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A new example of the trace fossil *Asteriacites quinquefolius* from Japan and the process of production as revealed by observations of an extant sea star

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Abstract. **A star-shaped trace fossil here assigned to *Asteriacites quinquefolius* (Quenstedt) was found in the Miocene Shirahama Formation, Wakayama Prefecture. This is the first report in Japan and stratigraphically youngest record for the ichnospecies. The fossil has five distinct arms and wide striations on both lateral sides of each arm, and the shape is bilaterally symmetrical. To clarify the fossil producing process, we conducted burial experiments of extant asteroids in aquarium and *in situ* for the first time. Asteroids buried themselves in the substratum using the tube-feet, and when asteroids were covered with thin sand, they escaped slantingly upward onto the sand tilting their body in a bilaterally symmetrical posture. As a result, the remaining trace was very similar to the fossil of *A. quinquefolius* from the Shirahama Formation. Accordingly, the results suggest the present fossil was formed by the behavior of escaping from thin sand cover by asteroids.**

Key words: asteroid, burial experiment, escape posture, Miocene, resting trace, Shirahama Formation

Introduction

Asteriacites quinquefolius (Quenstedt, 1876) is a well-known star-shaped trace fossil, with records from the Carboniferous to Triassic of India, Europe and USA (Seilacher, 1953; Hakes, 1977; Twitchett and Wignall, 1996; Röper and Rothgaenger, 1998; Patel *et al*., 2008; Ishida *et al*., 2013, 2017). The ichnospecies has wide arms with dense striations from an undifferentiated center, and was interpreted as a resting trace of asteroids on the basis of its morphology (Seilacher, 1953; Patel *et al*., 2008). Ishida *et al*. (2013, 2017) found an aberrant form of *A. quinquefolius* from the Jurassic Hienheim Formation in southern Germany. The specimen has one indistinct arm without striation and four distinct arms with wide and deep striations. Based on observations of the behavior of the extant asteroids, they demonstrated that this form of trace was produced when the asteroid moved horizontally on the trace (Ishida *et al.*, 2013, 2017).

Some time ago, an example of a star-shaped trace fossil of *Asteriacites quinquefolius* was found in the Miocene Shirahama Formation in Japan (Tanabe Research Group, 1985a, b). The trace has the typical form of *A. quinquefolius*, and has five distinct arms with only wide striations. The form is different from that of the Hienheim specimen (Ishida *et al.*, 2013, 2017) which suggests the trace was produced by a different process.

In this study, to clarify the producing process, we compared the detailed morphology of the new fossil from Japan and that of the trace produced by an extant asteroid. The fossil has no indistinct arm suggesting the asteroid moved vertically upward after producing the trace. We obtained the traces by laboratory observation of the behavior of an extant asteroid after burial of the asteroid by sand. There are the first laboratory and *in situ* observations of the behavior of extant asteroids after burial by sand.

Material and methods

A star-shaped trace fossil exposed on the surface of a boulder (10×20×10 cm) was found on the coast in Tonda, Shirahama-cho, Wakayama Prefecture, about 500 m south of the mouth of the River Takase (Site A in Figure 1; 33.62˚N, 135.39˚E). The boulder was composed of massive sandstone partly with mudstone on the surface. The boulder was interpreted to be autochthonous, because of the similar lithofacies of the outcrop in the immediate vicinity. In this area, the Shirahama Formation of the Tanabe Group is exposed. The lithofacies is composed mainly of massive sandstone and alternations of mudstone and sandstone with hummocky cross-lamination or planar cross-lamination, interpreted as storm or tidal current sediments (Tanabe Research Group, 1985a, b, 1992).

The Tanabe Group is of middle Miocene age on the basis of the planktonic foraminifera such as *Globigerinoides subquadratus*, *Globigerinoides sicanus*, *Praeorbulina glomerosa*, *Globorotalia birnageae*, and others (Tanabe Research Group, 1984).

The star-shaped trace fossil was preserved as a convex hyporelief and was composed of fine sandstone. The size of the trace fossil was measured by a vernier caliper. The detailed morphology of the present fossil was analyzed by taking molds using a synthetic resin and tracing it onto transparent paper placed upon the mold. Two synthetic resin molds of the trace fossil from the Shirahama Formation were made and housed at the Wakayama Prefectural Museum of Natural History (WMNH-Ge-2120160001) and National Museum of Nature and Science, Tsukuba, Japan (NMNS PA18450). The actual fossil belongs to Manabi Manabe, one of the authors.

Specimens of an extant asteroid, *Astropecten scoparius* Müller and Troschel, 1842, were collected by hand on the coarse sand bottom in the intertidal zone of Moroiso Bay, Miura-shi, Kanagawa Prefecture, Japan from April in 2016 to June 2017 (Site B in Figure 1). The asteroids were kept alive for one to 62 days in the laboratories (National Museum of Nature and Science, Ibaraki Prefecture and Misaki Marine Biological Station, the University of Tokyo, Kanagawa Prefecture) before observation. Twenty specimens were used in a total of twenty-three laboratory observations (Table 1). Their major radius (R) and body thickness at the center of disc were 28.5–55.5 mm and 5.2–9.0 mm, respectively, measured by a vernier caliper.

