Composite *Phymatoderma* from Neogene deep-marine deposits in Japan: Implications for Phanerozoic benthic interactions between burrows and the trace-makers of *Chondrites* and *Phycosiphon*

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Among composite trace fossils, one of the most common structures throughout the Phanerozoic are structures (e.g., dwelling trace, feeding trace) reworked by *Chondrites* and/or *Phycosiphon*. However, differences in the nature of the reworking behaviors of these two ichnogenera remain unknown. Thus, in this study, composite *Phymatoderma* specimens from the Neogene deep-marine Shiramazu Formation in Japan, particularly those reworked by *Chondrites* and *Phycosiphon*, were analyzed to reveal the specific conditions that might control the activities of these trace-makers. *Phymatoderma* reworked by *Phycosiphon* is significantly larger than non-reworked *Phymatoderma*, whereas *Phymatoderma* reworked by *Chondrites* shows no significant difference in burrow diameter compared with non-reworked *Phymatoderma*. The recognized size selectivity (i.e., preference for larger burrows) by the *Phycosiphon* trace-maker can be explained by considering the different feeding strategies of these two ichnogenera; namely deposit-feeding *Phycosiphon*-makers, which must have processed a significant mass of sediment to obtain sufficient organic matter, whereas chemosymbiotic *Chondrites*-producers did not require a lot of sediment to obtain nutrients. In order to test these interpretations, a dataset of Phanerozoic trace fossils reworked by *Chondrites*/*Phycosiphon* were compiled. Consequently, the *Phycosiphon*-producers' preference toward relatively larger burrows was recognized, quantitatively supporting the results of this study. The compilation also indicates that the burrow size might have become one of the important limiting factors for the *Phycosiphon*-producers that tried to rework the sediments within previous subsurface burrows, at least for 80 million years.

Key words: *Phymatoderma*, *Phycosiphon*, *Chondrites*, burrows, size, benthic interactions, Phanerozoic, Neogene, Japan.

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Introduction

Trace fossils are useful tools in various disciplines such as paleontology, sedimentology, and paleoceanography because they provide meaningful information about the paleoenvironments in which the trace-producing organisms lived and about the paleoecology of these organisms (Seilacher 1954, 1958, 1967a, b, 2007; Bromley 1996; Miller 2007; Buatois and Mángano 2011; Knaust and Bromley 2012). Composite trace fossils are particularly important because they provide direct evidence of benthic interactions during ancient times, as well as information about micro-environmental changes through time (Bromley and Ekdale 1986; Pickerill 1994;

Pickerill and Narbonne 1995; Gingras et al. 2002; Buatois and Mángano 2011).

Among composite trace fossils, one of the most common structures throughout the Phanerozoic are structures (e.g., dwelling trace, feeding trace) reworked by *Chondrites* and/or *Phycosiphon* (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). In particular, burrows completely reworked by *Chondrites* have been known as "Bandchondriten" (Eh-
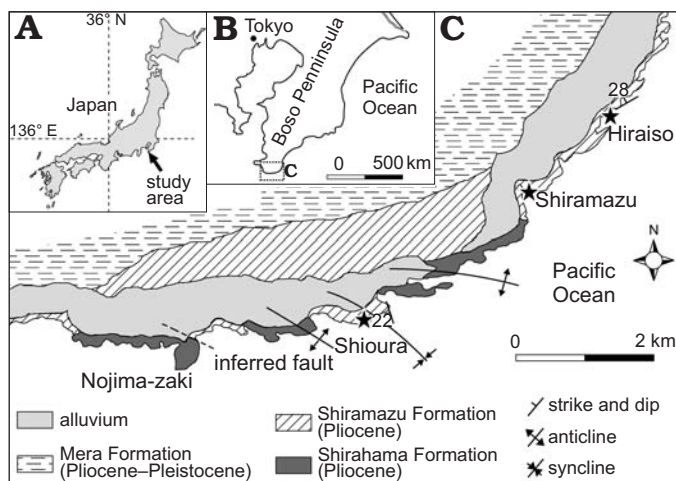
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Fig. 1. **A**, **B**. Maps of Japan and Boso Peninsula illustrating the location of study area. **C**. Geological map of the southern coast of the Boso Peninsula, central Japan (modified after Kotake 1988, 1989; Izumi 2014). Fieldwork was carried out at the Hiraiso, Shioura, and Shiramazu sections (indicated by stars). Numbers in C indicate dips.

renberg 1941), and there are many reports of such composite trace fossils (see Fu 1991 and references therein). Fossil burrows reworked by *Chondrites*/*Phycosiphon* generally served as preferential "feeding sites" for the trace-makers of these two ichnogenera. This is because sediments in subsurface burrows are richer in labile organic matter than the surrounding sediments due to the presence of a mucus lining, active filling by the trace-makers, or passive filling by fresh surface sediments (Bromley 1996; Izumi 2012). Factors other than organic matter, such as grain size and pore-water oxygenation, might also be important for colonization. However, when analyzing trace fossils reworked by *Chondrites*/*Phycosiphon*, organic matter is the most important factor because of the following reasons. As for *Chondrites*, it locally shows a pronounced association with sites of organic richness (e.g., black shale), probably due to its chemosymbiotic feeding strategy (Seilacher 1990; Fu 1991; Bromley 1996). The *Phycosiphon*-producer generally colonized in sites enriched in organic matter due to highly selective deposit-feeding activity (Wetzel 2010).

Considering the difference in the feeding strategy between *Chondrites* (i.e., chemosymbiosis) and *Phycosiphon* (i.e., deposit feeding) (Kern 1978; Seilacher 1990, 2007; Fu 1991; Wetzel and Bromley 1994; Bromley 1996; Bednarz and McIlroy 2009), there must be significant differences in the nature of their reworking activities. Particularly, probing for nutrient/organic matter, competition for space, and adaptation to sedimentary environmental conditions (e.g., sedimentation rate; oxygen/H$_2$S availability) may have influenced the nature of composite burrows as hypothesized in Mazumdar et al. (2011). However, in spite of such significance, there are no studies that performed systematic and quantitative analysis in order to determine the differences in the reworking behavior of *Chondrites* and *Phycosiphon* trace-makers.

