Producing Processes of the Trace Fossil Asteriacites lumbricalis Revisited: Different Ophiuroid Behaviors Produce Different Trace Forms

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Producing processes of the trace fossil *Asteriacites lumbricalis* revisited: different ophiuroid behaviors produce different trace forms

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Abstract. The star-shaped trace fossil *Asteriacites lumbricalis* is produced by ophiuroids and has two different forms. One form has four distinct arms with transverse fine and parallel striations and one indistinct arm without striations, and the producing process has been studied already. In this study, we clarified the producing process of another form with five distinct radiating arms and fine striations by aquarium observations of extant ophiuroids. The form was produced when ophiuroids were covered with a thin sand layer (11–39% of the arm length in thickness). After covered by thin sand, ophiuroids raised their five arms with one to five tips protruded vertically above the sand cover, raised and slanted the disc in the sand, and then obliquely emerged onto the sand cover. Finally, they returned to horizontal postures creeping on the sand. The trace left on the substratum was very similar in shape to the trace fossil from Hettangian (Lower Jurassic) in Blumenrod, Germany. The producing process of the repetitive multiple traces of *A. lumbricalis* was revealed by aquarium observations. When an ophiuroid was alternately covered with a thin sand layer and then with a thin abrasive layer as mud substratum, the ophiuroid left a vertically stacked series of traces which gradually shifted the horizontal position. This unique form of *A. lumbricalis* was produced by escaping of ophiuroids from successive deposition events.

Keywords: aquarium observation, burial, escape behavior, extant ophiuroid, Hettangian, resting trace

Introduction

Asteriacites lumbricalis Schlotheim, 1820 is a well-known star-shaped trace fossil with many records from the Ordovician to Miocene of South Africa, Europe, Russia, Japan, USA, South America, and Greenland (Oppel, 1864; Seilacher, 1953; Lewarne, 1964; Chamberlain, 1971; Goldring and Stephenson, 1972; Hakes, 1977; Hess, 1983; Knoch, 1989; Dam, 1990; Mikuláš, 1990; West and Ward, 1990; Röper and Rothgaenger, 1995, 1998; Twitchett and Wignall, 1996; Mángano *et al.*, 1999; Twitchett, 1999; Wilson and Rigby, 2000; Bell, 2004; Ishida *et al.*, 2004, 2013, 2017; Fourie, 2009; Jagt *et al.*, 2009; Bernardi *et al.*, 2010; Bernardi and Avanzini, 2011; Baucon and Carvalho, 2016). The ichnospecies has a distinct central subcircular area and fine striations in narrow arms, and has been interpreted as a resting trace of ophiuroids on the basis of its morphology (Seilacher, 1953; Lewarne, 1964; Mángano *et al.*, 1999; Wilson and Rigby, 2000).

The producing process of *A. lumbricalis* was revealed based on the observations of ophiuroids in aquariums and *in situ* (Ishida *et al.*, 2004, 2017). In their works, the traces produced by extant ophiuroids were comparable with the traces of *A. lumbricalis* which have four distinct arms with fine and parallel striations and one indistinct arm without striations. Similar fossil traces were found in the Lower Triassic Hiraiso Formation of Japan (Ishida *et al.*, 2004, Figure 3; 2017, Figure 8A), Upper Jurassic Hienheim Formation of Germany (Ishida *et al.*, 2013, Figure 2; 2017, Figure 8B), Lower Triassic Lazurnaya Bay Formation of Russia (Ishida *et al.*, 2017, Figure 8C), and Upper Cretaceous Himenoura Group of Japan (Ishida *et al.*, 2017, Figure 8D). Ishida *et al.* (2004, 2017) clarified that this form was produced when the ophiuroids moved horizontally on the trace. However, some other *A. lumbricalis* have a different shaped trace of five distinct arms with fine striations, for example, found in the upper Carboniferous of USA (Mángano *et al*., 1999) and the Lower Triassic of Italy (Baucon and Carvalho, 2016), although the detailed morphology is not clear because of poor preservation of the fossils. Recently we discovered a new specimen of *A. lumbricalis* in the Lower Jurassic Hettangian of Germany. The trace has five, distinct, clearly recognizable arms with fine striations. Thus, the producing process of this form of *A. lumbricalis* is supposed to differ from that reported by Ishida *et al.* (2004, 2017).

Recently, using laboratory observations, Ishida *et al*. (2019) found that extant asteroids produced star-shaped traces with five distinct arms after burial by sand. Asteroids did not move horizontally but slantingly upward onto the sand. Asteroids did not destroy the trace and, as a result, the traces had five distinct arms with striations. That suggests the form of five distinct arms of *A. lumbricalis*, as seen in the Hettangian, can be produced without horizontal movement of ophiuroids.

In addition, a strange type of *Asteriacites lumbricalis* containing a vertical consecutive series of star-shaped traces on overlapping thin sandstone layers was found (Seilacher, 1953, 2007; Mángano *et al.*, 1999; Gurav *et al*., 2014). Seilacher (1953, 2007) assumed that the traces were produced by a repetitive escape reaction in response to the repeating deposition of sand layers in hours. However, the producing process of this type of traces has not yet been fully elucidated.

In this study, to clarify the producing processes of the traces with five distinct arms of *A. lumbricalis*, we observed the behavior and traces of extant ophiuroids after burial by sand, using the method applied to asteroids by Ishida *et al.* (2019). We provide a description of a new fossil of *A. lumbricalis* from the Hettangian and compare it with the traces observed for extant ophiuroids in the new experiments. Moreover, we also had another aquarium observation of the ophiuroid behavior after successive deposition to clarify the producing process of the consecutive traces reported by Seilacher (1953, 2007).

Material and methods

Observation of extant ophiuroids

Two extant ophiuroid species, *Stegophiura sladeni* (Duncan, 1879) and *Ophiuroglypha kinbergi* (Ljungman, 1866), were collected for the aquarium observations in central Japan. For *S. sladeni*, eight specimens (7.0–15.0 mm in disc diameter) were recovered at a depth of 85–93 m in Sagami Bay by R/V Rinkai-maru of Misaki Marine Biological Station, the University of Tokyo in May 2017 and March 2018, and one specimen (7.2 mm in disc diameter) was recovered at a depth of 90 m in Tateyama Bay in May 2018 by the fishing boat Hosaka-maru. For *O. kinbergi*, one specimen (7.0 mm in disc diameter) was recovered at a depth of 5.6–7.5 m in the Moroiso Inlet in May 2018 by the research boat of Misaki Marine Biological Station, the University of Tokyo, two specimens (4.9 and 6.8 mm in disc diameter) were recovered at a depth of 10 m in Tateyama Bay in July 2017 by the research boat Sea-star of Ochanomizu University, and one specimen (7.6 mm in disc diameter) was recovered at a depth of 10 m off Awakominato in May 2017 by the research boat of Chiba University. The ophiuroids were kept alive in the laboratories (National Museum of Nature and Science, Ibaraki Prefecture and Misaki Marine Biological Station, the University of Tokyo, Kanagawa Prefecture) for one day to one week before observations. A total of nine specimens of *Stegophiura sladeni* and four specimens of *Ophiuroglypha kinbergi* were used in eleven and eight aquarium observations, respectively (Table 1). Their disc diameter and arm length (from the disc edge to the arm tip) were measured using a vernier caliper to the nearest 0.1 mm.

