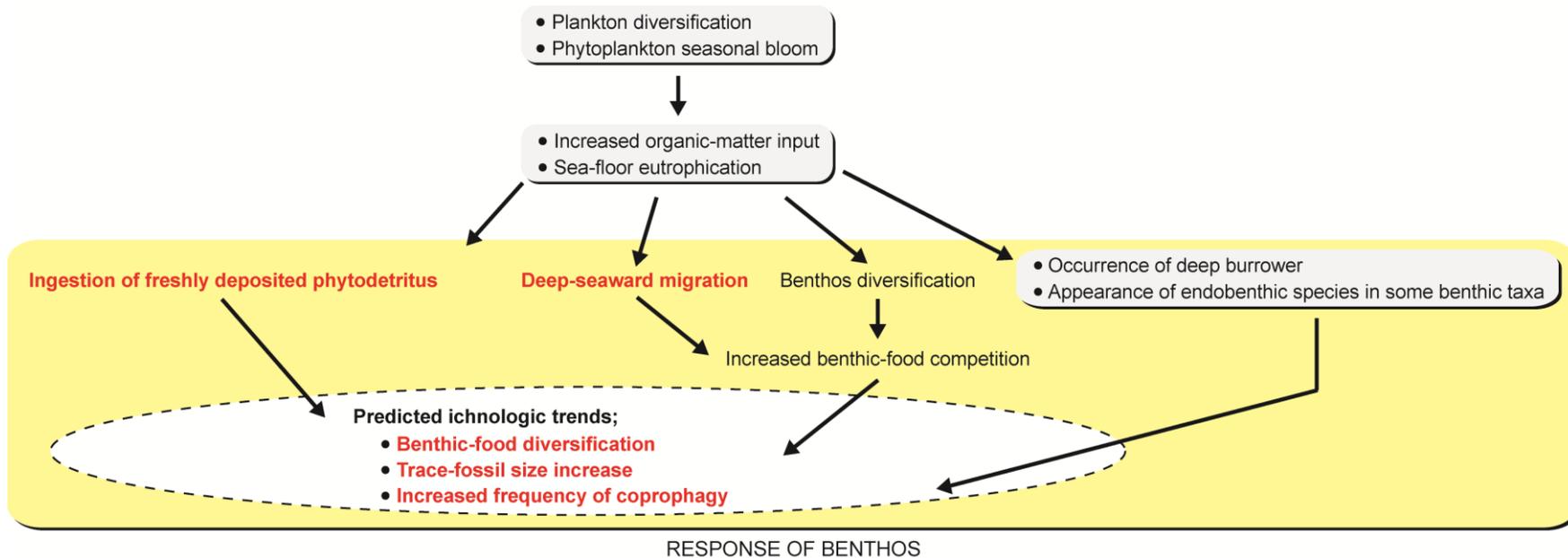


Fig. 1-3. Summary of the predicted trends (written in red color) that will be recognized from the chronological analysis of *Phymatoderma*. Yellow box emphasizes the benthic responses. It is predicted that the present study can further confirm the trends inferred from previous studies, and can also provide new perspectives that cannot be clarified by body-fossil evidence or experimental studies of benthos with skeleton.

## 第 2 章 (12～32 頁)

本章については、5 年以内に雑誌等で刊行予定のため、非公開。

## CHAPTER 3

### Identification of the trace-maker and formation process of *Phymatoderma*

THE BEST way to make obtained data, interpretations and discussion in the present study more significant and as solid as possible would be to reveal the paleobiology of *Phymatoderma*; especially, identification of the likely trace-maker and elucidation of the formation process are essentially important. The paleobiology of trace fossils is much less understood than that of body fossils because, in most cases, it is difficult to identify the trace-maker. However, in terms of some marine invertebrate ichnogenera (e.g., *Macaronichnus*, *Rosselia*, *Schaubcylindrichnus*), possible trace-makers can be identified by detailed observations of fossil specimens combined with the investigation of modern counterpart traces (e.g., Clifton and Thompson, 1978; Nara, 1995, 2006; Seike, 2007, 2008; Olivero and López Cabrera, 2010; Seike et al., 2011), thus making it possible to promote our understanding of the paleobiology of trace fossils.

Despite such successful examples of the identification of the trace-makers, the paleobiology of the *Phymatoderma*-producer has been poorly understood. *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 (e.g., Seilacher 2007). In addition, sedimentologic studies about *Phymatoderma* from deep-marine deposits (i.e., Pliocene Onzole Formation, Ecuador) have suggested that the trace-maker ingested the surface sediments and subsequently excreted fecal pellets into the subsurface burrows (e.g., Miller and Aalto, 1998; Miller and Vokes, 1998). However, paleobiological aspects of *Phymatoderma*, especially the mode of formation, from the epicontinental organic-rich black mudstones (i.e., black shales; see sections 2.2 and 2.3) have not been well understood. In particular, as Seilacher (2007) pointed out, the origin of pelletal infill has not yet been clarified; namely, it is still controversial whether the pellets were derived from the surrounding matrix (i.e., subsurface deposit-feeding trace-maker) or were imported from a food source at the sediment surface (i.e., surface deposit-feeding trace-maker).

In terms of the identification of the possible trace-maker, Kotake (1990, 1991) described the fecal pellet-filled ‘giant *Chondrites*’ from the Pliocene deep-marine Shiramazu Formation, central Japan. In the study conducted by Kotake (1990), an abyssal echiuran worm was suggested as a possible trace-maker of ‘giant *Chondrites*’ based on indirect, circumstantial evidence. Subsequently, based on the revision of ichnotaxonomy revised in the present study (see section 2.9), the pellet-filled ‘giant

*Chondrites*' is now reinterpreted as *Phymatoderma* based on the presence of many diagnostic features of this ichnogenus. Although the conclusion of Kotake (1990) about the possible trace-maker is highly probable, there was no direct trace-fossil evidence that clearly indicated echiuran activities. It is true that echiuran worms ingest marine sediments and generally excrete ellipsoidal fecal pellets (i.e., Goto et al., 2011). However, there are also many benthic animals such as polychaetes, holothurians and gastropods that ingest marine sediments and subsequently excrete ellipsoidal fecal pellets (e.g., Minoura and Osaka, 1992; see also Fig. 3-1).

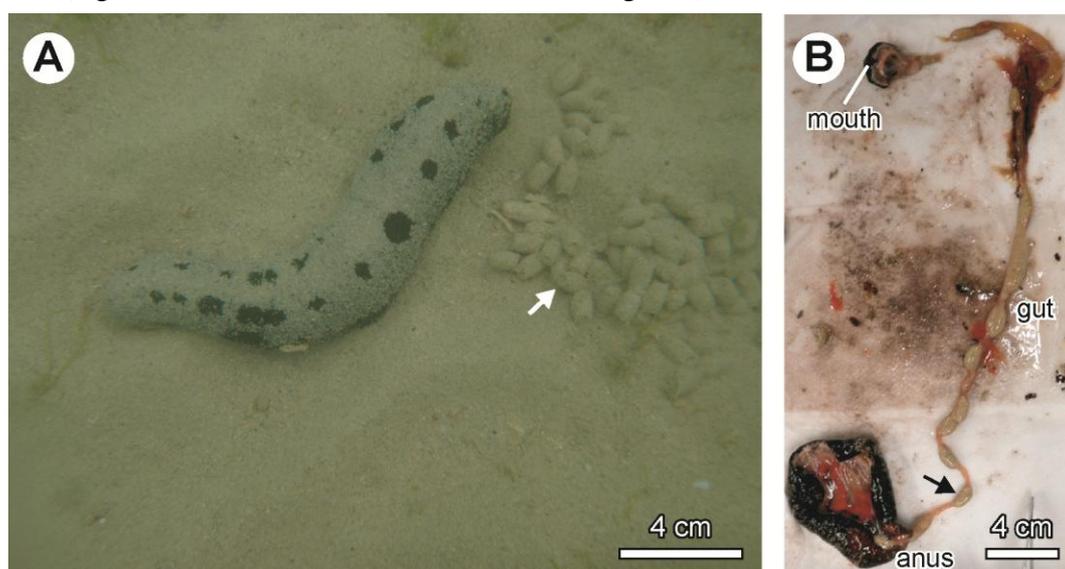


Fig. 3-1. Modern marine deposit-feeding holothurian worm and its fecal pellets. (A) General view of *Holothuria atra* and its surrounding ellipsoidal fecal pellets (white arrow), probably excreted by the same individual. Nashiro Beach, Okinawa Prefecture, Japan. (B) Anatomical image showing the digestive system of *Holothuria atra*. In some individuals, ellipsoidal sandy pellets are recognized in the gut (black arrow), confirming that the ellipsoidal pellets around the *Holothuria atra* (A) are fecal origin.

Instead, the most distinct evidence of echiuran feeding activities may be star-shaped (i.e., rosette-like shaped) surface traces spreading outward from the central hole(s) (i.e., Ohta, 1984; see also Fig. 3-2). Such characteristic star-shaped surface traces are produced when endobenthic echiuran worm ingests surface sediments using a proboscis, and are relatively common both in shallow-marine environments (i.e., tidal flat) and deep sea-floor (e.g., Ohta, 1984; de Vaugelas, 1989; Goto, 2012). Therefore, to identify *Phymatoderma* as echiuran fecal pellets, it is essentially important to find out both surface star-shaped trace fossil and *Phymatoderma* from the same lithological unit.



Fig. 3-2. Example of star-shaped feeding trace produced by modern echiuran worm of shallow-marine species, *Listriolobus riukiurnsis* (Courtesy of Dr. Ryutaro Goto).

In summary, to identify the likely trace-maker of *Phymatoderma*, the following points should be resolved; 1) the origin of the pelletal infill of *Phymatoderma* from the epicontinental black shale is unknown, and 2) trace-fossil evidence that directly reflects the feeding activities of echiuran worms has never been found. In this chapter, both problems are resolved by 1) carbon-isotope analysis to identify the origin of the pellets (discussed in section 3.1), and 2) discovery of co-occurrence of a star-shaped trace fossil and *Phymatoderma* from the same lithological unit (discussed in section 3.2).

### **3.1. Origin of the pelletal infill of *Phymatoderma* from epicontinental black shale**

#### **3.1.1. Materials and methods**

*Materials.*—*P. granulata* from the Lower Jurassic (Toarcian) epicontinental black shale (Posidonia Shale) exposed in Dotternhausen, southern Germany (see section 2.3). For locality map and detailed lithologic log, see Fig. 3-3. Geologic setting, depositional environment and age constraints of the Posidonia Shale have been summarized by many previous studies (e.g., Kauffman, 1981; Ziegler, 1982, 1988; Riegraf et al., 1984; Bassoulet et al., 1993; Röhl et al., 2001; Schmid- Röhl and Röhl, 2003; Frimmel et al., 2004; Schwark and Frimmel, 2004; Röhl and Schmid- Röhl, 2005)