To reveal these differences, this study presents detailed descriptions and measurements of numerous specimens of the deposit-feeding ichnogenus *Phymatoderma* from the Neogene deep-marine deposits, which were occasionally reworked either by *Chondrites* or *Phycosiphon*. This study is also the first detailed report of composite *Phymatoderma*, apart from one published photograph that captured a specimen reworked by *Phycosiphon* (Izumi 2014: fig. 3C). Fieldwork and measurements were carried out in several outcrops of the Pliocene continental slope deposits of the Shiramazu Formation, which are exposed in the southern part of the Boso Peninsula, Chiba Prefecture, central Japan (Fig. 1). Furthermore, a database highlighting Phanerozoic trace fossils reworked by *Chondrites*/*Phycosiphon* was constructed to test the obtained results and their interpretations. The implications for various benthic interactions within subsurface burrows and their paleoecological significance are also discussed.

Abbreviations.—D, burrow diameter; PW$_{max}$, maximum pellet width.

Geological setting

Pliocene to Pleistocene deep-marine deposits of the Chikura Group are exposed in the southern part of the Boso Peninsula, central Japan (Fig. 1A, B). The Chikura Group consists mainly of alternating beds of sandstone and siltstone, with many conglomerate and tephra layers (Kotake 1988). It contains eleven formations (Kotake 1988), but the Shirahama Formation (the lowermost formation of the Chikura Group), Shiramazu Formation, and the Mera Formation are exposed in the southernmost part of the Boso Peninsula (Fig. 1C).

The Shirahama Formation, up to 120 m thick, consists of alternating beds of conglomerate and parallel-laminated tuffaceous sandstone (Kotake 1988). The base of this formation ranges from 3.1 to 2.8 Ma on the basis of the planktonic microfossil assemblage such as planktonic foraminifera and calcareous nannoplanktons (Kotake 1988).

The Shiramazu Formation is approximately 450 m thick (Kotake 1989), and composed of alternating beds of parallel-laminated tuffaceous sandstone and siltstone (Kotake 1988). Siltstone is generally massive, but parallel and convolute laminae are recognized (Kotake 1988). Many well-preserved *Phymatoderma* specimens occur especially in this formation (Izumi 2013); those specimens that are reworked by either *Chondrites* or *Phycosiphon* are the focus of the present study.

The Mera Formation is approximately 400 m thick, and consists mainly of siltstone with tephra and thin sandstone layers with current ripples (Kotake 1988). The planktonic foraminifer *Discoaster tamalis*, with a known last occurrence datum at 2.5 Ma (Haq and Takayama 1984), disappears in the upper part of the Mera Formation (Kotake 1988), suggesting that the Pliocene/Pleistocene boundary occurs near the upper part of this formation.
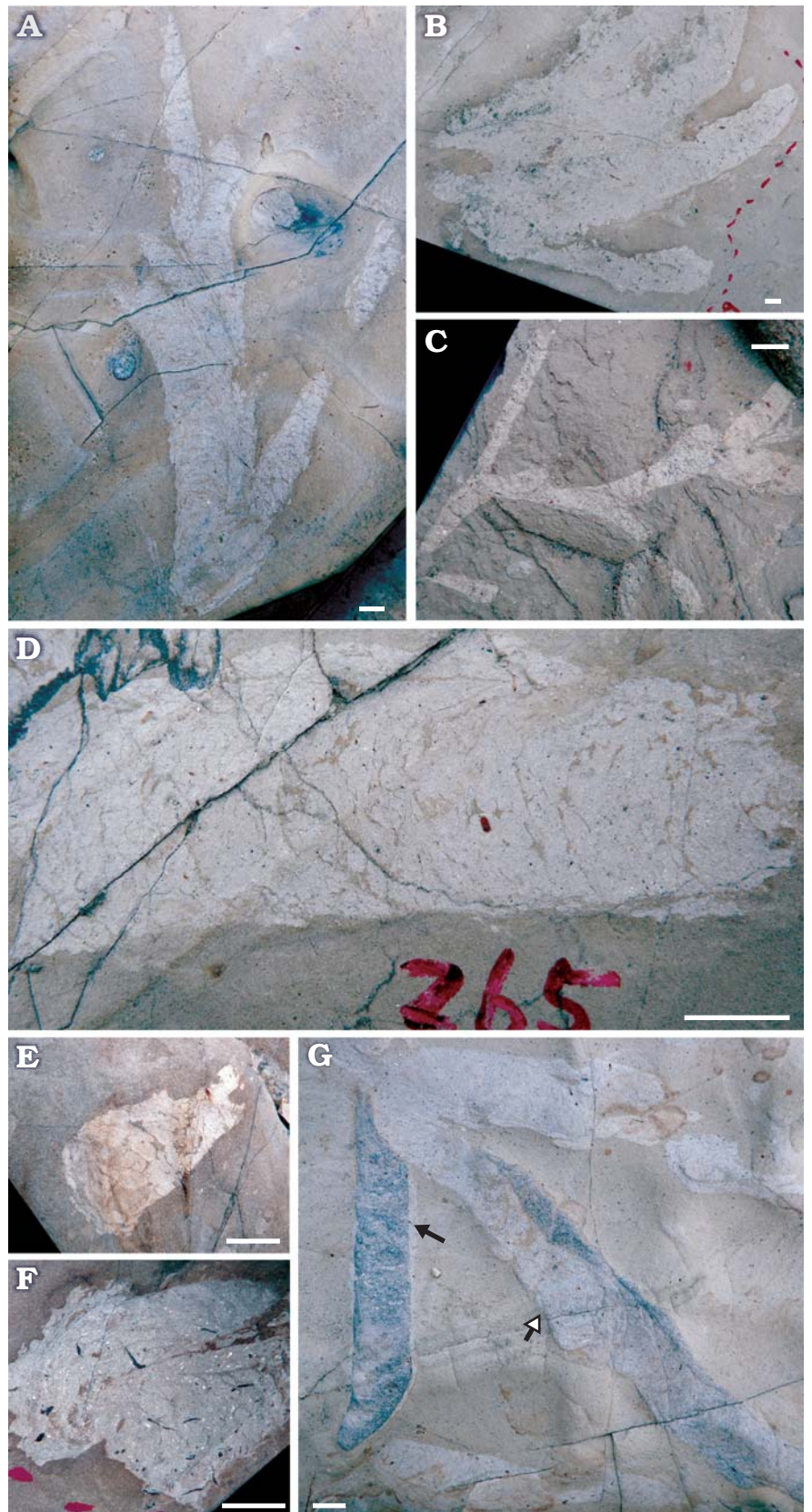
Fig. 2. *Phymatoderma* burrows from the Shiramazu Formation, Shioura (A–D) and Hiraiso (E–G) sections, Chiba Prefecture, central Japan. **A–C**. General views. Branched overlaping tunnels (**A**). Entire specimen representing a digitate morphology (**B**). Tunnels showing second-ordered branching (**C**). **D**. Magnified view of the burrow, focusing on the presence of the pelletal infill. **E**, **F**. Pellets with various kinds of compositions. White-colored volcanic-ash pellets (**E**) and light gray-colored muddy pellets (**F**). **G**. Specimen with revisiting structures. Note that white-colored tunnel first (black arrow), black-colored tunnel with scoriaceous infill second, and then white-colored tunnel (white arrow) came again. Field photos; all except E parallel (or nearly parallel) views to the bedding plane; E, obliquely cut vertical cross-sectional view. Scale bars 10 mm.