The behavior of ophiuroids was observed in aquaria of small (170 mm in diameter, 70 mm in height) and large (230 mm in diameter, 75 mm in height) hemisphere-shaped plastic bowls (Table 1). Aluminiferous abrasive powder (#1000 or #2000) was used as substratum following Ishida *et al.* (2019). The grain size (11.5 or 6.7 µm, respectively) was equivalent to mud. After on-site Seawater was filled in the aquaria, aluminiferous abrasive was laid on the bottom as a substratum of about 10–20 mm in thickness enough for ophiuroids to bury themselves (Figure 1A). One ophiuroid specimen was placed on the substratum in each observation. After the ophiuroids finished burying themselves shallowly in the substratum to be in their resting position (Figure 1B), they were quickly covered with sand (0.2–0.5 mm in grain size equivalent to fine-to medium-grained sand) in thickness of 2–33 mm (Figure 1C). Ophiuroids were removed after they successfully escaped onto the sand cover (Figure 1D). Water temperature was kept at 13–20°C throughout the observation. The substratum was dried for several days to a week to allow the abrasive substratum to harden. The upper parts of the plastic bowls were cut off above the sand by a heat iron thread (polystyrene foam cutter). Then, the sand cover was carefully removed with a spoon and a paint brush (Figure 1E). The morphology of the trace left on the hardened substratum (Figure 1F) was observed and recorded by making a sketch on a transparent paper placed upon a photo of the resulting traces. Exceptionally, in one case (Table 1, Observation no. 19), the ophiuroid did not appear on the sand cover. The ophiuroid was excavated by removing the sand cover and the trace was observed by the same method. During the process of escape, the movements of disc and arms of ophiuroids were recorded by a video camera.

Table 1. Aquarium observations of ophiuroids covered with sand. One specimen of *Ophiuroglypha kinbergi* and one specimen of *Stegophiura sladeni* (marked with asterisks) were repeatedly used in observations. The time is measured after the ophiuroid was covered with sand. ND: The ophiuroid did not appear on the sand cover in Observation no. 19.

Observation no.	Species	Disc diameter (mm)	Arm length (mm)	Size of aquarium bowl	Abrasive no. used for substratum	Thickness of cover sand (mm)	Thickness of cover/ arm length ratio (%)	Time when arm tip emarged on the sand (min)	Time when the whole body appeared on the sand (min)	Behavior		Trace	
										Pattern	Figure 3	Form	Figure 4
1	*Stegophiura sladeni*	7.2	18.8	small	#2000	2	11	1.8	8.2	arm-tip-first escape		radial symmetry	A
2	*Stegophiura sladeni**	13.2	31.0	small	#2000	4	13	0.2	1.1	arm-tip-first escape		radial symmetry	B
3	*Stegophiura sladeni*	8.0	22.0	large	#2000	3	14	29.9	47.7	arm-tip-first escape	A	radial symmetry	C
4	*Ophiuroglypha kinbergi**	7.0	12.0	small	#2000	3	25	0.1	0.3	arm-tip-first escape		radial symmetry	D
5	*Ophiuroglypha kinbergi*	6.8	19.6	small	#2000	5	25	0.1	1.8	arm-tip-first escape		radial symmetry	E
6	*Stegophiura sladeni*	9.0	19.2	small	#2000	5	26	0.3	34.8	arm-tip-first escape		radial symmetry	F
7	*Ophiuroglypha kinbergi*	7.6	18.3	large	#2000	5	27	10.0	12.2	arm-tip-first escape		radial symmetry	G
8	*Ophiuroglypha kinbergi*	4.9	12.9	small	#1000	5	39	0.1	1.1	arm-tip-first escape	B	radial symmetry	H
9	*Stegophiura sladeni*	8.5	18.6	small	#2000	10	54	0.7	2.0	direct escape		irregular	I
10	*Stegophiura sladeni*	15.0	29.0	small	#2000	20	69	1.0	1.5	direct escape		irregular	J
11	*Stegophiura sladeni**	13.2	31.0	small	#2000	25	81	0.5	1.5	direct escape	C	irregular	K
12	*Ophiuroglypha kinbergi**	7.0	12.0	small	#2000	10	83	0.3	0.7	direct escape		irregular	L
13	*Stegophiura sladeni**	13.2	31.0	small	#2000	33	106	1.0	1.4	direct escape		irregular	M
14	*Ophiuroglypha kinbergi**	7.0	12.0	small	#2000	13	108	0.2	0.4	direct escape		irregular	N
15	*Stegophiura sladeni*	12.5	22.0	small	#2000	26	118	0.8	1.3	direct escape		irregular	O
16	*Stegophiura sladeni*	9.2	18.4	small	#2000	23	125	2.5	4.0	direct escape		irregular	P
17	*Ophiuroglypha kinbergi**	7.0	12.0	small	#2000	15	125	0.2	0.4	direct escape		irregular	Q
18	*Ophiuroglypha kinbergi**	7.0	12.0	small	#2000	20	167	0.1	0.5	direct escape	D	irregular	R
19	*Stegophiura sladeni*	12.1	16.6	small	#2000	30	181	ND		direct escape	E	irregular	S

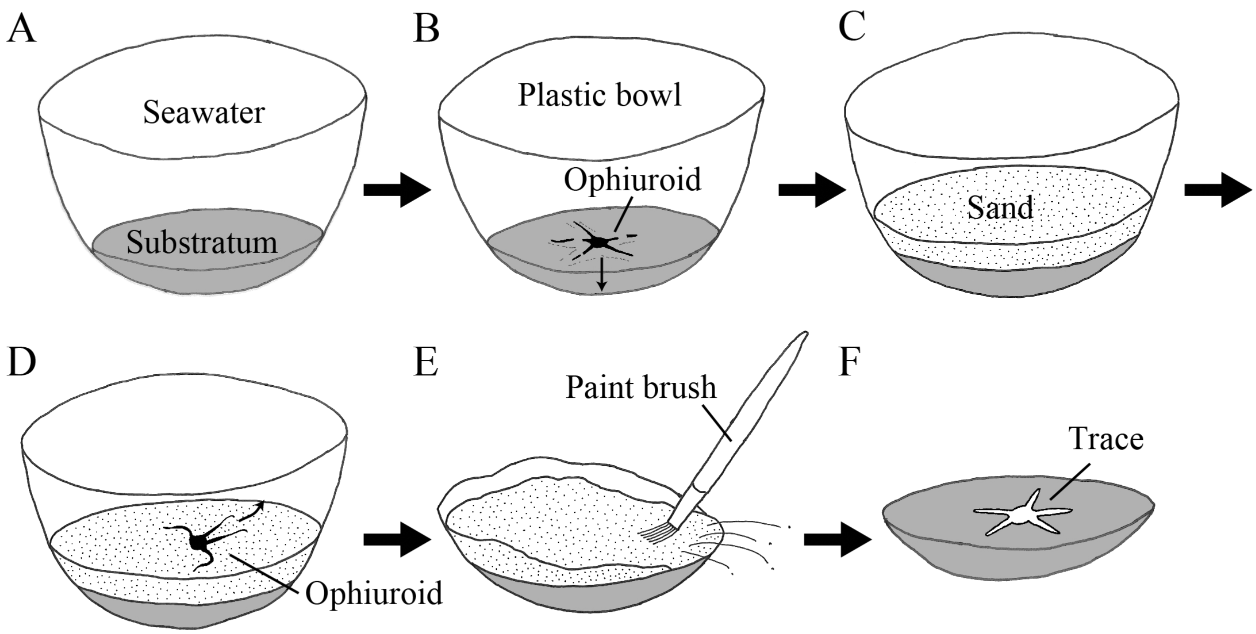

Figure 1. Experimental design for burial observations of the extant ophiuroid by sand. **A**, sea water and substratum were filled in a plastic bowl. **B**, an ophiuroid was put on the substratum and it buried itself in the substratum. **C**, the ophiuroid was covered with sand. **D**, the ophiuroid escaped onto the sand. **E**, the bowl was cut and the sand was removed. **F**, the trace was left on the substratum. Short arrows near ophiuroid show the moving direction of the ophiuroid.