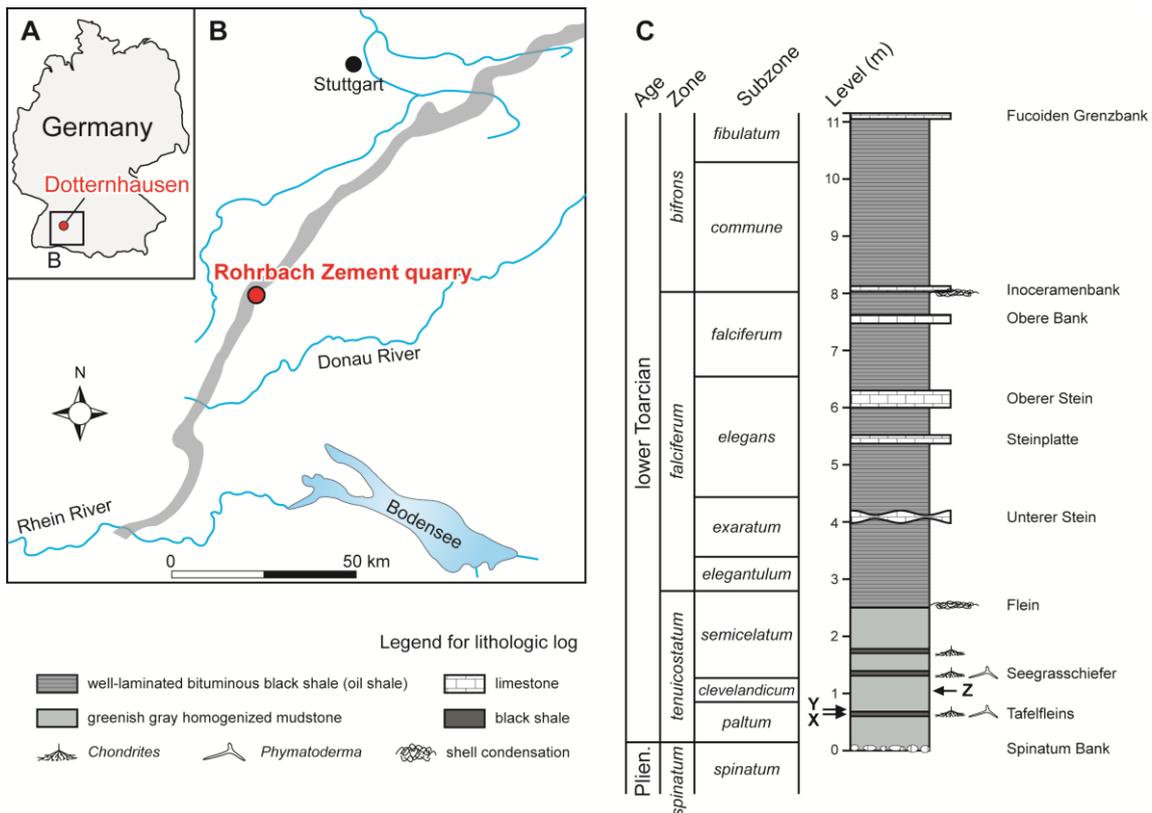


Fig. 3-3 (Slightly modified from Izumi, 2012). Geologic setting. (A) Map of Germany showing the Dotternhausen section. (B) Distribution of the Posidonia Shale (gray shade) across southern Germany, and the locality of the Dotternhausen section at the Rohrbach Zement quarry. Modified after Savrda and Bottjer (1989). (C) Litho- and bio-stratigraphy for the uppermost Pliensbachian to the lower Toarcian sequence at the Dotternhausen section. After Riegraf et al. (1984) for ammonite biostratigraphy. *Phymatoderma*-bearing black shale and the overlying mudstone for the carbon-isotope analyses were collected from horizons X and Y, respectively. The  $\delta^{13}\text{C}_{\text{org}}$  value of the greenish gray mudstone from horizon Z analyzed by Röhl et al. (2001) was used as the reference.

**Methods.**—In order to identify whether the pelletal infill of *P. granulata* from the Dotternhausen section was derived from the surrounding black shale or overlying greenish gray mudstone, carbon-isotope values of the pelletal infill, the ambient black shale, and the overlying mudstone were analyzed. *P. granulata* and the surrounding black shale collected from the horizon named ‘Tafelfleins’ bed (e.g., Röhl et al., 2001) and the mudstone from the overlying horizon were used for carbon-isotope analyses.

Carbon-isotope values of organic carbon ( $\delta^{13}\text{C}_{\text{org}}$ ) were used to identify the origin of the pelletal infill on the basis of the following hypothesis; namely, the  $\delta^{13}\text{C}_{\text{org}}$  values of ingested material do not change greatly throughout the passage through the gut of a trace-producing animal. It is highly likely because the carbon isotopic change

due to the decomposition of organic matter is quite small (e.g., Haines, 1977; Fenton and Ritz, 1988). For carbon-isotope analysis preparations, the pelletal infill of *P. granulata*, surrounding black shale, and overlying greenish gray mudstone were powdered using a microdrill, and the powders were then treated with 20% hydrochloric acid to remove all carbonates and other acid-soluble minerals. Each powder sample was sealed in a Sn foil for isotope analysis (approximately 1–2 mg for the pelletal infill, 0.3–0.5 mg for black shale, and 2–3 mg for mudstone). Bulk carbon-isotope values of organic carbon were measured using a Finnigan MAT253 isotope ratio mass spectrometer attached to an elemental analyzer (FLASH 2000, ThermoFinnigan) through an interface system (Conflo4, ThermoFinnigan) at the Department of Geology and Palaeontology, National Museum of Nature and Science, Tokyo. The measurements for each sample were carried out three times and the mean value of the results was used as the  $\delta^{13}\text{C}_{\text{org}}$  ratio of the sample. The precision of the measurements was  $\pm 0.15\text{‰}$  (1 SD). Isotope values are reported relative to the Vienna Pee Dee Belemnite (VPDB) standard.

### 3.1.2. Results

The carbon-isotope values for pelletal infill of *P. granulata*, surrounding black shale, and overlying greenish gray mudstone are summarized in Table 3-1 and Fig. 3-4. Although the  $\delta^{13}\text{C}_{\text{org}}$  value of each sample used in this study was the mean value of three measurements, the carbon-isotope ratios of the same sample show little variation (approximately 0.02 to 0.1‰).

Carbon-isotope ratios of pelletal infill of *P. granulata*, the surrounding black shale, and the overlying greenish gray mudstone vary between  $-27.02$  and  $-26.33\text{‰}$  ( $n = 21$ ),  $-28.73$  and  $-28.04\text{‰}$  ( $n = 8$ ), and  $-26.34$  and  $-26.22\text{‰}$  ( $n = 3$ ), respectively. Although many samples of the pelletal infill were analyzed for precisely evaluating the variability of the  $\delta^{13}\text{C}_{\text{org}}$  value among the *P. granulata* specimens from the same horizon, the sample standard deviation of the  $\delta^{13}\text{C}_{\text{org}}$  value of pelletal infill of *P. granulata* from horizon X is quite similar to that of the black shale (Table 3-1). As for the overlying greenish gray mudstone, the number of samples analyzed is small because the mudstone from horizon Y is nearly completely homogenized. Despite the small number of samples, sample standard deviation of the  $\delta^{13}\text{C}_{\text{org}}$  value of overlying mudstone is quite small (Table 3-1). The  $\delta^{13}\text{C}_{\text{org}}$  value of the pelletal infill is similar to that of the overlying mudstone, but is significantly different from that of the ambient black shale (Fig. 3-4).

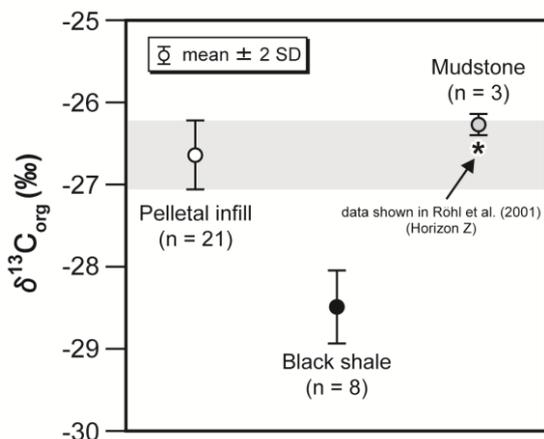


Fig. 3-4 (Modified from Izumi, 2012). Carbon-isotope values of the pelletal infill of *P. granulata*, the surrounding black shale, and the overlying greenish gray mudstone. Shade represents the 95% confidence interval of  $\delta^{13}\text{C}_{\text{org}}$  value of the pelletal infill. Note that the precision of the measurements was  $\pm 0.15$  ‰ (1 SD).

### 3.1.3. Interpretations: Origin of the pelletal infill of *P. granulata* and its formation process

Carbon-isotope values of the excreted material have been used as a reliable indicator of the ingested food source (e.g., Codron et al., 2005; Kuwae et al., 2008; Landrum and Montoya, 2009). This is because the isotopic change due to the degradation of organic matter through the passage of digestive organs is quite small (e.g., Haines, 1977; Fenton and Ritz, 1988). For these reasons, it seems likely that the  $\delta^{13}\text{C}_{\text{org}}$  value of the pelletal infill of *P. granulata* is close to or exactly that of the ingested material.

As shown in Fig. 3-4, the difference of  $\delta^{13}\text{C}_{\text{org}}$  value between the pelletal infill of *P. granulata* and the overlying mudstone (ca. 0.37‰) is much smaller than that between the pelletal infill and surrounding black shale (ca. 1.85‰). This fact indicates that the pelletal infill of *P. granulata* was not derived from the surrounding black shale but from the overlying mudstone. Because the pelletal infill of *P. granulata* consists of fecal pellets owing to the morphological similarity to fecal pellets of some modern marine deposit-feeding animals (e.g., Minoura and Osaka, 1992; Seilacher, 2007), the carbon-isotope data strongly indicate that *P. granulata* from the lower Toarcian black shale was formed as a product of surface deposit feeding and subsequent subsurface excretion, rather than subsurface deposit feeding. Such a formation process is similar to the previously proposed one for *Phymatoderma* from the continental slope deposits (e.g., Kotake, 1991a; Miller and Aalto, 1998;

Miller and Vokes, 1998). Furthermore, such a “reverse-conveyor strategy” (cf. Bromley, 1996) has also been reported in modern marine benthos such as the terebellid *Polycirrus eximius*, the cirratulid *Tharyx acutus*, and the spionids *Scolecolepis squammata* and *Pygospio elegans* (e.g., Myers, 1977; Reise, 1981).

This study revealed that the  $\delta^{13}\text{C}_{\text{org}}$  value of the pelletal infill of *P. granulata* is more similar to that of the overlying mudstone than that of the surrounding black shale (Fig. 3-4). Although there is a slight isotopic difference between the pelletal infill and the mudstone, this fact is not so important, because contamination of excreted pellets by the surrounding black muddy sediments could have happened to some extent. Since each fecal pellet might have been in a three-dimensional spherical form when excreted by the *Phymatoderma*-producer, the ambient organic-rich black mud might have slightly penetrated into interspace between pellets.

Furthermore, the difference of the mean  $\delta^{13}\text{C}_{\text{org}}$  value between the pelletal infill and overlying mudstone (ca. 0.37‰) has little palaeoecological significance for the following reasons. First, the isotope ratio mass spectrometer (ThermoFinnigan MAT253) has its own precision ( $\pm 0.3\%$  as  $2\sigma$ ). Second, the carbon-isotope values often show inherent variability. Namely,  $\delta^{13}\text{C}_{\text{org}}$  measurements for a sequence of marine sediments often show fluctuations of up to 0.5‰ even between adjacent data points (e.g., Kienast et al., 2001). Furthermore, as for the ichnofossil *Zoophycos*, whose infill was deposited as a result of downward transport from the surface sediments, the difference of  $\delta^{13}\text{C}_{\text{org}}$  value between the infill and overlying sediments can be approximately 0.4 to 0.5‰ (Löwemark et al., 2004). In this case, late Quaternary deep-sea *Zoophycos* was examined, and the  $^{14}\text{C}$  data demonstrated that the infill of such *Zoophycos* was introduced from the surface sediments (e.g., Löwemark and Schäfer, 2003). Therefore, these carbon-isotope data from the late Quaternary *Zoophycos* might provide a reliable example of the expected variability between the source and infill. Third, it is highly likely that the surface sediments, some of which were ingested by a *Phymatoderma*-producer as a food source, have been mixed almost entirely by bioturbation (Savrda and Bottjer, 1989). Because the greenish gray mudstone of the Dotternhausen section is well homogenized,  $\delta^{13}\text{C}_{\text{org}}$  value of any horizon from the mudstone between the “Tafelfleins” and “Seegrasschiefer” beds can be used as good reference data for the carbon-isotope value of ingested sediments. Accordingly, the  $\delta^{13}\text{C}_{\text{org}}$  value of horizon Z (Fig. 1C) analyzed by Röhl et al. (2001) is shown in Fig. 3-4. According to Röhl et al. (2001), the lithofacies at horizon Z is “light bioturbated marls,” and this lithofacies is interpreted to correspond with the greenish gray homogenized mudstone in this study. Although horizon Z is

approximately 0.3 m above horizon Y, it is within the 95% confidence interval of the  $\delta^{13}\text{C}_{\text{org}}$  value from the pelletal infill of *P. granulata* (Fig. 3-4). This evidence further confirms that the pelletal infill of *P. granulata* was derived from the overlying mudstone.

In summary, fecal pellets of *P. granulata* within the Posidonia Shale are interpreted to have been derived mainly from the overlying mudstone as a result of the surface deposit-feeding activity of a producer, as is schematically shown in fig. X in Miller and Vokes (1998).