Detailed fieldwork and measurements were performed at three localities (Hiraiso, Shioura, and Shiramazu) of the Shiramazu Formation (Fig. 1C). The depositional setting of the study area has been interpreted as a middle bathyal trench-slope basin of approximately 2000 m in water depth, based on the benthic foraminiferal assemblage (Kotake 1988).
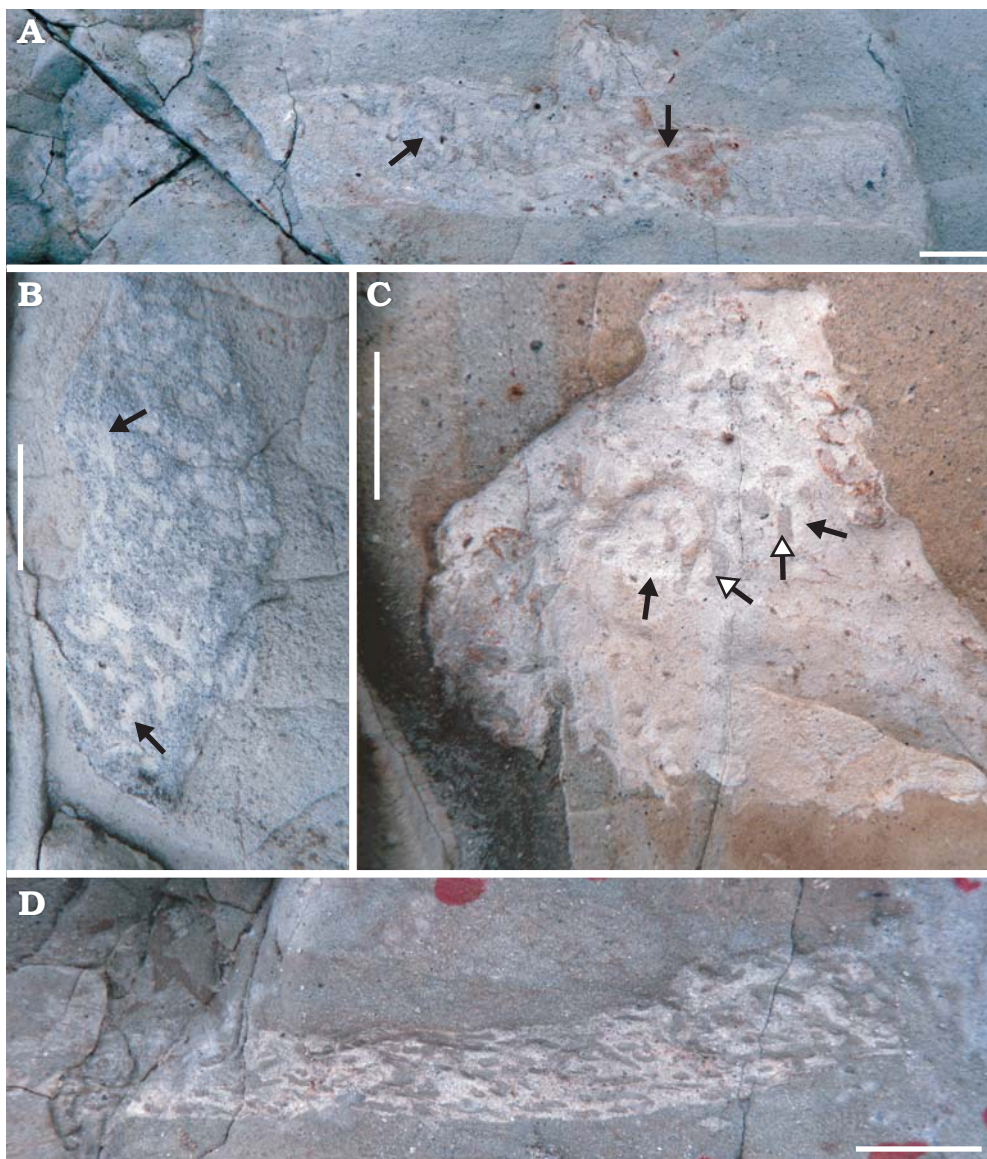
Fig. 3. Composite *Phymatoderma* burrows from the Shiramazu Formation, Hiraiso section, Chiba Prefecture, central Japan. **A**, **B**. *Phymatoderma* reworked by *Chondrites*. *Phymatoderma* tunnels with dark gray-colored scoriaceous infill reworked by white-colored *Chondrites* (arrows). **C**, **D**. *Phymatoderma* reworked by *Phycosiphon*. Even within the pelletal infill of *Phymatoderma*, cores (white arrows) and surrounding mantles (black arrows) of *Phycosiphon* are sometimes clearly recognized (**C**). Field photos; A, B, parallel to the bedding plane; C, obliquely cut vertical cross-sectional view; D, vertical cross-sectional view. Scale bars 10 mm.