An additional experiment was designed to observe the response to repeated burial (Table 2). Aluminiferous abrasive (#2000) was laid as a substratum (about 15 mm in thickness) after on-site seawater was filled in an aquarium (Figure 2A). After the ophiuroid finished burying itself shallowly in the substratum (Figure 2B), it was covered with sand in thickness of 5–8 mm (Figure 2C). Shortly after that, the ophiuroid raised arm tips onto the sand cover (Figure 2D), and then it was covered with abrasive (#2000) in thickness of 7 mm (Figure 2E). The ophiuroid escaped onto the abrasive cover (Figure 2F) and buried itself shallowly in the abrasive again (Figure 2G). This sand and abrasive cover was repeated once more (Figure 2H–I). After finally covered by sand, the ophiuroid escaped onto the sand (Figure 2J), then it was retrieved. The sand and abrasive covers were carefully removed one after another (Figure 2K). The resulting traces on the three abrasive substrata were observed (Figure 2L).

A new trace fossil of *Asteriacites lumbricalis*

A well-preserved star-shaped trace fossil was examined here, found in the sandstone layers of the Lower Jurassic Hettangian in a former landfill site near Blumenrod, Coburg County, Germany (see Knoch, 1989 for the site and stratigraphy). The trace fossil was preserved as a convex hyporelief and was composed of fine sandstone, partly covered with thin mudstone. The detailed morphology of the present fossil was observed by producing a synthetic resin mold and retracing it using a camera lucida. The arm length (from the edge of central depression to the arm tip) was measured using a vernier caliper on the mold. The fossil and its synthetic resin mold are housed at the National Museum of Nature and Science, Tsukuba (NMNS PA18691).

Results

Aquarium observation of behavior and traces by extant ophiuroids

In all laboratory observations, ophiuroid specimens of *Stegophiura sladeni* and *Ophiuroglypha kinbergi* buried into the substratum shallowly at depths of about 20–100% of body thickness by moving their tube-feet, and formed resting traces of five arms with crescent-shaped mounds along the arms (Figure 3A1, B1, C1, D1, E1). The mounds finally remained in the traces on the substratum (Figure 4). When ophiuroids were covered with sand, they showed two different behavior patterns to escape onto the sand cover depending on the thickness of sand cover (Table 1).

When ophiuroids were covered with relatively thin sand (11–39% of the arm length in thickness), they showed “arm-tip-first escape” behavior (Table 1, Observation nos. 1–8). The ophiuroids first raised the arms with

Table 2. Aquarium observation of an ophiuroid repeatedly covered with sand and #2000 abrasive. The ophiuroid used is the same as in Observation no. 3 (*Stegophiura sladeni*, disc diameter 8.0 mm, arm length 22.0 mm).

Sequence (in Figure 5)	Elapsed time (min)	Event/ophiuroid behavior	Thickness of cover (mm)	Thickness of cover/arm length (%)	Trace left	
					Form	Figure 6
A	0	ophiuroid set				
B	11.6	resting			radial symmetry	A1
C	11.9	sand cover	6	27		
D	14.0	raising arm tips				
E	14.2	abrasive cover	7	32		
F	15.3	escaping				
G	21.4	resting			radial symmetry	A2
H	21.7	sand cover	5	23		
I	35.1	raising arm tips				
J	35.5	abrasive cover	7	32		
K	35.8	escaping				
L	46.8	resting			radial symmetry	A3
M	47.5	sand cover	8	36		
N	51.0	raising arm tips				
O	51.2	escaping				
P	51.5	escaping				

one to five (mostly five) tips protruded vertically above the sand cover (Figure 3A2, B2), raised and slanted the disc in the sand, and then obliquely emerged onto the sand cover (Figure 3A3, B3). Finally, they returned to horizontal postures creeping on the sand (Figure 3A4, B4). The escape behavior is relatively slow and ophiuroids fully emerged on the sand cover in 13.4 minutes on average (0.3–47.7 minutes) after covered. The ophiuroids left "radial symmetrical" traces on the original substratum (Figure 4A–H). The traces had five distinct, nearly radiating arms bending slightly (Figure 4C–H) or straight (Figure 4A–B) with fine parallel striations perpendicular to the arm axis, and a deeper (Figure 4C, F, H) or shallower (Figure 4A–B, D–E, G) central depression with striations in nearly radial symmetry.

On the other hand, when ophiuroids were covered with relatively thick sand equaling to 54–167% of the arm length in thickness, they showed "direct escape" behavior (Table 1, Observation nos. 9–18). The ophiuroids first bent two arms slightly aborally, and held up the disc and the two arms almost vertically above the sand cover (Figure 3C2, D2). The other three arms remained in the sand; probably damaging the resting trace on the substratum. The three arms were slanted and pulled out obliquely from the sand (Figure 3C3, D3). Finally the ophiuroids returned to horizontal postures on the sand (Figure 3C4, D4). The ophiuroids fully emerged on the sand cover very quickly in 1.4 minutes on average (0.4–4.0 minutes) after covering. The ophiuroids left "irregular" traces on the substratum. The traces had mostly five (Figure 4I–P) or sometimes only three (Figure 4Q, R) arm depressions, with fine striations partly left in a few arms (Figure 4I–J, L–O). The form of arm depressions was sharply bent (Figure 4J, K, M, P), or slightly curved (Figure 4I, L, N, O, Q, R). Exceptionally, after maximum covering (181% of the arm length in thickness), the ophiuroid did not emerge from the sand even 31 minutes after being covered (Table 1, Observation no. 19). When the cover sand was removed, the ophiuroid remained in "direct escape" posture, slanting disc and arms nearly vertically (Figure 3E2). The trace left on the substratum was "irregular", with almost straight and sharply curved arms without striations (Figure 4S).