#### **3.1.4. Implications for the formation process of other *Phymatoderma***

Carbon-isotope analysis of *P. granulata* from the Lower Jurassic epicontinental black shale (Fig. 3-4) clearly confirmed the surface deposit-feeding trace-maker. Although it is generally well recognized by ichnologists that the same ichnotaxon may be produced by more than one organism, it is likely that the specific ichnotaxon may reflect the same ethology and formation process because trace fossils are primarily evidence of animal behavior (e.g., Seilacher, 1967; Bromley, 1996; Buatois and Mángano, 2011). With respect to *Phymatoderma*, this basic ichnologic concept may be applicable; namely, since previous authors (e.g., Kotake, 1991a; Miller and Aalto, 1998; Miller and Vokes, 1998) have demonstrated that the trace-maker of deep-sea *Phymatoderma* was also a surface deposit feeder, now it is highly reasonable to assume that the trace-makers of every *Phymatoderma* were surface deposit-feeding animals.

### **3.2. Identification of the trace-maker of *Phymatoderma* from deep-sea deposits**

#### **3.2.1. Materials and methods**

**Materials.**—Trace-fossil specimens yielded from the Neogene (Miocene–Pliocene) deep-sea Misaki Formation, Miura Peninsula, central Japan. For locality map of the studied sections, see Fig. 3-5. Geologic setting, depositional environment and age constraints of the formation have been summarized by many papers published mostly in 1980s to 1990s (Yoshida et al., 1984; Soh et al., 1989; Akimoto et al., 1991; Kanie and Hattori, 1991; Kanie et al., 1991; Taniguchi et al., 1991; Kitazato, 1997; Lee and Ogawa, 1998; Stow et al., 1998; Yamamoto et al., 2009).

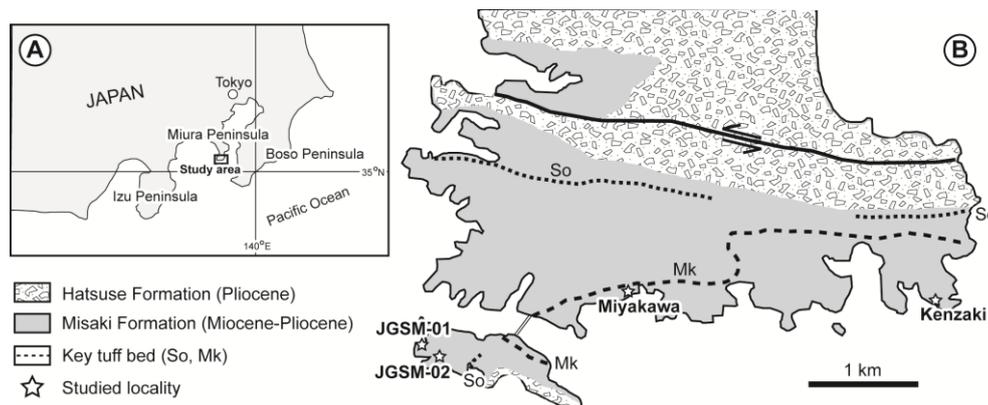


Fig. 3-5 (Slightly modified from Izumi and Yoshizawa, in press). Locality map and geologic setting. (A) Map of Japan showing the study area (southern part of the Miura Peninsula, central Japan). (B) Simplified geologic map of the southern part of the Miura Peninsula illustrating the detailed localities of the four study sites (white stars). Modified from Yamamoto et al. (2009). GPS coordinates of each locality are provided below; JGSM-01: N35°08'09.7" E139°36'40.7", JGSM-02: N35°08'01.1" E139°36'43.5", Miyakawa: N35°08'28.2" E139°38'10.9", Kenzaki: N35°08'26.7" E139°40'32.6".

**Methods.**—Field observations at four sections (JGSM-01, JGSM-02, Miyakawa, and Kenzaki; see Fig. 3-5).

### 3.2.2. Star-shaped trace fossil and *Phymatoderma* recognized in the Misaki Formation

As a result of the field observations, co-occurrence of star-shaped surface trace fossil and *Phymatoderma* (i.e., branched fecal pellet-filled burrow) was discovered in the Misaki Formation for the first time. Because *Phymatoderma* from the Misaki Formation was described in previous chapter (see section 2-8), a star-shaped trace fossil is newly described herein.

Indeterminate star-shaped trace fossil (Fig. 3-6)

**Specimens.**—Two specimens studied in the field (JGSM-02 section).

**Description.**—The nearly complete specimen (Specimen 1; Fig. 3-6) 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. 3-6). The overall size of the specimen 1 is 18 × 19 cm (Fig. 3-6). Some spokes show sharp contours; however, other spokes amalgamates with contiguous spokes, leading to ambiguous contours (Fig. 3-6). In some cases, several spokes overlap near the center, resulting in branched morphology (Fig. 3-6). Spokes are filled with light gray to yellowish-colored

fine-grained sediments, and filled also with less abundant black-colored coarse scoria grains (Fig. 3-6). Infilling fine-grained sediments are homogenous (Fig. 3-6). 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. 3-6, 3-7). The exact number of spokes cannot be counted because of the overlapping and/or amalgamation of the spokes, but at least 10 spokes can be clearly recognized in specimen 1 (Fig. 3-6). On the other hand, at least 3 spokes are preserved in the case of the incomplete specimen (specimen 2; Fig. 3-6). The spoke diameters, which were measured nearly parallel to the bedding plane, range from 11.49–20.96 mm for the specimen 1 (mean value = 15.94 mm; n = 10) and 12.40–16.20 mm for the specimen 2 (mean value = 13.77 mm; n = 3). Morphometric parameters are also summarized in Table 3-2.

**Remarks.**—Found and described for the first time by Izumi and Yoshizawa (in press) and the present study. The present specimens are generally similar to the other ichnogenus *Estrellichnus* Uchman and Wetzel, 2001, which is a horizontal trace composed of either straight narrow ridges or grooves radiating from a central mound or depression. However, neither central mound nor depression was recognized in the studied specimens. An alternative candidate may be the ichnogenus *Glockerichnus* Pickerill, 1982, which is a star-shaped sole trail with numerous ribs radiating from the center. However, rare occurrence of the specimens from Misaki Formation and relatively poor preservation of central area prevent three-dimensional interpretations; thus, an accurate classification is difficult.

**Occurrence.**—Top surface of black-colored scoriaceous conglomerate (Fig. 3-7), Misaki Formation, Neogene (Moicene–Pliocene), Miura Peninsula, central Japan.

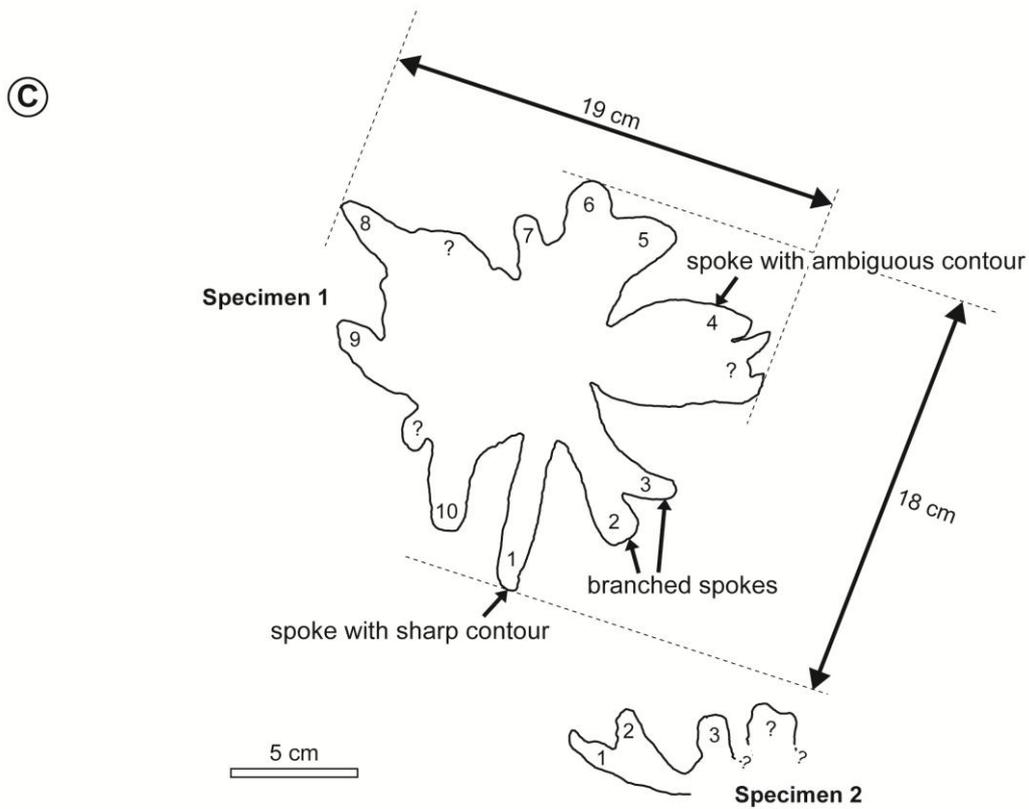
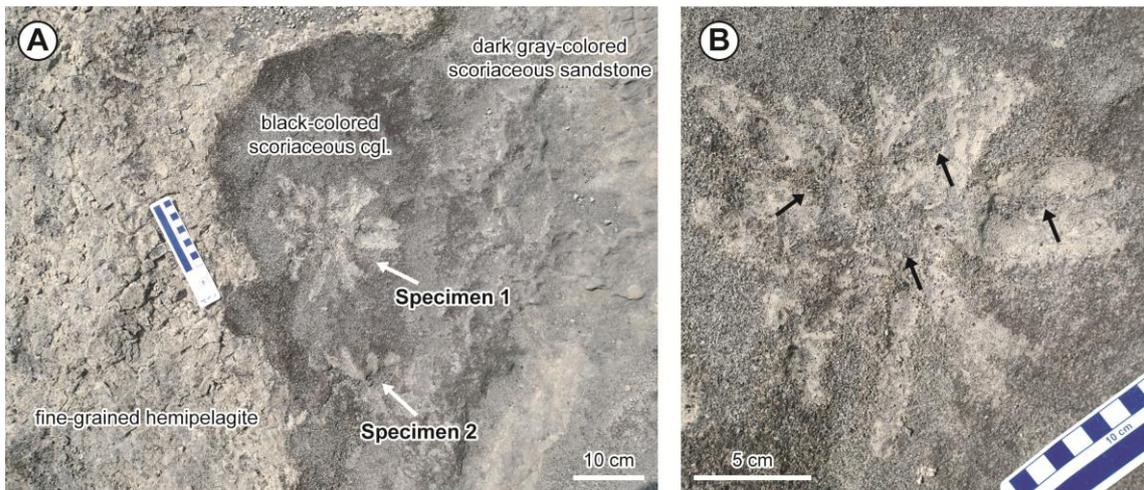


Fig. 3-6 (Slightly modified from Izumi and Yoshizawa, in press). Star-shaped trace fossils from the Misaki Formation. View parallel to the bedding plane. JGSM-02 section. (A) General view of the two specimens. (B) Magnified view of the relatively well-preserved specimen (specimen 1). Note that the spokes are mainly filled with light gray to yellowish fine-grained sediments (i.e. hemipelagite), with minor amounts of coarser scoria grains (arrows), which might have been derived from the overlying scoriaceous sandstone. (C) Sketch of specimen contours. Note that each obvious spoke is numbered serially.