Material and methods

Description of *Phymatoderma*.—*Phymatoderma* from the Shiramazu Formation was first reported formally by Izumi (2013), who reinterpreted "giant *Chondrites*" in previous works (Kotake 1990, 1991) as *Phymatoderma* (probably *P. granulata* Schloteim, 1822). More detailed and updated descriptions are provided below.

Phymatoderma from the Shiramazu Formation is a burrow system, which consists of horizontal, straight to slightly curved tunnels with an ellipsoidal cross-section. The tunnels are generally parallel to the bedding planes, showing first order, and less commonly second order branches (Fig. 2A–C), which are overlapped in some cases (Fig. 2A). Entire specimens often have digitate general morphology (Fig. 2B). Each tunnel is filled with ellipsoidal pellets, which have light gray-colored muddy, black-colored scoriaceous, or white-colored volcanic-ash compositions (Fig. 2D–F). The branching angle is generally constant in a single specimen (Fig. 2A–C); however, the tunnel contors can be poorly defined due to the pelletal infill. Both the tunnels and pellets have no linings. Locally within the tunnels, pellets distribute along with arcs of menisci, resulting in meniscate structures (Fig. 2A). However, in some other tunnels, meniscate structures are only weakly recognized (Fig. 2D). Nearly completely-overlapped tunnels (= re-visiting structures) are occasionally recognized (Fig. 2G). *Phymatoderma* specimens are often cut by other trace fossils such as *Scolicia* and *Zoophycos*, but *Phymatoderma* never cuts these ichnogenera. Tunnels completely or partly reworked by other smaller-sized ichnogenera (e.g., *Chondrites* or *Phycosiphon*) are also observed in some cases (Fig. 3). Among these composite *Phymatoderma*, tunnels reworked by *Chondrites* are less common.

Burrow measurements.—In order to reveal the differences in the nature of the reworking activities of *Chondrites* and *Phycosiphon* trace-makers, several parameters were mea-

sured using a caliper in the field or an image-processing program called Image J in the laboratory. These values include, burrow diameter (D_{Pm}) and maximum pellet width (PW_{max}) of non-reworked *Phymatoderma* specimens, and burrow diameters of: reworked *Phymatoderma* specimens, reworking *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 Fig. 4. An unpaired t-test was used for statistic analysis.

Results

The results of burrow measurements are summarized in Figs. 5 and 6, as well as Table 1. Through numerous measurements (n = 445), the burrow diameters of non-reworked *Phymatoderma* range from 4.30–45.80 mm (mean = 18.14 mm; Fig. 5A). Although the number of *Phymatoderma* specimens reworked by *Chondrites* and *Phycosiphon*, which were recognized during fieldwork, are much smaller than the number of non-reworked *Phymatoderma*, *Phymatoderma* specimens reworked by *Chondrites* and *Phycosiphon* have 8.30–30.95 mm (n = 13; mean = 18.54 mm; Fig. 5B), and 9.70–40.65 mm in diameter (n = 34; mean = 28.39 mm; Fig. 5C), respectively. The mean values of non-reworked *Phymatoderma* specimens and tunnels reworked by *Chondrites* show no significant difference (Fig. 5D). On the other hand, *Phymatoderma* burrows reworked by *Phycosiphon* have significantly (p < 0.001) larger diameters compared to non-reworked specimens (Fig. 5D).

Table 1. Diameters (in mm) of trace fossils within the host siltstone of the Pliocene Shiramazu Formation, central Japan. n, number of measured burrows; * *Phymatoderma* reworked by *Phycosiphon* has significantly (p <0.001) larger diameter than *Phymatoderma* without reworking or reworked by *Chondrites*, whereas mean diameter of *Phymatoderma* reworked by *Chondrites* has no significant difference from non-reworked *Phymatoderma*; ** *Phycosiphon* has significantly (p <0.001) larger mean diameter than *Chondrites*.

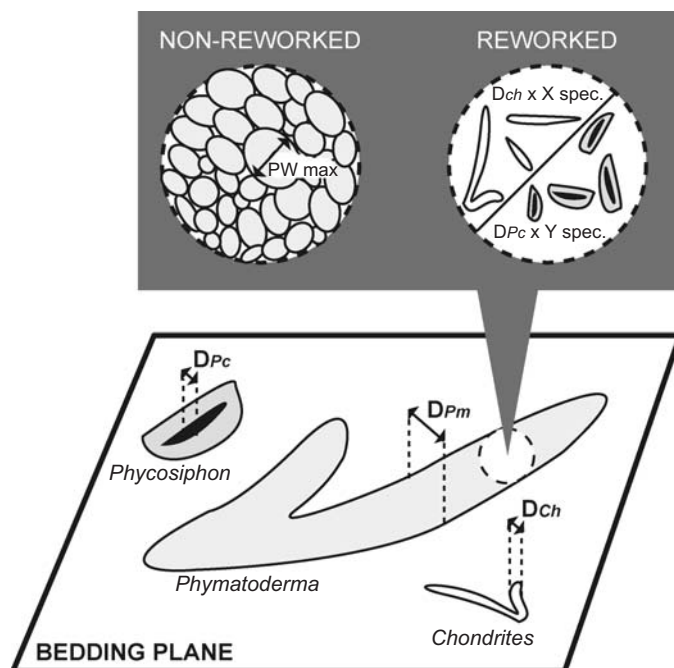| Ichnogenus		mean	min.	max.	n
Phymato-derma	non-reworked	18.14*	4.30	45.80	445
	reworked by *Chondrites*	18.54*	8.30	30.95	13
	reworked by *Phycosiphon*	28.39*	9.70	40.65	34
Chondrites		1.20**	0.55	2.00	85
Phycosiphon		1.38**	0.75	2.00	135

Fig. 4. 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 and Y are the numbers of measured specimens, X ranges from 4–10, Y from 2–37.