In the repeated burial experiment with sand and abra-

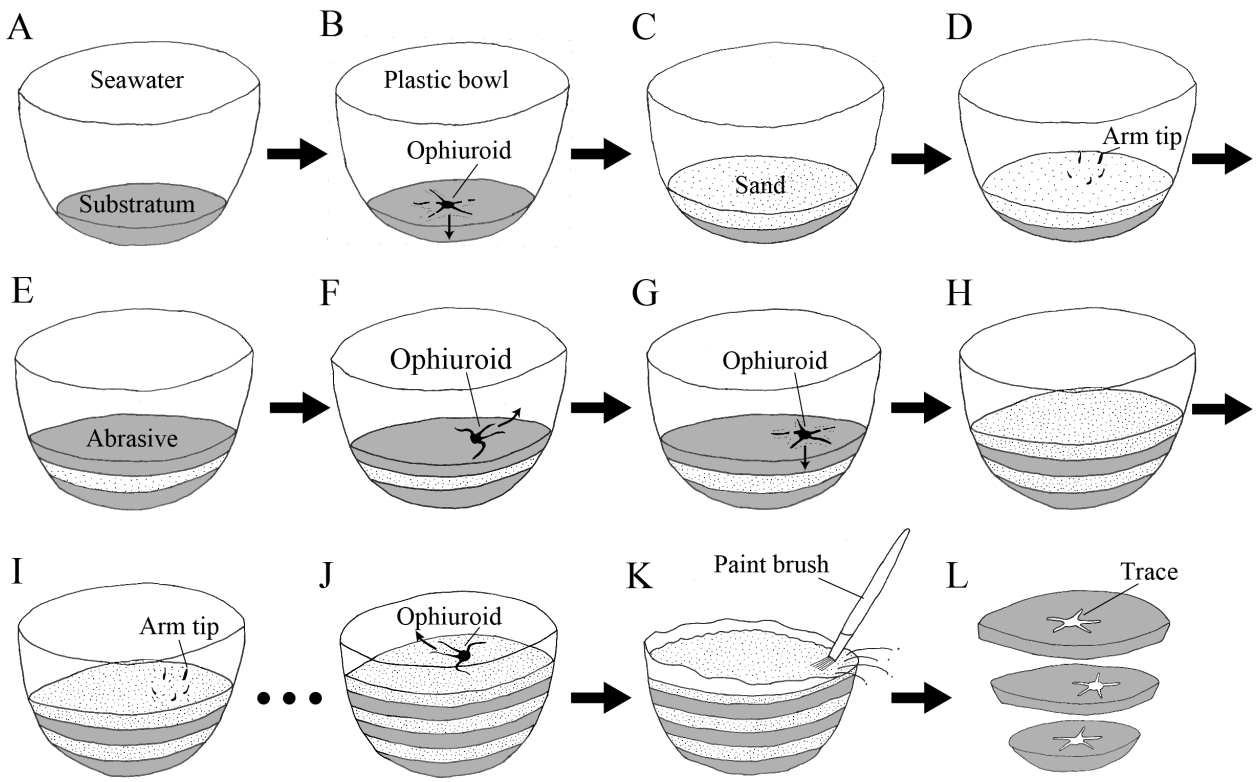

Figure 2. Experimental design for a repeated burial observation of the extant ophiuroid by sand and abrasive substratum. **A**, sea water and abrasive were filled in a plastic bowl. **B**, an ophiuroid was put on the abrasive and it buried itself in the abrasive. **C**, the ophiuroid was covered with sand. **D**, the ophiuroid raised arm tips onto the sand. **E**, the ophiuroid was covered with abrasive. **F**, the ophiuroid escaped onto the abrasive. **G**, the ophiuroid buried itself in the abrasive. **H**, the ophiuroid was covered with sand. **I**, the ophiuroid raised arm tips onto the sand. The same sequential process covered by abrasive and sand was repeated. **J**, finally the ophiuroid escaped onto the sand. **K**, the bowl was cut and the sand layers were removed. **L**, the traces were left on the substratum and two abrasive layers. Short arrows show the moving direction of the ophiuroid. See Table 2 for the details of the time course.

sive (Table 2), *Stegophiura sladeni* first buried itself shallowly in abrasive about 40–80% of disc thickness, resting for 11.6 minutes (Figure 5A–B). After that, the ophiuroid was covered with thin sand three times, equaling 23–36% of the arm length in thickness, and covered with thin abrasive twice, equaling 32% of the arm length in thickness, alternately (Table 2).

After the ophiuroid was covered by sand (Figure 5C, H, M), it raised three to five arms vertically with arm tips appearing on the sand cover (Figure 5D, I, N). When the ophiuroid was covered by abrasive (Figure 5E, J), it escaped onto the abrasive cover slanting the disc and arms (Figure 5F, K) and then buried itself shallowly in the abrasive (Figure 5G, L). It took a total of 39.6 minutes after the first sand cover of the ophiuroid to the third and final escape from the sand. The ophiuroid left star-shaped traces on the three abrasive layers (Table 2; Figure 6). They had five distinct, nearly radiating arms, which were curved slightly (Figure 6A1) or straight (Figure 6A2–3). The thickness of arms varied (Figure 6A1–3). The arms had fine parallel striations, perpendicular to the arm axis and the striations in the disc were nearly radially symmetrical (Figure 6A1–3). The horizontal position of the three traces partly overlapped (Figure 6B).

Morphology of *Asteriacites lumbricalis* from Hettangian

The star-shaped trace fossil of the Hettangian has five clear radiating arms and a differentiated center (Figure 7). The shape shows a nearly radial symmetry. The arms are slightly curved and narrow with pointed tips and have well-spaced fine parallel striations, perpendicular to each arm axis. The central depression has fine radial striations. The length of five arms measures 7.7–10.2 mm (mean 9.2 mm), and the width of the arm base is 2.2–2.8 mm (mean 2.5 mm). The diameter and depth of central depression are 5.6 mm and 1.4 mm, respectively.