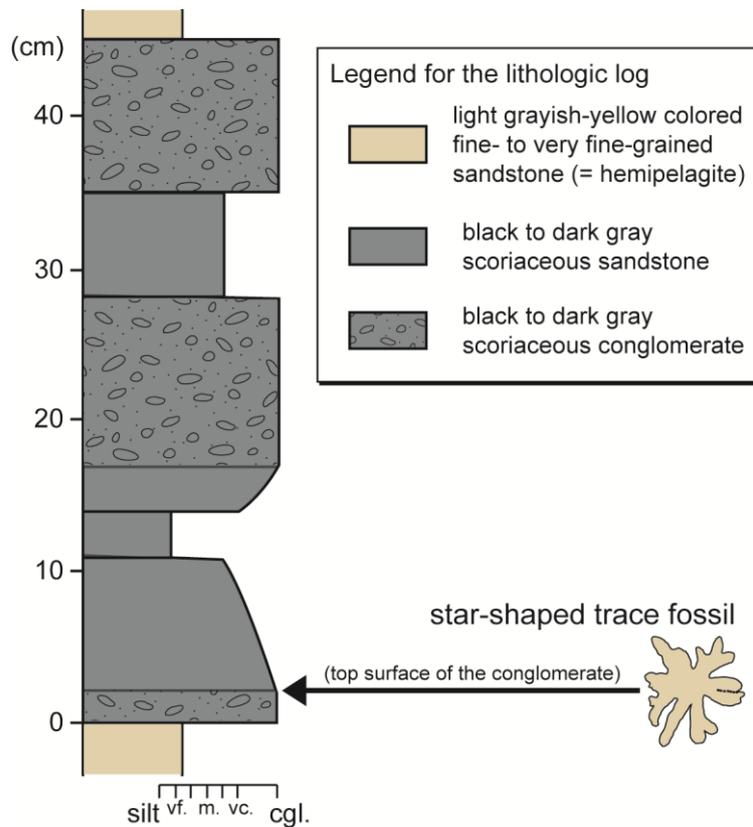


Fig. 3-7 (Slightly modified from Izumi and Yoshizawa, in press). Lithologic column near the occurrence horizon of the star-shaped trace fossils. Note that the star-shaped trace fossil occurs horizontally in the bedding plane (top surface) of the black-colored scoriaceous conglomerate, which is indicated by a black arrow. *Phymatoderma* does not occur around this level, but it is relatively common throughout the Misaki Formation.

### 3.2.3. Interpretations: Comparison with modern analogues and likely trace-maker of the star-shaped trace fossil and *Phymatoderma* from the Misaki Formation

To identify the animal that most likely produced the specific trace fossils, it is useful to compare them to modern similar traces. The relatively large star-shaped horizontal trace fossils, which were newly found from the Misaki Formation (Fig. 3-6), are closely similar to the surface feeding traces produced by echiuran worms, which have been commonly recognized on modern deep sea-floor (e.g., Ohta, 1984; Herring, 2002). Besides echiuran worms, similar star-shaped surface traces are produced by various kinds of animals (e.g., bivalve, polychaete, asteroid, ophiuroid; Ohta, 1984), but it is generally considered that echiuran worms are the most probable trace-makers than other candidates especially if the star-shaped traces are found in

deep-sea environments (Gaillard, 1991).

Bivalves have much greater preservation potential than trace fossils, but in the Misaki Formation fossil bivalves have not been recognized in or just around the star-shaped trace fossil or *Phymatoderma*, excluding bivalves as the trace-maker. Asteroid and ophiuroid are easily excluded because the star-shape traces produced by these animals have only 5 spokes (Ohta, 1984), which are much smaller than the star-shaped trace fossils from the Misaki Formation. It is impossible to completely exclude polychaetes as the potential trace-maker, at least in the case of the trace-fossil specimens from the Misaki Formation, but polychaetes might be unlikely. Ohta (1984) observed the star-shaped traces on the deep-sea floor of the Indian Ocean (i.e., 3025 m in water depth) that are produced by polychaetes with long palps. However, central structure of the star-shaped traces made by an abyssal polychaete is a tube, not a hole as in the case of echiuran's star-shaped traces (Ohta, 1984). Although the star-shaped trace fossil from the Misaki Formation (Fig. 3-5) lacks any observable central structure probably due to the taphonomic processes, it must have been preserved if there was a distinct central tube.

Considering these lines of evidence, abyssal echiuran worms are the most likely trace-maker. Among the modern analogous star-shaped surface feeding traces by echiuran worms, Type IV traces described by Ohta (1984) are most similar to the present fossil specimens (Figs. 3-6, 3-8; see also fig. 4 in Ohta, 1984).

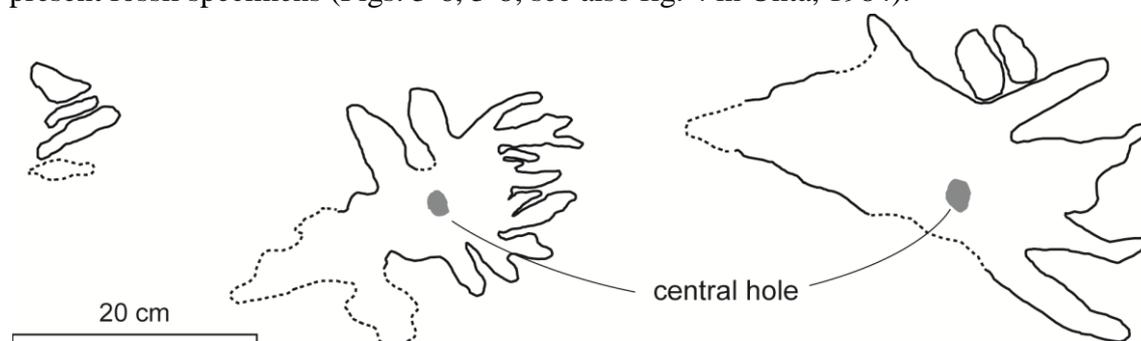


Fig. 3-8 (Slightly modified from Izumi and Yoshizawa, in press). Sketch of modern star-shaped feeding traces produced by abyssal echiuran worms (Type IV traces). Central holes are present (arrows). Dotted lines represent the ambiguous contour of the traces. Note the general similarity of the overall morphology between these traces and the star-shaped trace fossil from the Misaki Formation (Fig. 6). Figure 4 in Ohta (1984) was redrawn.

Not only are overall morphologic similarities between the fossil specimens and modern analogues evident (Figs. 3-6, 3-8), but dimension and the number of spokes are also similar, which are discussed below and summarized in Table 3-3. Namely,

lengths of spokes of modern Type IV star-shaped traces range from 86–152 mm (table 1 in Ohta, 1984). Although Ohta (1984) did not describe the overall size of the Type IV traces, it seems reasonable to assume that the overall size ranges from approximately 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 approximately 18 × 19 cm (Fig. 3-6), 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 3-3). In the case of fossil specimen 1 from the Misaki Formation, the spokes are 11.49–20.96 mm in diameter (Table 3-2), which is also within the range of the recorded spoke diameters of the modern Type IV traces (i.e. 10.70–26.50 mm; Ohta, 1984). Regarding the number of spokes observed, both fossil and modern star-shaped traces are also comparable (Table 3-3). At least 10 spokes can be distinguished in the fossil specimen 1 (Fig. 3-6), 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 (i.e. Type II, III; Ohta, 1984), but are quite similar to the fossil specimen 1. Lastly, bathymetry of both modern and fossil traces is quite similar (Table 3-3), 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. 3-9).

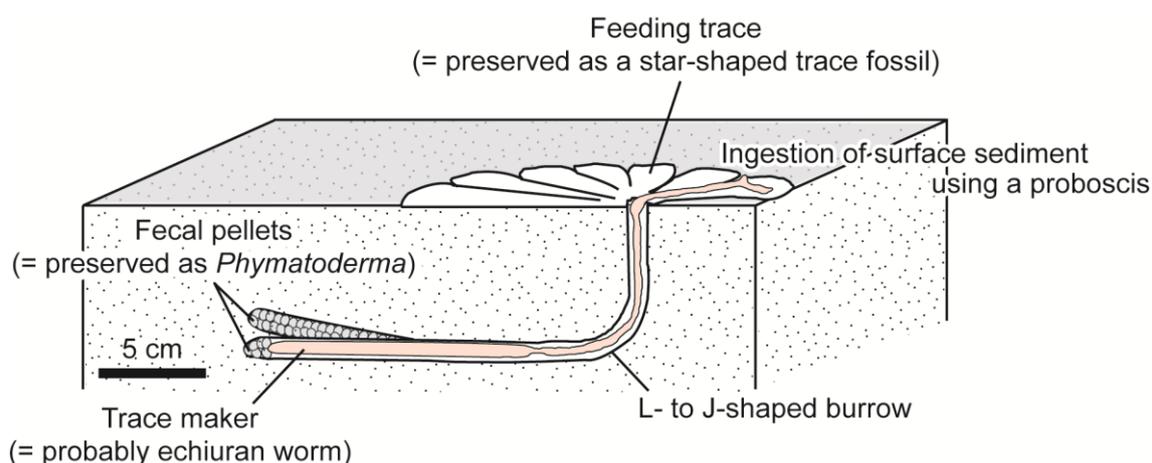


Fig. 3-9 (Slightly modified from Izumi and Yoshizawa, in press). Schematic diagram reconstructing the formation process of the star-shaped trace fossil and *Phymatoderma* from the Misaki Formation. Both types of trace fossils were probably produced by abyssal echiuran worms. Star-shaped trace fossil might have been 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 trace fossil is a surface biogenic structure, the preservation potential might be much lower than that of the subsurface fecal pellets.

On the other hand, 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 (e.g., Miller and Aalto, 1998; Miller and Vokes, 1998). Considering that both *Phymatoderma* and star-shaped trace fossils occur in the same lithologic unit (i.e., Misaki Formation), it is reasonable to presume that *Phymatoderma* from the Misaki Formation is fecal pellets excreted by deposit-feeding echiuran worms (Fig. 3-9). This interpretation is likely because of the following reasons. First, 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 (i.e., fecal pellets stuffed within the burrow) has been known also for shallow-water echiuran worm, *Echiurus* (Elders, 1975); thus, this may be considered a common excretion mode of echiurans. In addition, fecal pellets excreted by a modern shallow-water echiuran species *Ikegosoma gogoshimense* show ellipsoidal overall morphology (Goto et al., 2011; see also Fig. 3-10), which is highly similar to pellets of *Phymatoderma* from the Misaki Formation. Ellipsoidal pellets are also associated with the exceptionally well-preserved fossil specimen of echiuran worm *Coprinoscolex ellogimus* from the Middle Pennsylvanian shallow-marine Francis Creek Shale (Jones and Thompson, 1977). Based on all these lines of evidence, some of the subsurface fecal pellets excreted by ancient deep-sea echiuran worms might have been preserved as *Phymatoderma*, as illustrated in Figure 3-9.



Fig. 3-10. Fecal pellets excreted by *Ikegosoma gogoshimense*, which are scattered around the burrow opening (Courtesy of Dr. Ryutaro Goto).

Another supporting evidence is the morphological similarity between the Misaki *Phymatoderma* and burrows of the selected modern echiuran species. Vertical cross-sectional views of *Phymatoderma* from the Misaki Formation occasionally show upward branching (Fig. 3-11), which implies that the trace-maker of *Phymatoderma* roduced J-shaped burrow in some cases (Fig. 3-9). J-shaped burrows made by echiuran worms have been observed in *Maxmuelleria lankesteri* (see fig. 2c in Nickell et al., 1994), although this species lives in the muddy sediments of shallow marine environments (Nickell et al., 1994).

Furthermore, 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 (fig. 4 in Ohta, 1984) were measured using the image-processing program Image J, resulting in the ranges of 15.16–21.95 mm and 25.75–26.73 mm, respectively (Table 3-3). Those are within the range of the tunnel diameter of *Phymatoderma* (i.e., 5.30–27.25 mm; see section 2.9). This similarity in size may also support the interpretation that both star-shaped trace fossils and *Phymatoderma* from the Misaki Formation are feeding and fecal traces of ancient abyssal echiuran worms (Fig. 3-9).