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. 6; Table 1). 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 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-reworked *Phymatoderma* tunnels increase their size with increasing the tunnel diameters (Fig. 6).

Discussion

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; Izumi 2012), were attractive for other benthos; thus *Phymatoderma* reworked by other ichnogenera such as *Chondrites* and *Phycosiphon* were recognized (Fig. 3). Although some *Phymatoderma* specimens from the Shi-
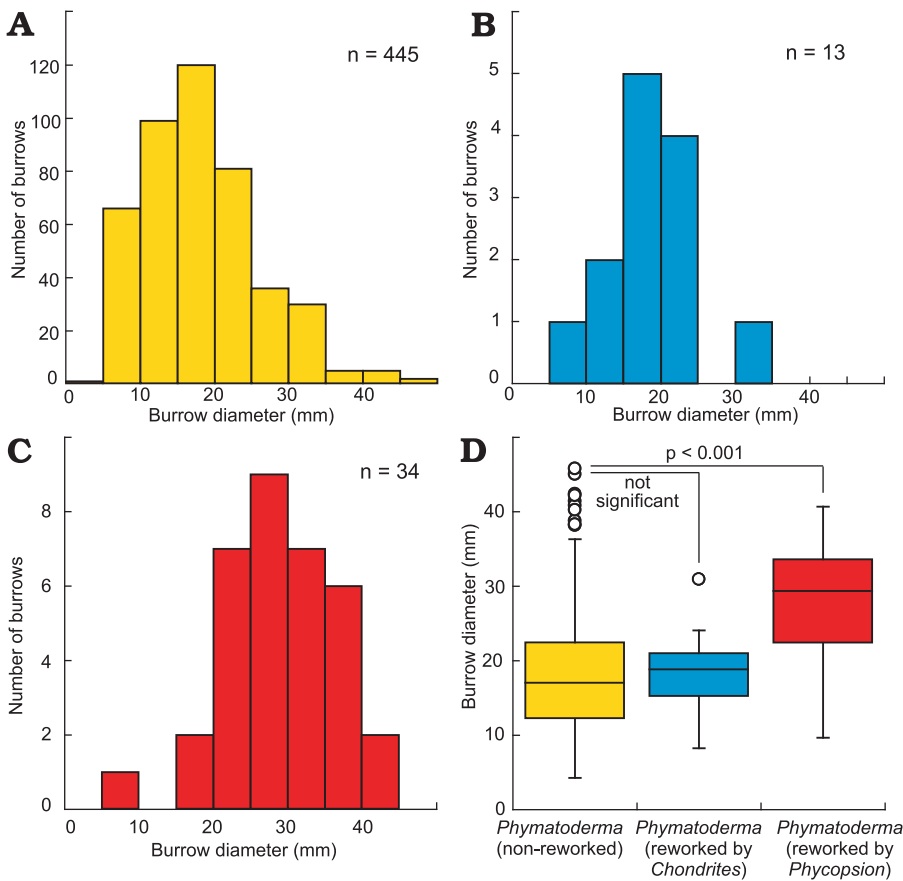
Fig. 5. Size distributions of *Phymatoderma* from the Shiramazu Formation. **A**. Non-reworked *Phymatoderma*. **B**. *Phymatoderma* reworked by *Chondrites*. **C**. *Phymatoderma* reworked by *Phycosiphon*. **D**. Comparison of burrow diameter between non-reworked *Phymatoderma*, and tunnels reworked by *Chondrites* and *Phycosiphon*. Note that *Phymatoderma* reworked by *Phycosiphon* has significantly larger size. n, number of measured burrows.

ramazu 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) reworked 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 reworked by *Chondrites* and *Phycosiphon*. *Phymatoderma* reworked by *Phycosiphon* has significantly larger burrow diameters compared with non-reworked *Phymatoderma* tunnels and those reworked by *Chondrites* (Fig. 5D). It is true that there is a significant difference in the mean diameter between *Chondrites* and *Phycosiphon* (Table 1), however, it may not be an important factor since the difference is very tiny. Furthermore, although mean diameter of *Phycosiphon* from the Shiramazu Formation is approximately 1.15 times larger than that of *Chondrites*, average size of *Phymatoderma* reworked by *Phycosiphon* has ca. 1.53 times larger

than that of *Phymatoderma* reworked by *Chondrites* (Table 1). Therefore, these results (Fig. 5D) 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).