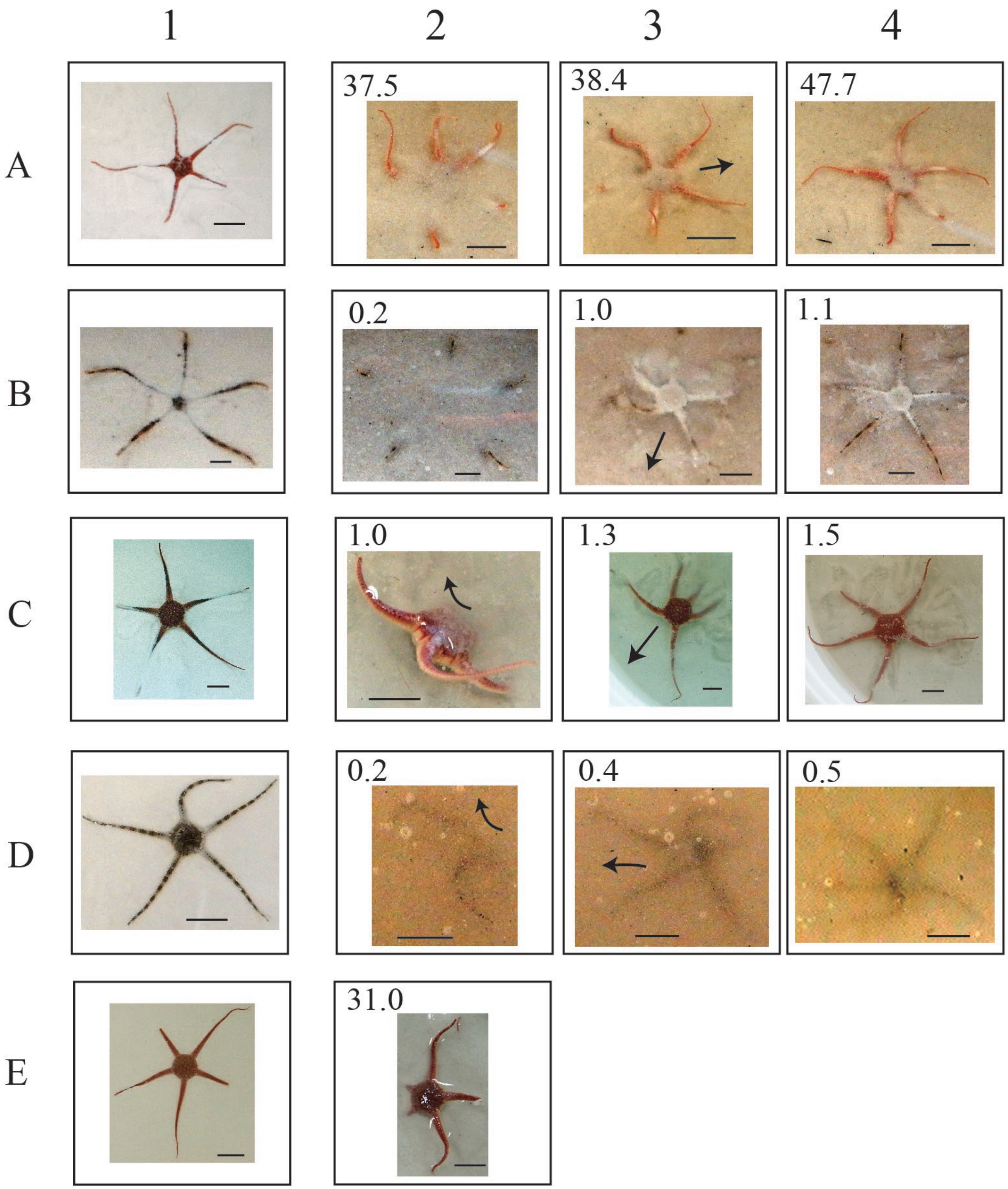

Figure 3. Two behavior patterns of ophiuroids after sand cover. **A**, **B**, arm-tip-first escape; **C–E**, direct escape. (1) Resting posture on the substratum. (2) Arm tips (A, B) or arms (C, D) emerging above the sand. (3) Disc emerging on the sand. (4) Whole body emerged on the sand. Time (minutes) after sand covering is shown in each photo. In Observation 19, the ophiuroid failed to escape and figure E2 shows the posture observed when sand cover was removed. *Stegophiura sladeni* (A, C, E) and *Ophiuroglypha kinbergi* (B, D). Arrows show moving direction of ophiuroids. See Table 1 for the detailed experimental data. Scale bars: 1 cm (A, C–E), 5 mm (B).

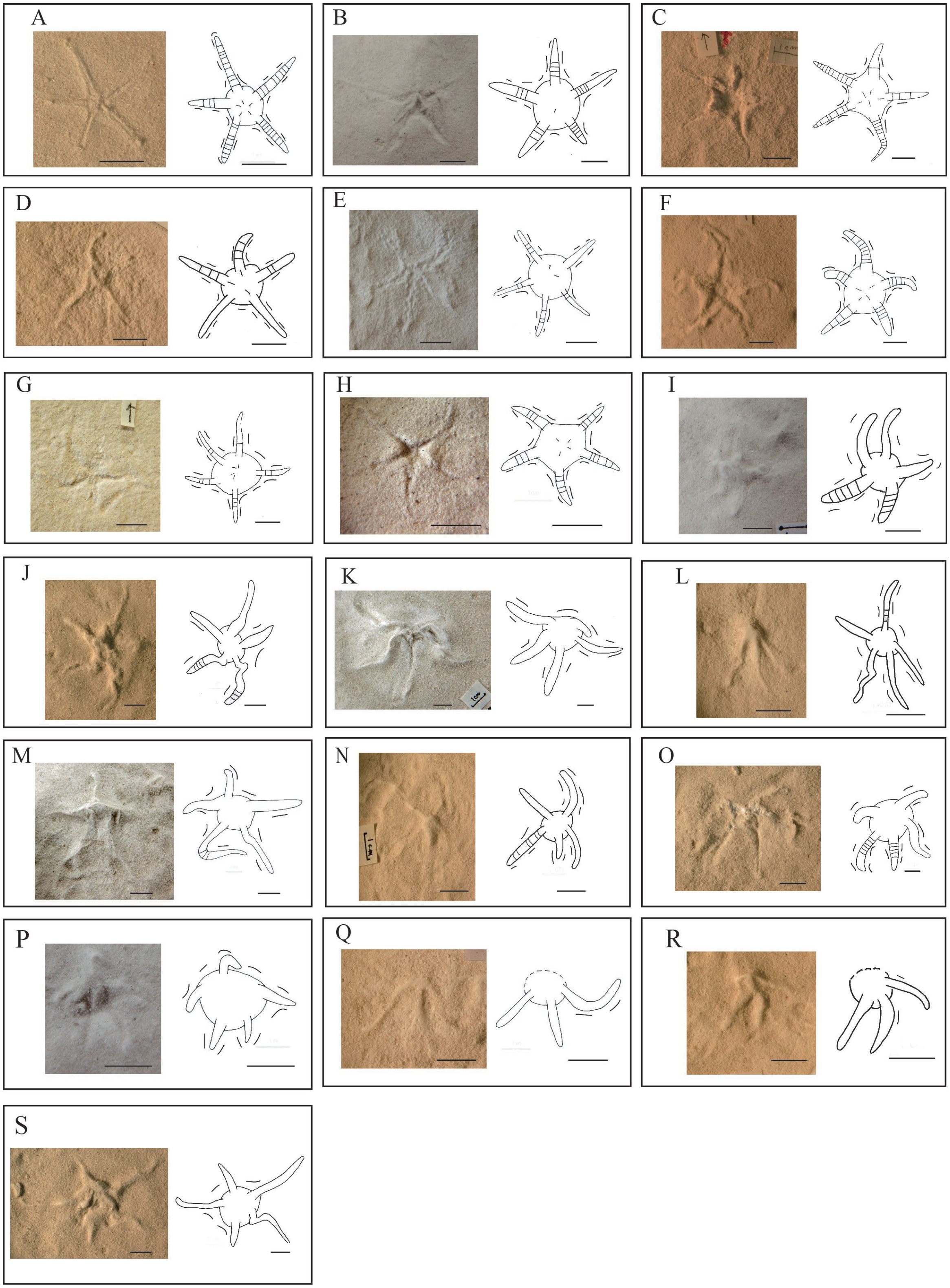

Figure 4. Traces of ophiuroids left on the substratum in aquarium observations. **A–H,** radial symmetry form. **I–S,** irregular form. Sketches of the photographs show the trace outlines, striation on the traces, and mound around traces. See Table 1 for the experimental data. Scale bars: 1 cm.