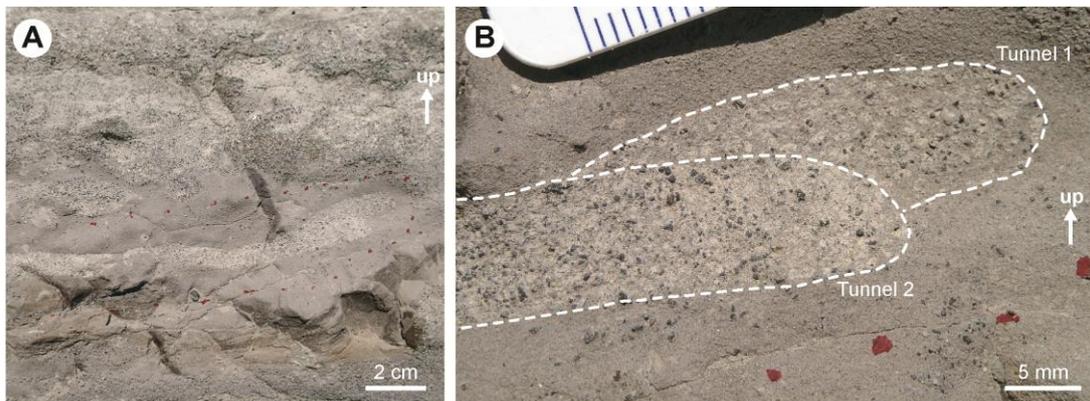


Fig. 3-11. Field photograph of *Phymatoderma* tunnels extending in a slightly upward direction (Slightly modified from Izumi and Yoshizawa, in press). Vertical cross-sectional view. JGSM-01 section. (A) Overall view. (B) Magnified photograph of the tunnels displaying an upward direction. Pellets are relatively well preserved and consists of white-colored sediments with minor amounts of black-colored scoria grains. Note that partial overlap of tunnel 1 and tunnel 2. White-colored dashed lines represent the contour of the tunnels.

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 the fieldwork at the Kenzaki section. However, regarding the Misaki *Zoophycos*, pellets are only weakly visible or nonvisible. Although this study cannot exclude the possibility that *Zoophycos* was also fecal trace made by deep-sea echiuran worm, the overall complex morphology of pellet-filled *Zoophycos* (Kotake, 1989, 1992, 1995) does not resemble the previously known echiuran burrow morphology (e.g., de Vaugelas, 1989; Nickell et al., 1994); thus, our interpretation that the deep-sea *Phymatoderma* was produced by echiuran worms (Fig. 3-9) seems more probable.

#### **3.2.4. Implications for the trace-maker of other *Phymatoderma*, and proposal for future research direction**

Several different kinds of animals are able to produce star-shaped surface trace similar to the specimens from the Misaki Formation (i.e., bivalves, polychaetes, echiuran worms, asteroids, ophiuroids; Ohta, 1984; Gaillard, 1991; Bromley, 1996; Goto, 2012) and sub-horizontally branched burrows stuffed with ellipsoidal fecal pellets similar to *Phymatoderma* (i.e., polychaete, echiuran worms; Myers, 1977; Reise, 1981; de Vaugelas, 1989; Nickell et al., 1994; Goto, 2012). Thus, if co-occurrence of a star-shaped trace fossil and *Phymatoderma* is recognized from the specific lithologic unit, the most likely trace-maker of both ichnogenera was echiuran worms or polychaete. As discussed above, especially in the case of deep-sea deposits, echiuran worms are more probable (Gaillard, 1991), although polychaetes cannot be completely excluded. Therefore, to identify the trace-maker of *Phymatoderma*, co-occurrence of a star-shaped trace fossil and *Phymatoderma* from the same lithologic unit is the most ideal case. However, even in the case of the Misaki Formation, the direct evidence of the connection between the star-shaped trace fossil and *Phymatoderma* has not found so far; thus, further studies are required to discover the direct connection.

One example that is worthy to discuss morphometric parameters of *Phymatoderma* in detail is from the Hayama Group (see section 2.8). This is because the Hayama Group and Misaki Formation are tectonically, paleoenvironmentally, and paleogeographically closely related (e.g., Ogawa et al., 1985; Akimoto et al., 1991,

1995; Kitazato, 1997; Shibata, 2012; Fig. 3-12).

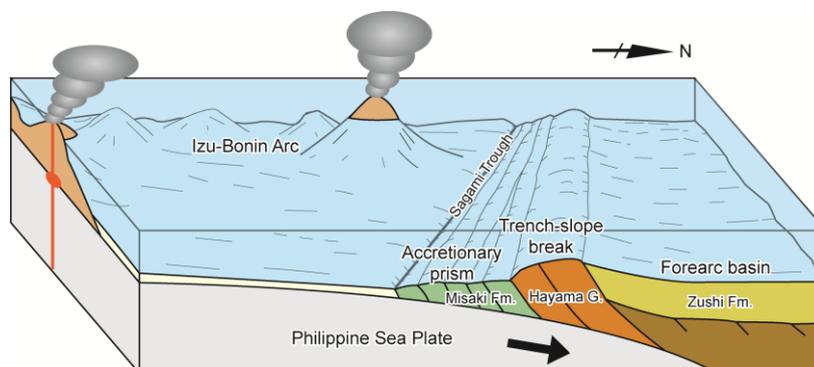


Fig. 3-12. Schematic and simplified reconstruction of the tectonic setting and paleogeography around the Miura Peninsula, central Japan during the late Miocene to early Pliocene (ca. 5 Ma). Note to scale. Slightly modified from Shibata (2012). Note that sedimentation of the Hayama Group and Misaki Formation had already occurred in the hemipelagic realm prior to 5 Ma.

Morphological similarity of *Phymatoderma* between the Hayama Group and Misaki Formation was confirmed by the comparison of morphometric parameters (Fig. 3-13). As Figure 3-13 clearly indicates, both the tunnel diameter and pellet aspect ratio have no significant differences ( $p > 0.05$ ) between *Phymatoderma* specimens from the Hayama Group and those from the Misaki Formation. Although a characteristic star-shaped trace fossil was not found from the Hayama Group, the morphometric similarity (Fig. 3-13; Table 3-4) probably suggests that the trace-makers of *Phymatoderma* from the both units (i.e., Hayama Group, Misaki Formation) were the same or closely related animal species.

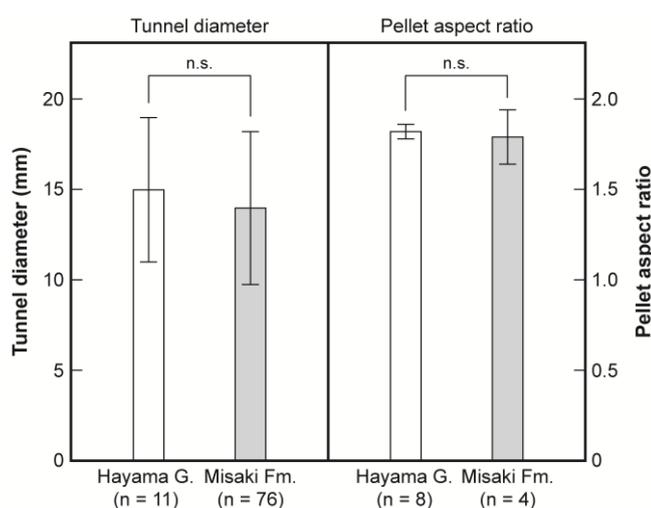


Fig. 3-13. Comparison of morphometric parameters of *Phymatoderma* between the Hayama Group and Misaki Formation. Data are represented as the mean value  $\pm$  SD (sample standard

deviation), and n.s. means not significant ( $p > 0.05$ ). Note that the Misaki Formation is tectonically, paleogeographically, and paleoenvironmentally closely related to the Hayama Group (Fig. 3-12).

Finally however, it must be pointed out that, except for the case of the Misaki Formation, other examples of such co-occurrence have never been reported nor recognized. This fact suggests that, when strictly considering, the trace-makers of *Phymatoderma* from localities other than the Misaki Formation cannot be identified. One must be always aware of the ichnologic principle that “producers are commonly soft-bodied animals that are rarely preserved” (Buatois and Mángano, 2011). Despite the ichnologic principle, one promising future direction to confirm the possibility that *Phymatoderma* are echiuran’s burrow filled with its fecal pellets (see section 3.2.3) is experimental studies using modern echiuran worms. In particular, to observe the morphologies of experimentally produced echiuran’s burrows and pellets is highly promising approach. Besides, burrow casting method (cf. Seike et al., 2012) may be applied to both shallow- and deep-sea echiurans.

Table 3-1. Results of the carbon-isotope analysis of *Phymatoderma granulata* from the Dotternhausen section (Lower Jurassic, Germany). SD means the sample standard deviation. Data has already been published in Izumi (2012).

	C-isotope ratio (‰)		n
	mean	SD	
pelletal infill	-26.64	0.21	21
overlying mudstone	-26.27	0.06	3
surrounding black shale	-28.49	0.22	8

n: number of measured samples

Table 3-2. Morphometric parameters of the studied star-shaped horizontal trace fossils from the Misaki Formation. SD means the standard deviation. Data will be published in Izumi and Yoshizawa (in press).

Locality (Fig. 3-5)	Specimen (Fig. 3-6)	Spoke number (Fig. 3-6)	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

Table 3-3. Comparison of the present star-shaped trace fossils with their modern analogous echiuran feeding traces. Data will be published in Izumi and Yoshizawa (in press).

	Star-shaped traces	
	*Fossil specimen	*Modern counterpart
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. 3-6	Fig. 3-8; 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).

Table 3-4. Morphometric comparison of *Phymatoderma* between the Hayama Group and Misaki Formation.

	Tunnel diameter (mm)	Pellet aspect ratio
Hayama Group	14.98 ± 3.99 (n = 11)	1.82 ± 0.04 (n = 8)
Misaki Formation	13.97 ± 4.13 (n = 76)	1.79 ± 0.15 (n = 4)

#### 第4章（56～79頁）

本章については、5年以内に雑誌等で刊行予定のため、非公開。

## CHAPTER 5

### Role of *Phymatoderma* as a feeding site for other small benthos

IN THE previous chapters (Chapters 3, 4), the pelletal infill of *Phymatoderma* was investigated as fecal pellets of the trace-maker itself, to interpret the mode of formation, mode of feeding, and diets. This is because these lines of evidence must be significant to reveal the Phanerozoic history of the benthic-pelagic coupling; namely, the interaction between marine deposit feeders (i.e., the *Phymatoderma*-producers) and phytoplankton diversification. Then, in this section (Chapter 5), special attention is paid to the trace fossils reburrowing selectively into the fecal pellets of *Phymatoderma*-producer, which may indicate the coprophagous activity of their trace-makers.

Fecal materials may provide a direct piece of evidence for the actual dietary source of the fecal-producing animals in the case of both vertebrates and invertebrates (i.e., both vertebrates and invertebrates) (e.g., Chin et al., 2003, 2008; Hollocher et al., 2010; Nakajima and Izumi, 2014; see also subchapter 4.1). On the other hand, it is well known that some animals, of both terrestrial and marine, feed on fecal matter excreted by other animals because feces, of especially herbivorous and omnivorous mammals, represent a rich source of nutrients based in large part on the bacterial content, sometimes high nitrogen content, abundant complex carbohydrates and also vitamins and minerals (e.g., Philips, 2011). Feces provide a certain ecological niche for such coprophagous animals, and many papers have reported the paleontological evidence that feces of ancient animals were actually excavated and fed on by other smaller organisms (e.g., Chin and Gill, 1996; Eriksson et al., 2011). Therefore, the trace-fossil evidence for the coprophagous behavior of marine benthic invertebrates provides significant information on the paleobiological interactions, which are also expected to have been affected by the Mesozoic phytoplanktonic diversification and subsequent biological/environmental changes; thus, for the purpose of the present study, ichnologic signatures representing coprophagous behavior of marine benthic invertebrates should be investigated in detail.

However, one serious problem is that evidence for the ancient coprophagous behavior has been mostly provided by trace fossils preserved in the terrestrial coprolites (i.e., vertebrate fossil feces); on the other hand, much fewer examples of coprophagous behavior recorded in marine invertebrate fossil feces have been recognized so far. Under such circumstances, the present study discovered and described, for the first time, the coprophagous features produced by marine benthic organisms; namely, the *Phymatoderma* pelletal infill reburrowed by smaller ichnogenes (i.e., *Chondrites*, *Phycosiphon*; see Chapter 2). Thus, in this chapter, ichnologic characteristics of such

reburrowed trace fossils (e.g., relationships between reburrowing and reburrowed ichnogenera) were examined in detail.

### 5.1. Materials and methods

**Materials.**—*Phymatoderma* specimens from the Neogene deep-marine Shiramazu Formation, central Japan. Among studied specimens from various ages and localities, only *Phymatoderma* specimens from the Shiramazu Formation were reburrowed by both *Chondrites* and *Phycosiphon* (Plate 2-10; Fig. 5-1); thus, this is an ideal example to reveal the relationship between reburrowing and reburrowed ichnogenera.