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., oli-
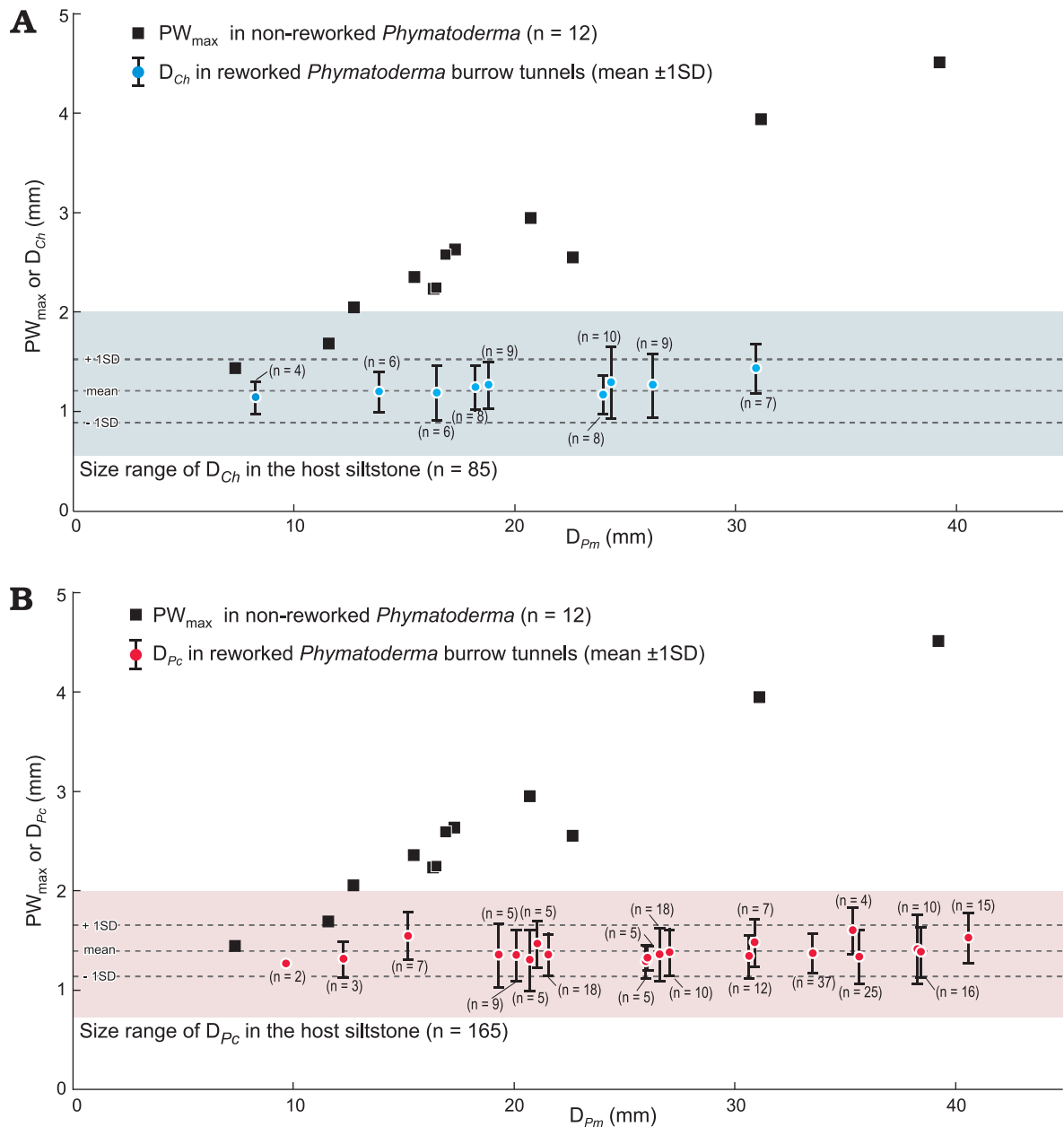
Fig. 6. Scatter plots showing the relationships between *Phymatoderma* burrow diameter and its maximum pellet width (black plot) and reworking trace-fossil diameter. **A**. *Chondrites*. **B**. *Phycosiphon*. Note that diameters of both ichnogenera that reworked *Phymatoderma* tunnels are within the size-range of them occurring in the host siltstone (shade), although pellet width increases with increasing *Phymatoderma* burrow diameter. 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; n, number of measured burrows.

gotrophic) 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. 5D). 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 reworking various-sized *Phymatoderma* have similar-sized diameter, which are within the size range of those from the host siltstone (Fig. 6B), despite the increase of fecal-pellet size with increasing *Phymatoderma* burrow diameter (Fig. 6). This fact suggests that there was no size bias in terms of the *Phycosiphon*-pro-