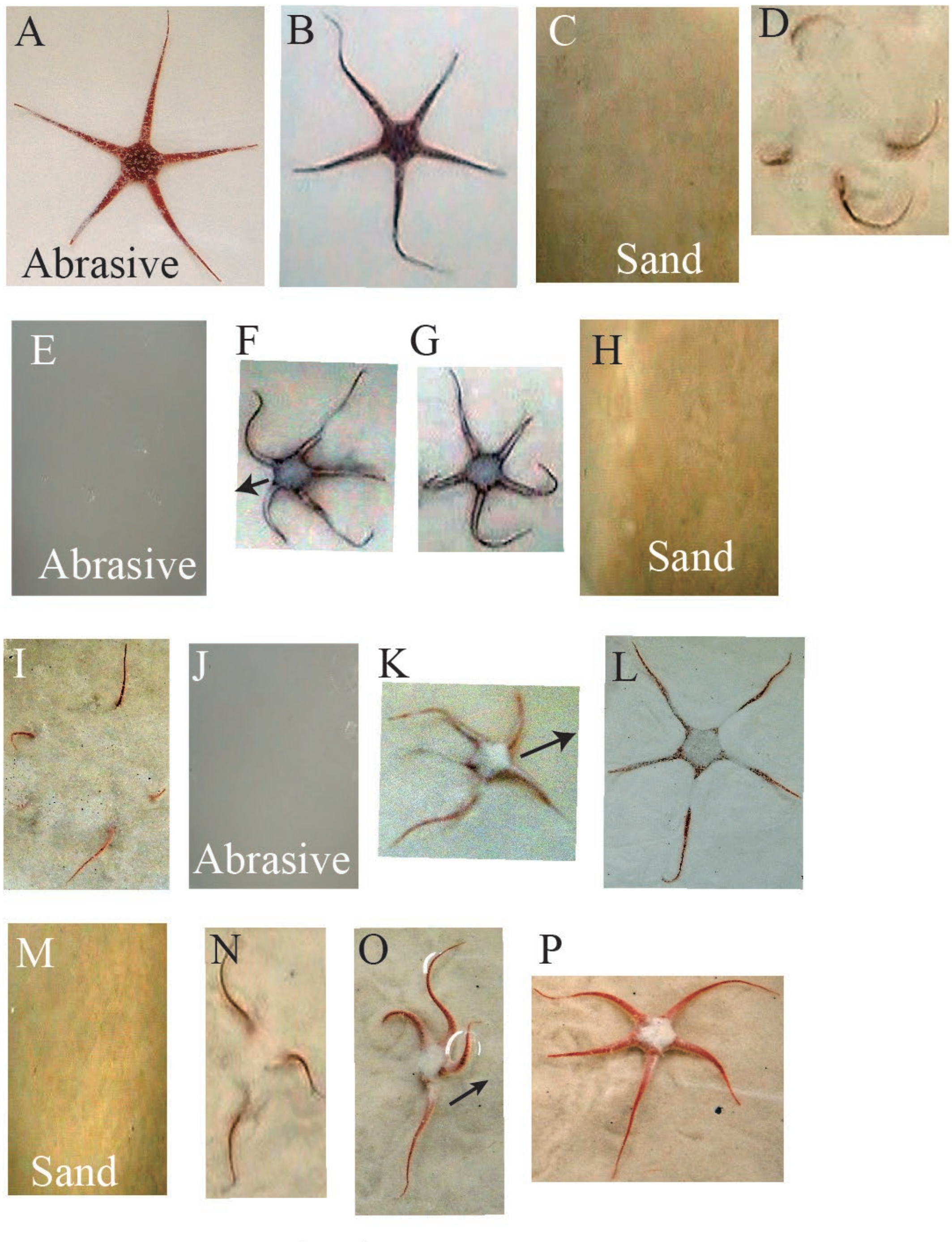

Figure 5. Behavior of an ophiuroid in the repeated burial observation in aquarium. The ophiuroid is not seen shortly after being covered by sand (C, H, M) or abrasive (E, J). *Stegophiura sladeni*. See Table 2 for the experimental design and data. Arrows show moving direction. Scale bar: 1 cm.

Discussion

Two different trace forms have been found in *Asteriacites lumbricalis*. Ishida *et al.* (2004, 2017) studied the producing process of the trace form with four distinct arms and one indistinct arm found in the Devonian to Cretaceous, of South Africa, USA, Germany, Russia, and Japan (Seilacher, 1953; Hakes, 1976; Röper and Rothgaenger,

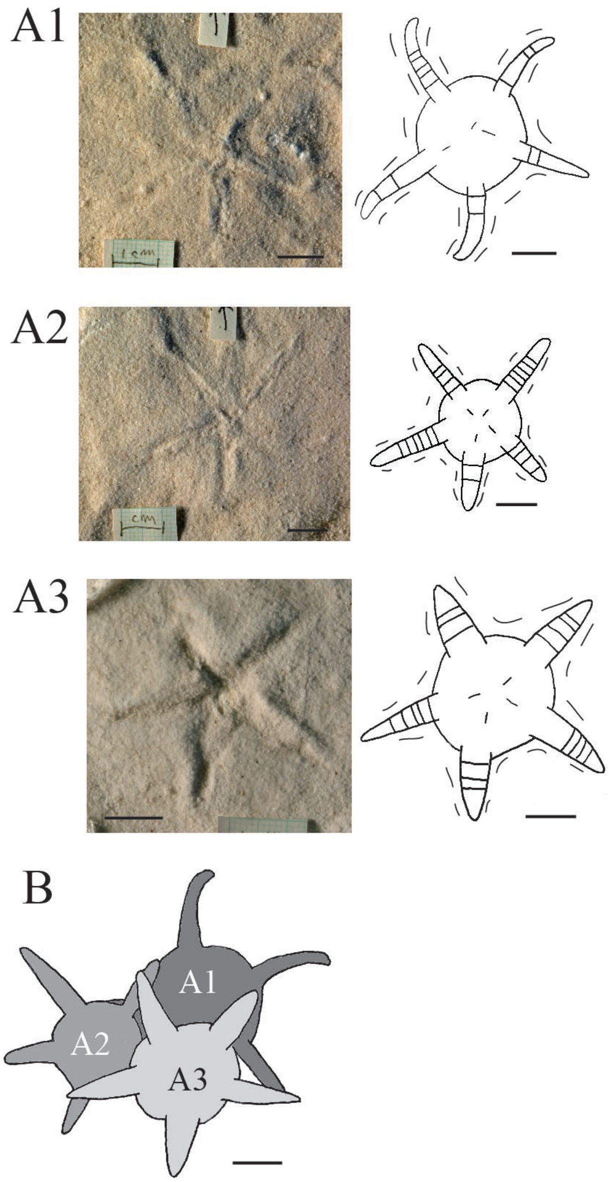

Figure 6. Traces in the repeated burial experiment. **A**, three traces left on the abrasive substratum. Sketches of the photographs show the trace outlines, striation on the traces, and mound around traces. **B**, diagram showing horizontal position of traces from above. See Table 2 for the experimental design and data. Scale bars: 1 cm.

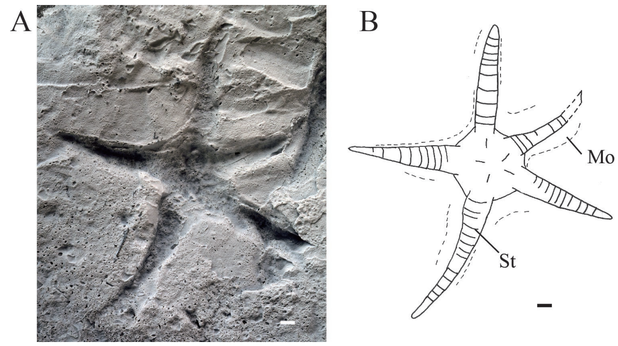

Figure 7. *Asteriacites lumbricalis* from the Hettangian, Germany. **A**, synthetic resin mold; **B**, sketch showing striations and mounds. Abbreviations: Mo, mound of substratum; St, striation. Scale bars: 1 mm.

1998; Wilson and Rigby, 2000; Fourie, 2009; Ishida *et al.*, 2017). Another form with five distinct arms has been rarely found in the Carboniferous to Jurassic, of USA, Italy and Germany (Mángano *et al.*, 1999; Baucon and Carvalho, 2016; present paper). In this study, burial observations using extant ophiuroids in aquaria revealed that the latter form was produced by ophiuroids' escape behavior after burial by a thin (less than *ca.* 5 mm) sand layer (Figure 8). Seilacher (1953, fig. 3) also found this form from less than 4 mm thick sandstone layers in a vertical repetition of *A. lumbricalis*. The trace morphology (Figure 4A–H) is strikingly similar to *Asteriacites lumbricalis* from the Hettangian (Figure 7). The Hettangian sandstones including the present fossil exhibited ripple marks upon their depositional surfaces suggesting beach or shallow-water sandy bottom environments (Knoch, 1989). The sandstone layers were only a few mm thick, and a fossil ophiuroid *Palaeocoma escheri* (Heer, 1865) was found in the same layers (Knoch, 1989). *P. escheri* might be a producer species of *A. lumbricalis* in the Hettangian.