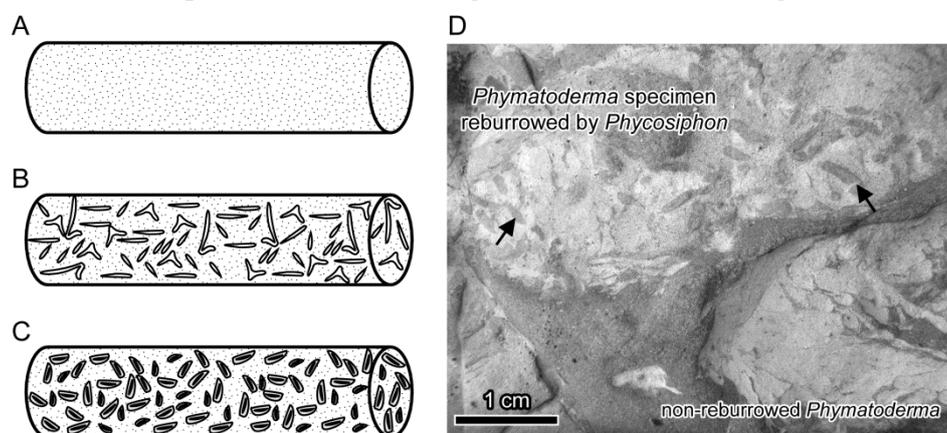


Fig. 5.1. Schematic diagrams (A–C) and field example (D) of the reburrowed trace fossils. (A) Non-reburrowed trace-fossil specimen. (B) Trace-fossil specimen that was reburrowed with *Chondrites*. (C) Trace-fossil specimen that was reburrowed with *Phycosiphon*. (D) Field photograph showing the *Phymatoderma* specimen that was reburrowed with *Phycosiphon* (black arrows), Neogene (Pliocene) Shiramazu Formation, central Japan. Modified from fig. 3C in Izumi (2014).

**Methods.**—In order to reveal the differences in the nature of the reworking activities of *Chondrites* and *Phycosiphon* trace-makers, several kinds of parameters were measured using a caliper in the field or the image-processing program Image J in the laboratory. These values include, burrow diameter ( $D_{Pm}$ ) and maximum pellet width ( $PW_{max}$ ) of non-reburrowed *Phymatoderma* specimens, and burrow diameters of: reburrowed *Phymatoderma* specimens, reburrowing *Chondrites* ( $D_{Ch}$ ) and *Phycosiphon* ( $D_{Pc}$ ), and the two ichnogenera (*Chondrites* and *Phycosiphon*) within the host siltstone of the Shiramazu Formation. In cross section, burrows of *Phycosiphon* are composed of a fine-grained, dark-colored central core and a surrounding coarser mantle (Kern 1978; Goldring et al. 1991; Wetzel and Bromley 1994; Bromley 1996). ‘Burrow diameter’ measured in this study is the width of the central core because it has been interpreted to

represent the body width of its trace-maker (Ekdale and Lewis 1991; Wetzel and Bromley 1994; Seilacher 2007; Bednarz and McIlroy 2009). Only  $PW_{max}$  and its associated  $D_{Pm}$  were measured using Image J because it is usually difficult to evaluate the largest pellet for each specimen in the field. Detailed measurement information is also summarized in Figure 5-2. An unpaired t-test was used for statistic analysis.

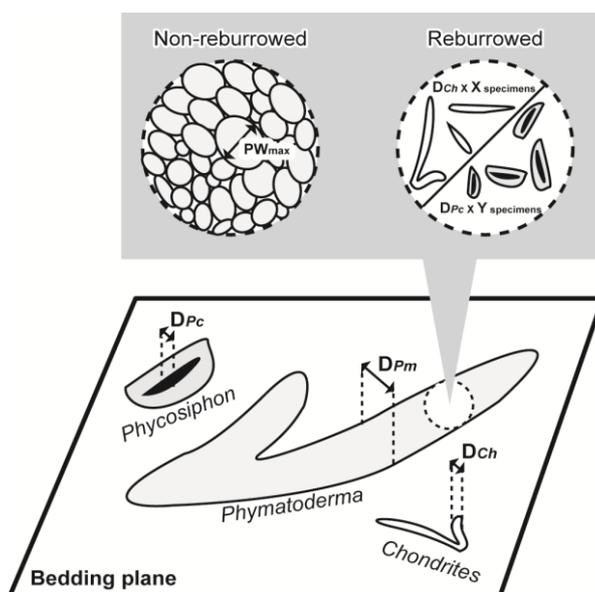


Fig. 5-2 (Slightly modified from Izumi, in press). Schematic diagram showing the measured parameters.  $D_{Ch}$ : burrow diameter of *Chondrites*,  $D_{Pc}$ : burrow (i.e. central core) diameter of *Phycosiphon*,  $D_{Pm}$ : burrow diameter of *Phymatoderma*,  $PW_{max}$ : maximum pellet width. X ranges from 4–10, Y from 2–37.

## 5.2. Results

The results of burrow measurements are summarized in Figures 5-3 and 5-4, as well as Table 5-1. Through numerous measurements ( $n = 445$ ), the burrow diameters of non-reburrowed *Phymatoderma* range from 4.30–45.80 mm (mean = 18.14 mm; Fig. 5-3A). Although the number of *Phymatoderma* specimens reburrowed by *Chondrites* and *Phycosiphon*, which were recognized during fieldwork, are much smaller than the number of non-reburrowed *Phymatoderma*, *Phymatoderma* specimens reburrowed by *Chondrites* and *Phycosiphon* have 8.30–30.95 mm ( $n = 13$ ; mean = 18.54 mm; Fig. 5-3B), and 9.70–40.65 mm in diameter ( $n = 34$ ; mean = 28.39 mm; Fig. 5-3C), respectively. The mean values of non-reburrowed *Phymatoderma* specimens and tunnels reburrowed by *Chondrites* showed no significant difference (Fig. 5-3D). On the other hand, *Phymatoderma* burrows reburrowed by *Phycosiphon* have significantly ( $p < 0.001$ ) larger diameters compared to non-reburrowed specimens (Fig. 5-3D).

The burrow diameters of *Chondrites* and *Phycosiphon* occurring in the host siltstone

of the Shiramazu Formation range from 0.55–2.00 mm ( $n = 85$ ; mean = 1.20 mm), and 0.75–2.00 mm ( $n = 135$ ; mean = 1.38 mm), respectively (Fig. 5-4). Mean diameters of *Phycosiphon* and *Chondrites* within the host siltstone have a significant ( $p < 0.001$ ) difference, although the difference itself is very tiny (ca., 0.18 mm; Table 5-1). Burrows that rework the *Phymatoderma* tunnels have highly constant diameters regardless of varying *Phymatoderma* diameters and are within the ranges of diameters of *Chondrites/Phycosiphon* from the host siltstone, whereas, fecal pellet diameters of non-reburrowed *Phymatoderma* tunnels increase their size with increasing the tunnel diameters (Fig. 5-4).

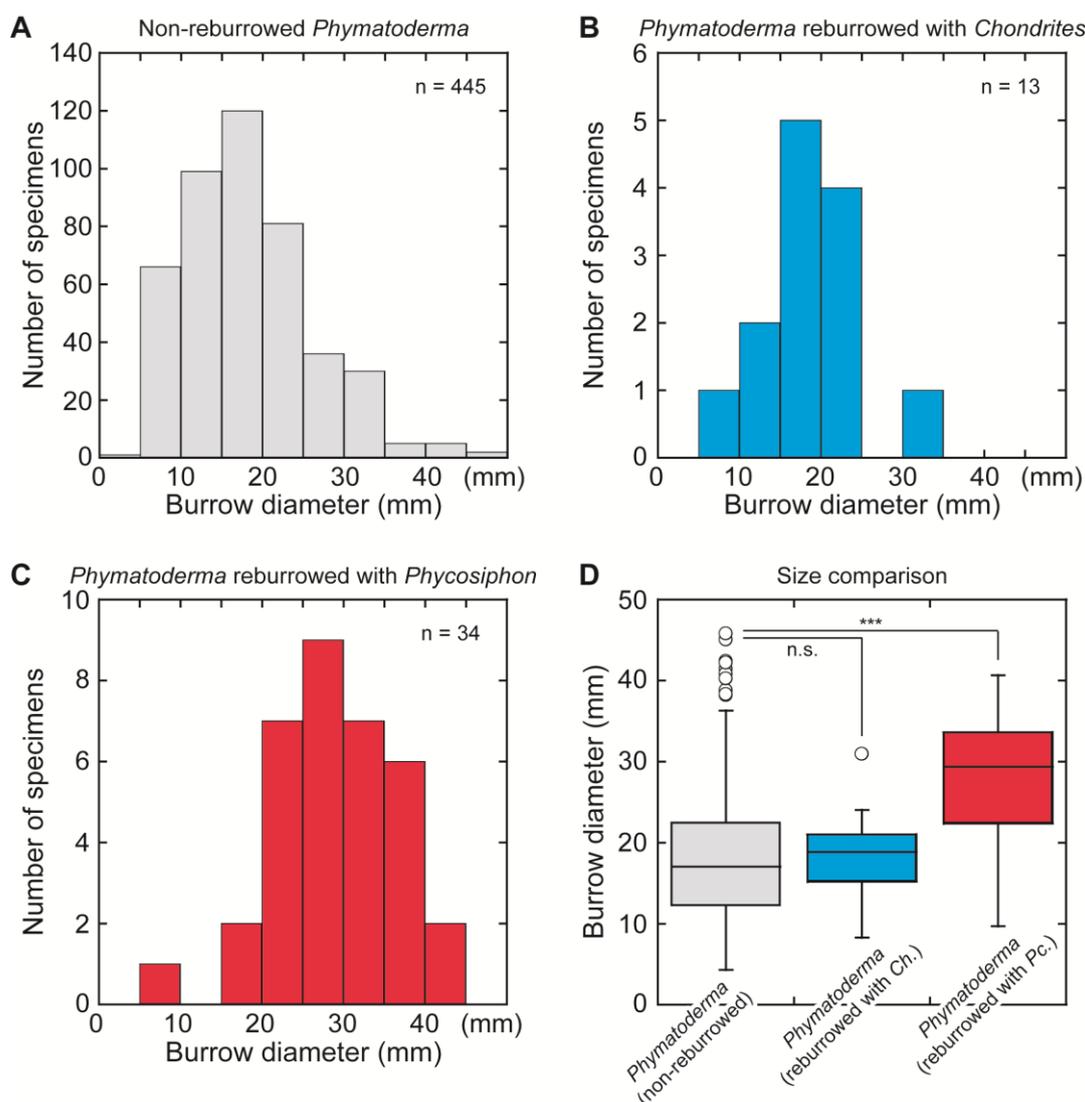


Fig. 5-3 (Slightly modified from Izumi, in press). Size distributions of *Phymatoderma* from the Shiramazu Formation. (A) Non-reburrowed *Phymatoderma*. (B) *Phymatoderma* reburrowed by *Chondrites*. (C) *Phymatoderma* reburrowed by *Phycosiphon*. (D) Comparison of burrow diameter

between non-reburrowed *Phymatoderma*, and tunnels reburrowed by *Chondrites* and *Phycosiphon*. Note that *Phymatoderma* reburrowed by *Phycosiphon* has significantly larger size. *Ch.*: *Chondrites*, *Pc.*: *Phycosiphon*, n.s.: not significant, \*\*\*:  $p < 0.001$ , n: number of measurements.