ducers. This is probably because *Phymatoderma* from the Shiramazu Formation is much larger than *Phycosiphon* (Table 1). The diameter of the smallest *Phymatoderma* specimen reworked by *Phycosiphon* is approximately 8-times larger than that of the *Phycosiphon* itself (Fig. 6B); 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⁻ 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. 5A, 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. 5D). In spite of the increase of fecal-pellet size with increasing *Phymatoderma* burrow diameter (Fig. 6), all *Chondrites* burrows reworking varying *Phymatoderma* have similar-sized diameter and within the size range of those from the host siltstone (Fig. 6A), which also indicates that there was no size bias in terms of the *Chondrites*-producers.
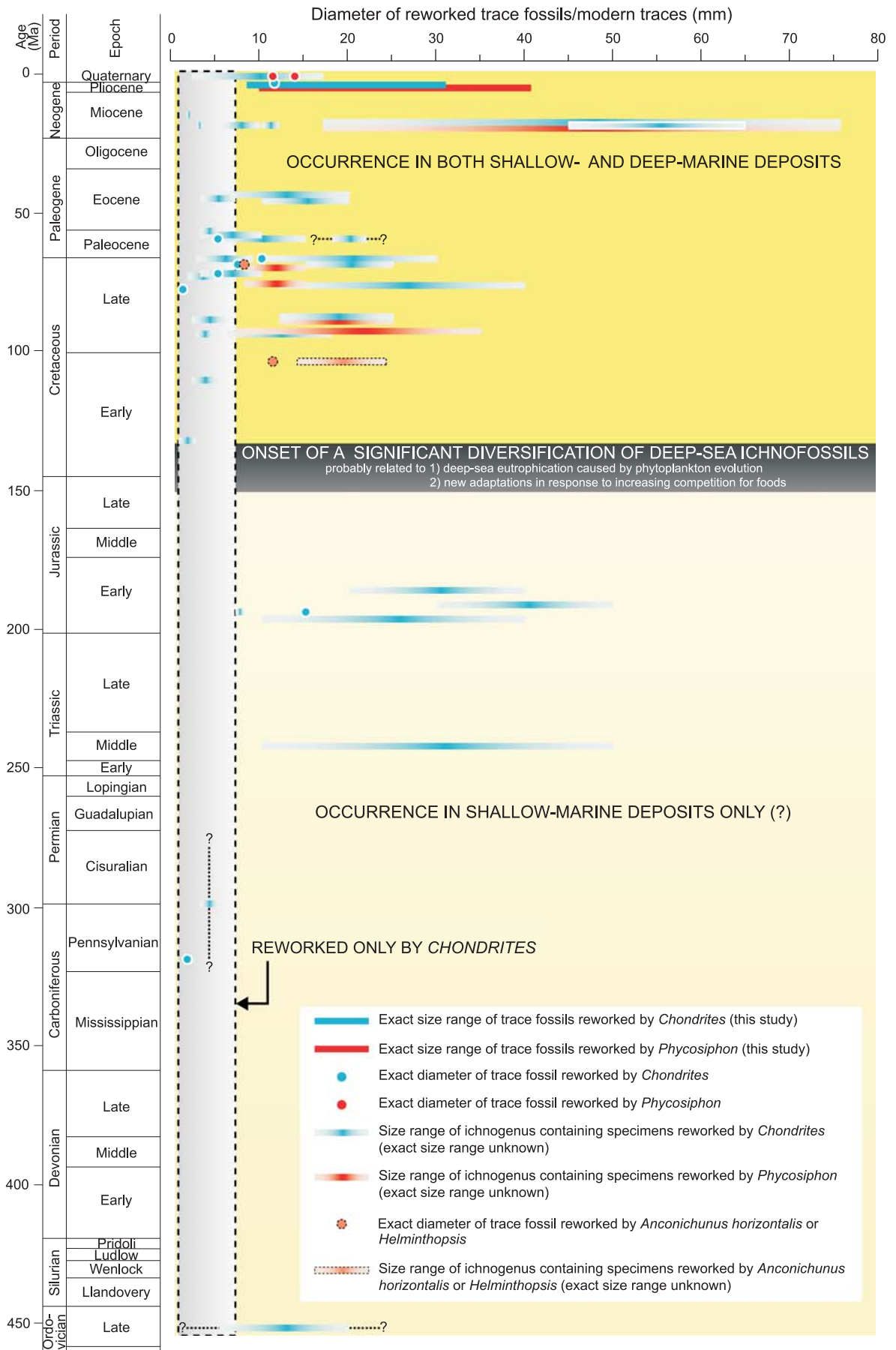
Although the explanation about the reworking activities discussed here seems to be highly likely, frequency of reworked *Phymatoderma* is not so high with respect to non-reworked *Phymatoderma* (i.e., approximately 10%; Fig. 5), suggesting that the trace-makers of both *Chondrites* and *Phycosiphon* 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 reworked trace fossils. Difference in frequency of *Phymatoderma* reworked by *Chondrites* or *Phycosiphon* (Fig. 5B, C) may be related to sequential colonization of turbidites (Wetzel and Uch-

man 2001). The *Phycosiphon*-producer penetrate substrates earlier than the *Chondrites*-producer (Wetzel and Uchman 2001), which can explain higher frequency of *Phymatoderma* reworked by *Phycosiphon* (Fig. 5). *Phymatoderma* tunnels reworked 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.

Phanerozoic records of trace fossils reworked by *Chondrites/Phycosiphon*.—It is difficult to evaluate whether the composite *Phymatoderma* recognized in this study (Fig. 3) is common in the long Phanerozoic stratigraphical records, because there are no other reports of reworked *Phymatoderma* specimens other than those from the Shiramazu Formation. However, there is a noteworthy report of pellet-filled branched trace fossils from the Recent (ca. 46–58 kya) continental slope deposits in the Krishna–Godavari basin, Bay of Bengal (Mazumdar et al. 2011), which closely resemble *Phymatoderma melvillensis* Uchman and Gaździcki, 2010 in appearance (see Mazumdar et al. 2011: fig. 2 and Uchman and Gaździcki 2010: figs. 3, 4). These "*P. melvillensis*-like" pellet-filled branched ichnofossils are occasionally reworked by *Chondrites* (Mazumdar et al. 2011: fig. 2e, f). The authors did not recognize reworking structures by *Phycosiphon*, probably due to the burrow diameters of "*P. melvillensis*-like" trace fossils (i.e., 4–17 mm; Mazumdar et al. 2011), which are relatively smaller than *Phymatoderma* from the Shiramazu Formation (Fig. 5A). However, it is also important to note that these "*P. melvillensis*-like" burrows were collected by a Giant Calypso piston corer (Mazumdar et al. 2011), which cannot take larger burrows if any.

Despite the lack of reports focusing on the composite *Phymatoderma*, it is worthwhile to compile published data of other trace fossils and modern traces reworked by *Chondrites* or *Phycosiphon* for testing the implications of size selectivity inferred from the results of this study (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app60-Izumi_SOM.pdf). Consequently, throughout the Phanerozoic, *Chondrites* reworked trace fossils with various sizes including approximately 1–76 mm in diameter, whereas relatively larger trace fossils (i.e., 7–76 mm in diameter) were preferentially reworked by *Phycosiphon* (Fig. 7). Furthermore, there are no records of tiny (i.e., a few mm in diameter) burrows that were reworked by *Phycosiphon* (Fig. 7). The recognized trend (i.e., larger burrow preference by the *Phycosiphon*-producers) is highly obvious, even if *Chondrites* and *Phycosiphon* generally have similar burrow diameters of approximately 0.5–2 mm throughout the Phanerozoic (Gerard

Fig. 7. Stratigraphical distribution of trace fossils reworked by *Chondrites* and *Phycosiphon*. Note that trace fossils with tiny diameter were reworked → only by *Chondrites* throughout the Phanerozoic (gray shade with dotted line). Particularly, *Anconichnus horizontalis* has been interpreted as a synonym of *Phycosiphon incertum* (Wetzel and Bromley 1994). Although ichnofossils reworked by these two ichnogenera have been only known from shallow-marine deposits before the Cretaceous except for one controversial case, these are common in both shallow- and deep-marine deposits in the Cretaceous and Cenozoic. This is probably related to significant deep-sea trace-fossil diversification in the Late Jurassic to Early Cretaceous periods, which might have been caused by eutrophication of seafloor due to the evolution of various phytoplankton.