On the other hand, when the sand cover was thick, the traces were neither radially symmetrical nor uniform in length, shape, and number of arms (Figure 4I–S). Such an irregular-shaped form has once been reported as *Asteriacites lumbricalis* in its vertical repetition traces (Seilacher, 1953, plate 9). One of the authors also found a similar shaped trace fossil in the Lower Triassic Lazunaya Bay Formation of Russia though unidentified (Y. I. unpublished data). These irregularly star-shaped fossils were produced also by escape behavior when covered by relatively thick sand layers, 20 mm (Seilacher, 1953) and 12 mm (Y. I. unpublished data).

Stegophiura sladeni failed to escape from the sand cover when buried with 30 mm thick (181% of the arm length) sand cover (Figure 3E). The previous laboratory study showed extant *Ophiura sarsii sarsii* also failed to escape from sand cover of similar thickness (60 mm, 180% of the arm length) (Ishida, 1999). Around 180% may be a limit for these ophiuroids to escape from sand deposition which covers them. The observed escape posture when covered by sand in this thickness (Figure 3E2) was very similar to the posture of well-preserved fossil *Ophiura sarsii sarsii* of the late Miocene Hongo Forma-

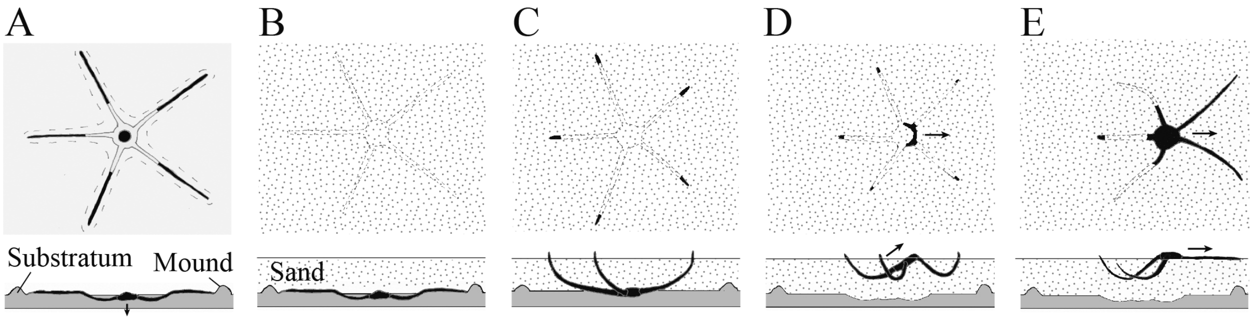

Figure 8. Schematic diagram of the producing process of *Asteriacites lumbricalis* with five distinct arms showing ophiuroid behavior after thin sand cover. Horizontal view (upper row) and vertical view (lower row). Arrows show moving direction of the ophiuroid disc.

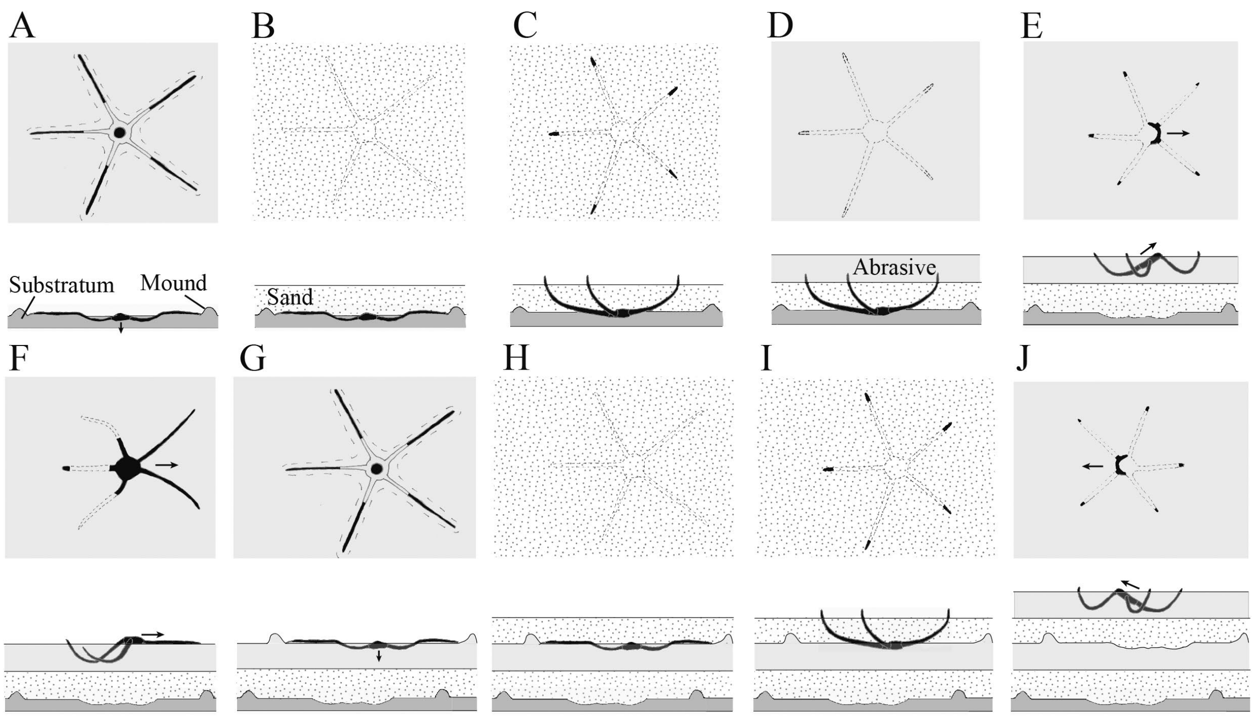

Figure 9. Schematic diagram of the producing process of the vertical consecutive series of *Asteriacites lumbricalis* with five distinct arms showing ophiuroid behavior after thin sand and abrasive covers. Horizontal view (upper row) and vertical view (lower row). Arrows show moving direction of the ophiuroid disc.

tion in Japan (Ishida, 1999).

The repeated burial observation (Table 2, Figure 9) revealed the producing process of the vertical consecutive series of *Asteriacites lumbricalis* (Seilacher, 1953, 2007; Mángano *et al.*, 1999; Gurav *et al.*, 2014). Seilacher (1953, 2007) suggested that the vertical repetitive traces were produced by the escape reaction of ophiuroids in response to the deposition of new sand layers. Our aquarium experiment verified his interpretation based on the mode of occurrence of traces: the repetitive escape behavior was induced by successive thin sand and abrasive covers (Figure 5) and the behavior produced radial symmetrical traces in slightly different shape and position on the abrasive layers (Figure 6).

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References

Baucon, A. and Carvalho, C. N., 2016: Stars of the aftermath: *Asteriacites* beds from the Lower Triassic of the Carnic Alps (Werfen Formation, Sauris di sopra), Italy. *Palaios*, vol. 31, p. 161–176.

Bell, C. M., 2004: Asteroid and ophiuroid trace fossils from the Lower Cretaceous of Chile. *Palaeontology*, vol. 47, p. 51–66.

Bernardi, M. and Avanzini, M., 2011: *Asteriacites lumbricalis* from the Anisian (Middle Triassic) of Vallarsa (Southern Trentino, NE Italy). *Studi Tridentino di Scienze Naturali*, vol. 88, p. 187–190.

Bernardi, M., Petti, F. M., Ferretti, P. and Avanzini, M., 2010: *Asteriacites lumbricalis* von Schlotheim, 1820 from the Coste dell'Anglone Lower Jurassic (Sinemurian) dinosaur ichnosite (Valle del Sarca, Trentino, NE Italy). *Bollettino della Societa Paleontologica Italiana*, vol. 49, p. 119–122.