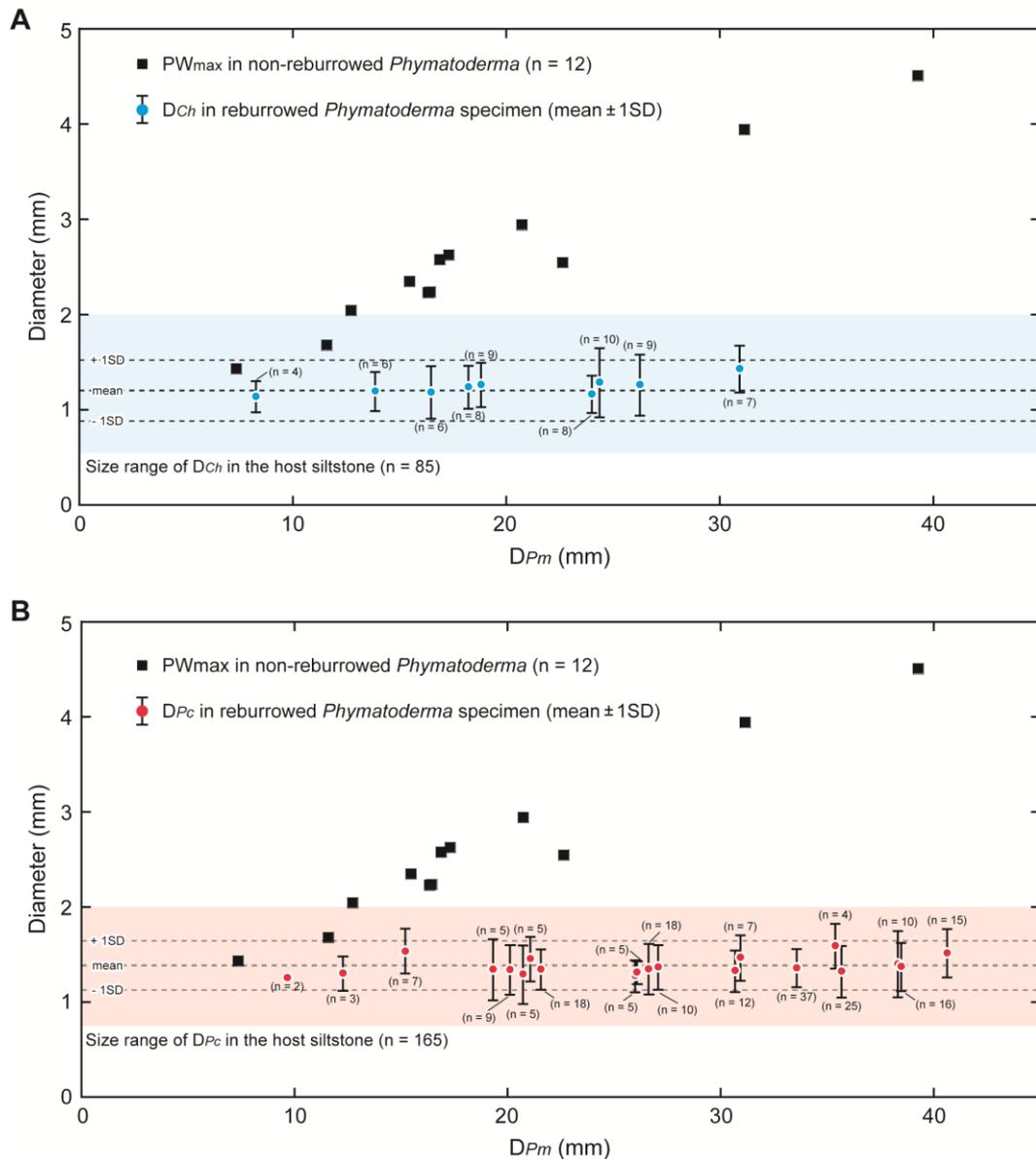


Fig. 5-4 (Slightly modified from Izumi, in press). Scatter plots showing the relationships between *Phymatoderma* burrow diameter and its maximum pellet width (black plot) and reburrowing trace-fossil diameter. (A) *Chondrites*. (B) *Phycosiphon*. Note that diameters of both ichnogenera that reburrowed *Phymatoderma* tunnels are within the size-range of them occurring in the host siltstone (shade), whereas pellet width increases with increasing *Phymatoderma* burrow diameter. D<sub>Ch</sub>: burrow diameter of *Chondrites*, DP<sub>c</sub>: burrow (i.e. central core) diameter of *Phycosiphon*, DP<sub>m</sub>: burrow diameter of *Phymatoderma*, PW<sub>max</sub>: maximum pellet width, n: number of measurements.

### 5.3. Interpretations: Size preference by the *Phycosiphon/Chondrites*-producers related with their feeding strategies

Burrows and feces of marine benthic animals are usually coated by mucus or mucus membrane (Bromley 1996), which contains abundant reactive organic matter (Lalonde et al. 2010; Petrash et al. 2011). Therefore, it is reasonable that *Phymatoderma* pellets, which have been interpreted as fecal pellets excreted by a surface deposit-feeding producer (Miller and Aalto 1998; Miller and Vokes 1998; see also subchapter 3-1), were attractive for other benthos; thus *Phymatoderma* reburrowed by other ichnogenera such as *Chondrites* and *Phycosiphon* were recognized (Fig. 5-1D). Although some *Phymatoderma* specimens from the Shiramazu Formation are cross-cut by other ichnogenera such as *Zoophycos*, these specimens do not construct the composite structures. This cross-cutting relationship along with the presence of composite *Phymatoderma* are consistent with the previous interpretation that *Phymatoderma* is emplaced at relatively shallow tier (Miller and Vokes 1998). Apart from *Phymatoderma*, the trace fossil record provides many examples of various deposit-feeding traces (i.e., some burrows, feces) reburrowed by *Chondrites* or *Phycosiphon* (e.g., Bromley and Frey 1974; Ekdale and Bromley 1991; Wetzel 1991, 2010; Buatois and Mángano 1992, 2011; Bromley 1996; Kędzierski and Uchman 2001; Buatois et al. 2002; Leszczyński 2004; Rotnicka 2005; Rodríguez-Tovar and Uchman 2006; Carmona et al. 2008; Rodríguez-Tovar et al. 2011a, b; Olivero and López Cabrera 2013; Uchman et al. 2013a, b).

This study is the first report to reveal systematically and quantitatively the differences in nature between trace fossils reburrowed by *Chondrites* and *Phycosiphon*. *Phymatoderma* reburrowed by *Phycosiphon* has significantly larger burrow diameters compared with non-reburrowed *Phymatoderma* tunnels and those reburrowed by *Chondrites* (Fig. 5-3D). Although there is a significant difference in the mean diameter between *Chondrites* and *Phycosiphon* within the host siltstone (Table 5-1), it may not be an important factor because the difference is tiny (0.18 mm). Furthermore, although mean diameter of *Phycosiphon* from the Shiramazu Formation is approximately 1.15 times larger than that of *Chondrites*, average size of *Phymatoderma* reburrowed by *Phycosiphon* has ca. 1.53 times larger than that of *Phymatoderma* reburrowed by *Chondrites* (Table 5-1). Therefore, these results (Fig. 5-3D) may be explained in terms of feeding strategies of *Chondrites* and *Phycosiphon* trace-makers, which have been interpreted to be different. The *Chondrites*-producer has been considered as a chemosymbiotic worm-like animal (Seilacher 1990; Fu 1991; Bromley 1996), whereas,

the *Phycosiphon*-producer has long been interpreted as a deposit-feeding vermiform organism (Kern 1978; Wetzel and Bromley 1994; Bromley 1996; Seilacher 2007; Bednarz and McIlroy 2009; Izumi, 2014).

As marine sediments are mainly composed of various types of mineral grains (i.e., quartz, feldspar, calcite, and clay minerals) and their organic matter content is generally low (Rabouille and Gaillard 1991; Boudreau 1997), deposit feeders appear to be faced with the common problem of obtaining food from sediments (Lopez and Levinton 1987). Potential food for deposit-feeding animals is fresh organic fraction in ingested sediment, phytodetritus and meiofauna (Lopez and Levinton 1987). Although the surface sediments contain abundant fresh organic matter at the time of deposition on the seafloor (Hartnett et al. 1998), the labile organic material may have been rapidly decomposed within the top few centimeters of sediments by microbial metabolisms (Druffel et al. 1992; Burdige 2006; Sarmiento and Gruber 2006). Furthermore, organic-matter flux to the seafloor generally varies depending on the water depth and the distance from the shore (Suess 1980; Romankevich 1984; Rabouille and Gaillard 1991), thus deep-sea settings have been regarded as low nutrition (i.e., oligotrophic) input areas (Jumars et al. 1990; Seiter et al. 2004). Therefore, in order to get sufficient organic matter under such severe conditions, the trace-maker of *Phycosiphon*, which was a subsurface deposit feeder (Kern 1978; Wetzel and Bromley 1994; Bromley 1996; Seilacher 2007), must have successively processed significant amounts of sediments during its life span. Since fecal pellets generally contain abundant fresh organic material compared to surrounding host sediments (Henriksen et al. 1983), *Phymatoderma*, especially larger sized specimens must have been an ideal locus of deposit-feeding activity by the *Phycosiphon*-producer, resulting in the significant size selectivity recognized herein (Fig. 5-3D). Preference for larger tunnels might have been critical to the *Phycosiphon*-producer considering the fact that *Phymatoderma* with twice the diameter has 8-times the volume of fecal aggregates.

It seems to be reasonable that a larger deposit feeder has to process larger amount of sediment to obtain sufficient organic matter. However, this trend cannot be recognized in this study; namely, all *Phycosiphon* burrows reburrowing various-sized *Phymatoderma* have similar-sized diameter, which are within the size range of those from the host siltstone (Fig. 5-4B), despite the increase of fecal-pellet size with increasing *Phymatoderma* burrow diameter (Fig. 5-4). This fact suggests that there was no size bias in terms of the *Phycosiphon*-producers. This is probably because *Phymatoderma* from the Shiramazu Formation is much larger than *Phycosiphon* (Table 5-1). The diameter of the smallest *Phymatoderma* specimen reburrowed by

*Phycosiphon* is approximately 8-times larger than that of reburrowing *Phycosiphon* (Fig. 5-4B); therefore, 512-times the volume of sediment, which seems enough volume even for relatively larger *Phycosiphon*-producer.

Alternatively, the most important factor for a chemosymbiotic *Chondrites*-producer might be HS<sup>-</sup> content within the pore water (Bromley 1996). Symbiotic sulfur-oxidizing bacteria utilized energy generated from the oxidation of sulfide to produce organic matter (Sarmiento and Gruber 2006). Decomposition of labile organic matter by sulfate-reducing bacteria within the excreted fecal sediments might have produced sulfide (Jørgensen 1977), since inner microenvironments of feces are generally anoxic (Reise 1985). In contrast to a deposit feeder, chemosymbiotic burrowers probably did not need to process large amounts of sediment; thus, space was not a limiting factor for the *Chondrites* trace-makers. Rather, probing itself within the *Phymatoderma* tunnels (i.e., aggregate of fecal pellets) may have been critically important for the *Chondrites*-producers. Since *Chondrites* is much smaller than *Phymatoderma* (Fig. 5-3A, B), even a relatively small *Phymatoderma* tunnel has enough space for the *Chondrites*-producer to uptake sufficient nutrients, which explains why the trace-makers of *Chondrites* did not show any size selectivity in terms of the *Phymatoderma* tunnel diameters (Fig. 5-3D). In spite of the increase of fecal-pellet size with increasing *Phymatoderma* burrow diameter (Fig. 5-4), all *Chondrites* burrows reburrowing varying *Phymatoderma* have similar-sized diameter and within the size range of those from the host siltstone (Fig. 5-3A), which also indicates that there was no size bias in terms of the *Chondrites*-producers.

Although the explanation about the reburrowing activities discussed here seems to be highly likely, frequency of reburrowed *Phymatoderma* is not so high with respect to non-reburrowed *Phymatoderma* (i.e., approximately 10 %; Fig. 5-3), suggesting that the trace-makers of both *Chondrites* and *Phycosiphon* also obtained foods from the host sediment (and pore water). This might be explained by the fact that the mass of *Phymatoderma* must be significantly low compared with that of the whole host sediment, even if *Phymatoderma* is a common trace fossil from the Shiramazu Formation. Consequently, the probability of reaching *Phymatoderma* (i.e., preferential 'feeding site') was low, although it is difficult to evaluate the validity of this probability (i.e., 10 %) due to the lack of any quantitative data of reburrowed trace fossils. Difference in frequency of *Phymatoderma* reburrowed by *Chondrites* or *Phycosiphon* (Fig. 5-3B, C) may be related to sequential colonization of muddy turbidites (Wetzel and Uchman 2001). The *Phycosiphon*-producer penetrate substrates earlier than the *Chondrites*-producer (Wetzel and Uchman 2001), which can explain higher frequency

of *Phymatoderma* reburrowed by *Phycosiphon* (Fig. 5-3). *Phymatoderma* tunnels reburrowed both by *Chondrites* and *Phycosiphon* are not recognized. This fact indicates that once colonized by the *Phycosiphon*-producer, *Phymatoderma* tunnel could not be colonized by the *Chondrites*-producer, probably due to some sort of exclusion.