Diameter of reworked trace fossils/modern traces (mm)

OCCURRENCE IN BOTH SHALLOW- AND DEEP-MARINE DEPOSITS

ONSET OF A SIGNIFICANT DIVERSIFICATION OF DEEP-SEA ICHNOFOSSILS
probably related to 1) deep-sea eutrophication caused by phytoplankton evolution
2) new adaptations in response to increasing competition for foods

OCCURRENCE IN SHALLOW-MARINE DEPOSITS ONLY (?)

REWORKED ONLY BY *CHONDRITES*

Exact size range of trace fossils reworked by *Chondrites* (this study)

Exact size range of trace fossils reworked by *Phycosiphon* (this study)

Exact diameter of trace fossil reworked by *Chondrites*

Exact diameter of trace fossil reworked by *Phycosiphon*

Size range of ichnogenus containing specimens reworked by *Chondrites* (exact size range unknown)

Size range of ichnogenus containing specimens reworked by *Phycosiphon* (exact size range unknown)

Exact diameter of trace fossil reworked by *Anconichunus horizontalis* or *Helminthopsis*

Size range of ichnogenus containing specimens reworked by *Anconichunus horizontalis* or *Helminthopsis* (exact size range unknown)

and Bromley 2008). In terms of the size of *Chondrites*, however, it is ichnospecies specific at least in some cases (Uchman 1999; Uchman et al. 2012). The results of compilation not only support my interpretations but also provide further paleoecological implications. Namely, the burrow size might have become one of the important limiting factors for the *Phycosiphon*-producers, which tried to rework the sediments within previous subsurface burrows, at least for nearly 80 million years (Fig. 7), although probably other factors (i.e., depositional environment, sedimentation rate, pore-water oxygenation) also affected the mode of colonization.

In addition, it is important to note that all pre-Cretaceous trace fossils reworked by these two ichnogenera are known only from shallow-marine deposits except for one controversial example, whereas those from the Cretaceous and younger occurred in both shallow- and deep-marine deposits (Fig. 7). This may be related to the onset of a significant diversification of deep-sea trace fossils in the Late Jurassic to Early Cretaceous (Uchman 2004), which was probably related to new adaptations in response to increasing benthic competition for foods along with the deep-sea eutrophication caused by the evolution of various kinds of phytoplankton (Uchman 2003, 2004, 2007; Falkowski et al. 2004).

Potential for further research.—To expand the implications inferred from this study, it is worthwhile to discuss not only trace fossils but also body fossils that were reworked by *Chondrites* and/or *Phycosiphon*. There are several reports of ammonite fossils that were reworked by these ichnogenera (Maeda et al. 2010; García-Ramos et al. 2011).

According to García-Ramos et al. (2011), the Pliensbachian (Lower Jurassic) Rodiles Formation in Spain contains internal moulds of ammonites (and sometimes bivalves) that were traversed by *Chondrites*. These internal moulds must have acted as ideal feeding sites for the trace-makers of *Chondrites* due to the richness of decayed organic matter that may have been produced by the dissolution of ammonite shells. Although García-Ramos et al. (2011) did not described the size ranges of non-reworked and reworked internal moulds of ammonites, on the basis of the results of this study (i.e., Fig. 5D), it can be predicted that both non-reworked and reworked internal moulds have similar size distributions, or have no significant size difference.

Maeda et al. (2010) described the Campanian (Late Cretaceous) ammonoid species *Canadoceras kossmati* Matsumoto, 1954 from the Krasnoyarka Formation in Russia. In these ammonite specimens, *Phycosiphon* are commonly recognized within sediments infilling both body and air chambers (Maeda et al. 2010). Sediments stuffed in relatively restricted organic-rich spaces such as umbilical void, body and air chambers might have also been preferential feeding sites for deposit-feeding benthic animals (Maeda 1987). Shell diameter of *C. kossmati* from the Krasnoyarka Formation ranges from 5–80 cm (Maeda et al. 2010). Although any systematic/quantitative data about the shell size of ammonites whose sediment-infills are reworked by *Phycosiphon* is not available in their paper,

reworking by *Phycosiphon* seems to be present in relatively larger ammonite shells according to several figures (Maeda et al. 2010: figs. 5B, C, 6, 8A). This evidence might also support the size selectivity of *Phycosiphon* trace-makers inferred from this study (i.e., preference of larger sediment mass).

Conclusions

Composite *Phymatoderma* from the Pliocene deep-sea deposits (Shiramazu Formation in Chiba Prefecture, central Japan); particularly *Phymatoderma* reworked by *Chondrites* and *Phycosiphon*, was described in detail for the first time, and analyzed to reveal the difference in nature of the reworking activities by *Chondrites* and *Phycosiphon* trace-makers. *Phymatoderma* reworked by *Phycosiphon* has a significantly larger size than non-reworked *Phymatoderma*, whereas *Phymatoderma* reworked by *Chondrites* shows no significant difference in burrow diameter compared with non-reworked *Phymatoderma*. The recognized size selectivity (i.e., preference of burrows with relatively larger diameter) by the trace-makers of *Phycosiphon* may be well explained considering the difference in feeding strategies of the trace-makers; namely deposit-feeding *Phycosiphon*-makers must have processed a significant mass of sediment to obtain sufficient organic matter, while, chemosymbiotic *Chondrites*-producers did not require a lot of sediment for obtaining nutrients. To verify these interpretations, records of the Phanerozoic trace fossils reworked by *Chondrites*/*Phycosiphon* were compiled. As a result, the preference of relatively larger burrows by the trace-makers of *Phycosiphon* was also recognized, which supports the interpretations of this study and indicates that the burrow size might have become one of the important limiting factors for the *Phycosiphon*-producers, which tried to rework the sediments within previous subsurface burrows, for at least 80 million years. Furthermore, *Phycosiphon* reworking other kinds of fossils (e.g., sediments filled in body and/or air chambers of ammonites) might also be expected to show the preference of larger-sized ammonites; thus, this topic may have a potential for further studies.

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