Chamberlain, C. K., 1971: Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma. *Journal of Paleontology*, vol. 45, p. 212–246.

Dam, G., 1990: Palaeoenvironmental significance of trace fossils from the shallow marine Lower Jurassic Neill Klinter Formation, East Greenland. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 79, p. 221–248.

Duncan, P. M., 1879: On some Ophiuroidea from the Korean Seas. *Journal of the Linnean Society*, vol. 14, p. 445–482.

Fourie, P. H., 2009: Unique asterozoan trace fossils of the Gydo Formation (Bokkeveld Group, Cape Supergroup) near Nieuwoudtville, Northern Cape Province. *In*, Beukes, N. and Rajesh, H. M. *eds*., *The Annual Report of the Paleoproterozoic Mineralization Research (PPM) Group*, p. 33. Department of Geology, University of Johannesburg, Johannesburg.

Goldring, R. and Stephenson, D. G., 1972: The depositional environment of three starfish beds. *Neues Jahrbuch für Geologie und Paläontologie*, *Monatshefte*, Heft 10, p. 611–624.

Gurav, S. S., Kulkarni, K. G., Paranjape, A. R. and Borkar, V. D., 2014: Palaeoenvironmental implications of Middle Jurassic trace fossils from the Jaisalmer Formation, India, with emphasis on the ichnogenus *Asteriacites lumbricalis* von Schlotheim, 1820. *Annales Societatis Geologorum Poloniae*, vol. 84, p. 249–257.

Hakes, W. G., 1976: Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas. *University of Kansas Paleontological Contributions*, article 63, p. 1–46.

Hakes, W. G., 1977: Trace fossils in Late Pennsylvanian cyclothems, Kansas. *In*, Crimes, T. R. and Harper, J. C. *eds*., *Trace fossils 2*, p. 209–226. Seel House Press, Liverpool.

Heer, O., 1865: *Die Urwelt der Schweiz*, 622 p. Schulthess, Zürich.

Hess, R., 1983: Das Spurenfossil *Asteriacites* im klastischenä Permoskyth (Prebichl-Schichten) der südlichen Admonler Schuppenzone (Ostalpen) und seine palaogeographische Bedeutung. *Neues Jahrbuch für Geologie und Paläontologie*, *Monatshefte*, Heft 9, p. 513–519.

Ishida, Y., 1999: Escape behavior and postures of epifaunal ophiuroids from burial: Extant and late Miocene *Ophiura sarsii sarsii* as an example. *Memoir of the Geological Society of Japan*, no. 54, p. 161–173. (*in Japanese with English abstract*)

Ishida, Y., Fujita, T. and Kamada, K., 2004: Ophiuroid trace fossils in the Triassic of Japan compared to the resting behavior of extant brittle stars. *In*, Heinzeller, T. and Nebelsick, J. H. *eds*., *Echinoderms: München*, p. 433–438. Taylor and Francis Group, London.

Ishida, Y., Fujita, T., Kiyomoto, M., Röper, M., Komatsu, T., Kato, K., Kamada, K., Shigeta, Y. and Kumagae, T., 2017: How striations of ophiuroid and asteroid trace fossils were produced—Observations of tube-feet movement in living ophiuroids and asteroids. *Paleontological Research*, vol. 21, p. 27–36.

Ishida, Y., Fujita, T., Kohtsuka, H., Manabe, M. and Ohara, M., 2019: A new example of the trace fossil *Asteriacites quinquefolius* from Japan and its process of production as revealed by observations of extant sea star. *Paleontological Research*, vol. 23, p. 1–9.

Ishida, Y., Röper, M. and Fujita, T., 2013: Comparison of asteroid and ophiuroid trace fossils in the Jurassic of Germany with resting behavior of extant asteroids and ophiuroids. *In*, Johnson, C. *ed*., *Echinoderms in a Changing World*, p. 87–94. Taylor and Francis Group, London.

Jagt, J. W. M., Fraaije, R. H. B. and Bakel, B. W. M. van, 2009: A late Miocene astropectinid (Echinodermata, Asteroidea) and associated ichnofossils from Liessel, province of Noord-Brabant, the Netherlands. *Netherlands Journal of Geosciences*, vol. 88, p. 127–131.

Knoch, U., 1989: Die Schlangensterne von Blumenrod. *Fossilien. Zeitschrift für Sammler und Hobbypaläontologen*, vol. 6, p. 134–231.

Lewarne, G. C., 1964: Starfish traces from the Namurian of County Clare, Ireland. *Palaeontology*, vol. 7, p. 508–513.

Ljungman, A. V., 1866: Om några nya arter af Ophiurider. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, vol. 23, p. 163–166.

Mángano, M. G., Buatois, L. A., West, R. R. and Maples, C. G., 1999: The origin and paleoecologic significance of the trace fossil *Asteriacites* in the Pennsylvanian of Kansas and Missouri. *Lethaia*, vol. 32, p. 17–30.

Mikuláš, R., 1990: The ophiuroid *Taeniaster* as a tracemaker of *Asteriacites*, Ordovician of Czechoslovakia. *Ichnos*, vol. 1, p. 133–137.

Oppel, A., 1864: Über das Lager von Seestemen im Lias und Keuper. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, vol. 20, p. 206–212.

Röper, M. and Rothgaenger, M., 1995: Eine neue Fossillagerstätte in den Ostbayerischen Oberjura-Plattenkalken bei Brunn/Oberpfalz. *Jahresbericht 1994 und Mitteilungen der Freunde der Bayerischen Staatssammlung für Paläontologie und Historische Geologie München*, 23, p. 32–46.

Röper, M. and Rothgaenger, M., 1998: *Die Plattenkalke von Hienheim*, 110 p. Eichendorf Verlag, Eichendorf.

Schlotheim, E. F. von, 1820: *Die Petrefactenkunde auf ihrem Jetzigen Standpunkte durch die Beschreibung seiner Sammlung Versteinerter und Fossiler Überrestre des Thier-und Pflanzenreichs der Vorwelt Erläutert*, 437 p. Becher, Gotha.

Seilacher, A., 1953: Studien zur Palichnologie II. Die fossilen Ruhespuren (Cubichnia). *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen*, Band 98, p. 87–124.

Seilacher, A., 2007: *Trace Fossil Analysis*, 226 p. Springer, Berlin.

Twitchett, R. J., 1999: Palaeoenvironments and faunal recovery after the end-Permian mass extinction. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 154, p. 27–37.

Twitchett, R. J. and Wignall, P. B., 1996: Trace fossils and the aftermath of the Permo-Triassic mass extinction: evidence from northern Italy. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, vol. 124, p. 137–151.

West, R. R. and Ward, E. L., 1990: *Asteriacites lumbricalis* and a protasterid ophiuroid. *In*, Boucot, A. J. *ed*., *Evolutionary Paleobiology of Behavior and Coevolution*, p. 321–327. Elsevier, Amsterdam.

Wilson, M. A. and Rigby, J. K., 2000: *Asteriacites lumbricalis* von Schlotheim 1820: ophiuroid trace fossils from the Lower Triassic Thaynes Formation, central Utah. *Ichnos*, vol. 7, p. 43–49.

Author contributions

We declare that none of the material in this manuscript has been published or is under consideration for publication elsewhere. Y. I. did experiments in laboratory and identified the fossil. H. K. and M. K. collected extant specimens and analyzed the experimental data. T. F. analyzed the experimental data. All authors contributed to the writing of the manuscript.