#### **5.4. Size-dependent reburrowing behavior of deposit feeders: Insights from the Phanerozoic records of composite trace fossils**

The present study revealed, for the first time, the differences in the reburrowing behavior of *Chondrites* and *Phycosiphon* trace-makers quantitatively and systematically. In particular, preference for larger burrows by the *Phycosiphon*-producer than the *Chondrites*-producer was well recognized. The recognized difference can be explained by considering the different feeding strategies of these two ichnogenera; namely, deposit-feeding *Phycosiphon*-makers and chemosymbiotic *Chondrites*-makers; deposit-feeding *Phycosiphon*-producers (Kern, 1978; Wetzel and Bromley, 1994; Bednartz and McIlroy, 2009; Izumi, 2014) must have processed a significant mass of sediment to obtain sufficient organic matter, whereas chemosymbiotic *Chondrites*-makers (Seilacher, 1990; Fu, 1991; Bromley, 1996) did not require a substantial amount of sediment to obtain nutrients.

However, the differences in reburrowing behavior among organisms with a specific trophic type (e.g., deposit feeding) remain unknown. Given that all deposit feeders appear to have faced the common problem of obtaining food (i.e., organic matter) from ingested sediment (Lopez and Levinton, 1987), there must be a significant size-dependent relationship between reburrowing deposit-feeding organisms and reburrowed traces. In particular, a larger deposit feeder must ingest larger amounts of sediment to obtain sufficient organic matter than smaller ones (Cammen, 1989 and references herein), and this may have resulted in a preference for burrows with larger amounts of infilling sediment by larger deposit feeders.

To verify the idea, a systematic literature survey has been carried out particularly focusing on the occurrence reports of composite trace fossils from Phanerozoic marine deposits. In addition, the reports of trace fossils reburrowed by *Chondrites* were also investigated for comparison.

First, papers that reported the occurrence of trace fossils that were reburrowed with small deposit-feeding ichnogenera (*Phycosiphon*, *Planolites*, *Macaronichnus*) and with *Chondrites* were systematically investigated (Table 5-2). Then, the relationship between the sizes of the reburrowed and reburrowing trace fossils was evaluated (Fig. 5-5). There is a positive correlation ( $R^2 = 0.49$ ) between the diameter of the reburrowed trace

fossils and reburrowing deposit-feeding trace fossils, although the size data varied widely. The great variability observed might be due to the absence of works showing an exact size range of trace fossils that were reburrowed with small ichnogenera except for the present study (section 5.2), and to the small number of informative papers (i.e., 24 papers). On the other hand, the size of the reburrowed trace fossils and reburrowing *Chondrites* showed no correlation ( $R^2 = 0.08$ ; Fig. 1).

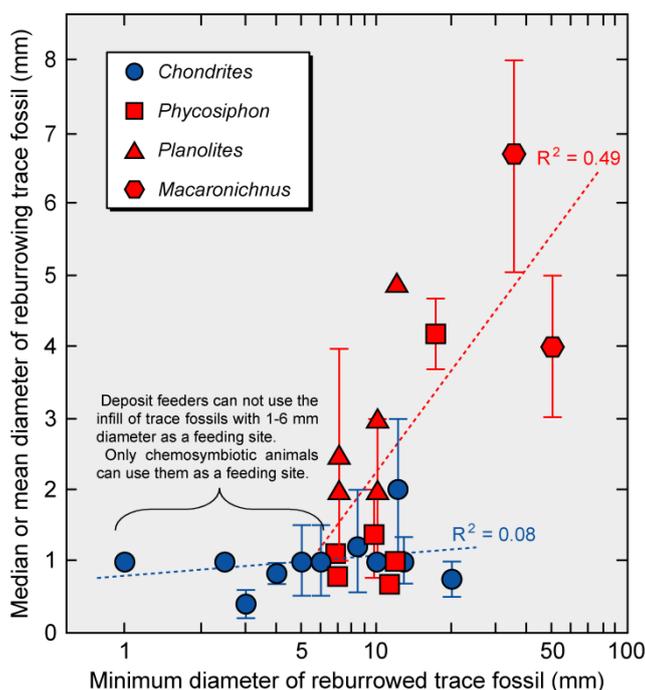


Fig. 5-5. Size relationship between reburrowing and reburrowed trace fossils based on the literature survey in the present study. Larger deposit feeder reburrowed larger trace-fossil infill as a feeding site, whereas chemosymbiotic *Chondrites*-producer was independent of the size of reburrowed trace fossils. Bars represent the range of diameter of the reburrowing ichnotaxa. In case of the average diameter of the reburrowing ichnotaxon is not available, median value is used instead.

Considering that larger deposit-feeding animals require more organic material (Cammen, 1987 and references herein), they may have ingested larger amounts of sediment to obtain organic matter, resulting in the positive correlation (Fig. 5-5). Small burrows, particularly with diameters of 1–6 mm (Fig. 5-5), have small amounts of infilling sediment and thus could not serve as a preferential feeding site for large deposit feeders. Therefore, burrow size, thus the amount of infilling sediment, is one of the most significant limiting factors for deposit feeders that tried to obtain organic matter in sediment-filled subsurface burrows, further supporting the inference described in

section 5.3.

On the other hand, *Chondrites*, whose producer was a chemosymbiotic animal (Seilacher, 1990; Fu, 1991; Bromley, 1996), showed no size-dependent relationship (Fig. 5-5), a part of which might be due to the small size range of *Chondrites* than other ichnogenera (Table 5-2). Even so, it is unlikely that the limiting factor for the reburrowing *Chondrites*-producer was a burrow size, because the infill of trace fossils with small diameter (i.e., 1–6 mm) could be used as a feeding site (Fig. 5-5). Instead, other aspects such as the  $\text{HS}^-$  concentration in the pore water might have been a limiting factor for the chemosymbiotic *Chondrites*-maker during reburrowing behavior.

In summary, as a result of the literature data compilation (Fig. 5-5), the idea that larger deposit feeder generally reburrowed larger trace-fossil infilling sediment to obtain sufficient food was verified.

Table 5-1. Diameters of each ichnogenus within the host siltstone of the Pliocene Shiramazu Formation, central Japan. Data will be published in Izumi (in press).

		mean	minimum	maximum	n
<i>Phymatoderma</i>	non-reburrowed	18.14*	4.30	45.80	445
	reburrowed with <i>Chondrites</i>	18.54*	8.30	30.95	13
	reburrowed with <i>Phycosiphon</i>	28.39*	9.70	40.65	34
<i>Chondrites</i>		1.20**	0.55	2.00	85
<i>Phycosiphon</i>		1.38**	0.75	2.00	135

n: number of measured burrows

\**Phymatoderma* reburrowed with *Phycosiphon* has significantly ( $p < 0.001$ ) larger diameter than *Phymatoderma* without reburrowed and reburrowed with *Chondrites*, whereas mean diameter of *Phymatoderma* reburrowed with *Chondrites* has no significant difference from non-reburrowed *Phymatoderma*.

\*\**Phycosiphon* has significantly ( $p < 0.001$ ) larger diameter than *Chondrites*.

Table 5-2. List of composite trace fossils with ichnotaxonomical and size data. The trace-fossil data in the present study represent the exact size range of the reburrowing trace-fossil diameters and the minimum diameter of the reburrowed trace fossils. Because other data provide the size (or size range) of trace fossils within the host rock, including composite specimens, the exact size of the reburrowing and reburrowed trace fossils is not available. In terms of the reburrowing trace fossils with their size range ‘less than X mm’, X mm is used in the present study because the minimum diameter is not available.

Reburrowing ichnogenus	Occurrence age	Min. diameter of reburrowed ichnogenus (mm)	Reburrowed ichnogenus	Mean or median diameter of reburrowing ichnogenus (mm)	Size range of reburrowing ichnogenus (mm)	Reference	Note
<i>Chondrites</i>	Pliocene	8.3	<i>Phymatoderma</i>	1.20	0.55–2.00	Izumi (in press); This thesis	
	early Miocene-late Pliocene	5	<i>Planolites</i>	1.0	less than 0.5–1.5	Ekdale (1980)	
	Paleocene-Eocene	4	<i>Planolites</i>	0.85	0.7–1.0	Rodríguez-Tovar et al. (2011b)	diameter of <i>Chondrites</i> (small)
	late Paleocene	20	<i>Palaeophycus</i>	0.75	0.5–1.0	Giannetti and McCann (2010)	
	Cretaceous-Paleogene	10	<i>Thalassinoides</i>	1	not described	Rodríguez-Tovar and Uchman (2006)	diameter of <i>Chondrites</i> isp.
	late Campanian-Maastrichtian	3	? <i>Radhostium</i>	0.4	0.2–0.6	Uchman (2007)	diameter of <i>Chondrites intricatus</i>
	Santonian-Maastrichtian	12	<i>Thalassinoides</i>	2.0	1.0–3.0	Phillips and McIlroy (2010)	

	early Campanian	ca. 1	<i>Gyrolites</i>	ca. 1	not described	Bromley and Frey (1974)	size of <i>Gyrolites</i> represents the diameter of burrow wall reburrowing <i>Chondrites</i> diameter was measured using fig. 7.2 in Bromley, 1996
	Cenomanian-Turonian	6	<i>Thalassinoides</i>	1.0	0.5–1.5	Rodríguez-Tovar et al. (2009)	diameter of <i>Chondrites</i> (small)
	Cenomanian-Turonian	2.5	<i>Planolites</i>	1	less than 1	Uchman et al. (2013a)	diameter of <i>Chondrites</i> (small)
	Cenomanian-Turonian	7	<i>Thalassinoides</i>	1	less than 1	Uchman et al. (2013b)	diameter of <i>Chondrites</i> (small)
	Late Cretaceous	12.67	?	1.0	0.67–1.33	Buatois and Mángano (2011)	diameters were measured using fig. 1.5b
<i>Phycosiphon</i>	Modern	11.25	<i>Planolites</i>	0.69	0.57–0.80	Wetzel (2010)	diameters were measured using text-fig. 4-2
	Pliocene	6.92	<i>Thalassinoides</i>	1.11	not described	Pickerill et al. (2002)	diameters were measured using fig. 14.3f
	Pliocene	9.70	<i>Phymatoderma</i>	1.38	0.55–2.00	Izumi (in press); This thesis	
	early Miocene	17	<i>Thalassinoides</i>	4.2	3.7–4.7	Carmona et al. (2008)	
	Turonian-Coniacian	12	<i>Thalassinoides</i>	ca. 1	not described	Kędzierski and Uchman (2001)	
	late Cenomanian-middle Turonian	7	<i>Thalassinoides</i>	0.8	less than 0.8	Rotnicka (2005)	diameter of <i>Chondrites</i> (small)

<i>Planolites</i>	late Miocene	10	<i>Ophiomorpha</i>	2	1–3	Hovikoski et al. (2005)	
	late Miocene	10	<i>Thalassinoides</i>	3	not described	Rebata et al. (2006)	
	late Oligocene-early Miocene	7	<i>Thalassinoides</i>	2	not described	Ghibaudo et al. (1996)	
	Santonian-Maastrichtian	12	<i>Thalassinoides</i>	4.9	5–12	Phillips and McIlroy (2010)	reburrowing <i>Planolites</i> diameter was measured using fig. 4B
	late Cenomanian-middle Turonian	7	<i>Thalassinoides</i>	2.5	1–4	Rotnicka (2005)	
<i>Macaronichnus</i>	Pleistocene	34.8	<i>Conichnus</i>	6.7	5–8	Mayoral et al. (2013)	reburrowed <i>Conichnus</i> diameter is the average between small and large forms
	middle Miocene	50	<i>Piscichnus</i>	4	3–5	Kotake (2007)	

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第 6 章 (95～123 頁)

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Appendix 1 (159～170 頁)

第 6 章の内容の一部であるため、非公開。

Appendix 2 (171～176 頁)

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Appendix 3 (177～183 頁)

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Appendix 4 (184 頁)

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Reference in Appendices (185～207 頁)

第 6 章の内容の一部であるため、非公開。