The behavior was observed in aquariums of small (170 mm in diameter, 70 mm in height) and large (230 mm in diameter, 75 mm in height) hemisphere-shaped plastic bowls or exceptionally of a square-shaped polystyrene foam box (250×160×140 mm) for thickest cover (100 mm) by sand. Aluminiferous abrasive (#2000 or #1500; equivalent to mud in grain size) or gypsum (equivalent to mud) was laid as substratum about 15–20 mm in thickness and on-site or artificial sea water was filled in the aquariums (Figure 2-1, Table 1). Water temperature was kept at 14–22˚C throughout the observation. One specimen of *Astropecten scoparius* was placed on the substratum in each aquarium. After the asteroids buried themselves shallowly in the substratum (Figure 2-2), they were quickly covered with sand (0.2–0.5 mm in grain size equivalent to fine to medium sand) in thickness of 5–100 mm (Figure 2-3). Asteroids were removed after they successfully escaped onto the sand cover (Figure 2-4). Asteroids did not appear on the sand cover in two observations (Table 1, Observation Nos. 22, 23), and then were excavated by removing the sand cover. The substratum was dried for several days to a few weeks to allow the abrasive or gypsum to harden. The upper part of the plastic bowls and polystyrene foam box were cut off above the sand by a heat iron thread (polystyrene foam cutter). Then, the cover sand was carefully removed with a spoon and paint brush (Figure 2-5). The morphology of the trace left on the hardened substratum was observed (Figure 2-6). During the process of escape, the movements of arms and tube-feet of asteroids were recorded by a video camera.

In situ observations by scuba diving were done for two separate specimens of *Astropecten scoparius* (about 40 mm in R) on the coarse sand bottom at a depth of 2 m in Moroiso Bay in November 2016 (Site B in Figure 1). In the experiments, when the asteroids slightly buried themselves in the substratum, sand on the sea floor in the immediate vicinity was scooped and dumped quickly on the two specimens about 20 mm thick by hand. Asteroid behavior was recorded using an underwater video camera.

The morphology of the traces left on the substratum was sketched on a transparent paper placed upon a photo of the traces.

Results

Morphology of *Asteriacites quinquefolius* from Japan

The star-shaped trace fossil has five clear radiating arms and an undifferentiated center (Figure 3). The arms are wide and deep rod-shaped with rounded or a slightly pointed tips. The shape does not reveal complete radial symmetry but rather in bilateral symmetry having 5 arms unevenly stretched. The arms have striations on both lateral sides of each arm. The striations are parallel and perpendicular to the arm axis, and wide and in contact with each other. The length (from the estimated center of the trace to the tip of the arm) of five arms measures 63.8–94.2 mm (mean 75.3 mm), and the width of the arm base is 22.8–28.8 mm (mean 25.9 mm). The depth of central depression of the specimen is 14.5 mm. The specimen had five triangular mounds on both sides of arms (Figure 3). The morphology completely matches the diagnosis of *A. quinquefolius* (Seilacher, 1953), and agrees well with previous descriptions (Hakes, 1977; Patel *et al.*, 2008). Ishida *et al.* (2013) reported an anomalous form of the ichnospecies from Germany: the here-described Japanese specimen differs in having five distinct arms and only wide striations on each arm.

Laboratory observations of the behavior of extant asteroids

In all laboratory observations, the asteroids buried themselves in the substratum shallowly at depths of about 20–90 % of body thickness, and formed crescent-shaped mounds along the arms (Figure 4). The mounds finally remained in the trace on the substratum (Figure 5).

When asteroids were covered with sand, they showed three different behavior patterns depending on the thickness of the sand cover (Table 1). When asteroids were covered with thin sand equalling 11–74 % of the major radius (R) in thickness (Table 1, Observation Nos. 1–11), they slantingly crawled up tilting their body by cyclic movement of tube-feet onto the sand cover in 0.7–19 minutes (Figure 4A, B; "slanting" in Table 1). The escape posture performed in bilateral symmetry: one arm preceded the body, two arms extended laterally on each side, and the other two arms extended obliquely backward (Figure 4A, B). All asteroids (n=11) left star-shaped traces on the substratum. They had five distinct arms with wide striations. Eight traces were not radially but bilaterally symmetrical similar to the posture of asteroids when escaping as described above (Figure 5B, D‐J; Table 1, Observation Nos. 2, 4‐10). The other three traces, on the other hand, were radially symmetrical (Figure 5A, C, K; Table 1, Observation Nos. 1, 3, 11). The striations were in contact with each other, arranged in parallel, perpendicular to the arm axis on both radial halves (Figure 5A–K).

On the other hand, when asteroids were covered with relatively thick sand equalling 75–136 % of R in thickness (Table 1, Observation Nos. 12–21), they escaped onto the sand cover in 1–27 minutes by a different behavior (Figure 4C–E; "vertical" in Table 1).

The asteroids lifted one or two arms almost vertically on the sand cover bending themselves aborally (Figure 4C2, D2, E2). They then heaved most of the body above the sand (Figure 4C3) and sometimes were nearly upside down (Figure 4D3, E3). Finally they returned to their original postures with the aboral side up (Figure 4C4, D4, E4). The traces left on the substratum had five irregular arm depressions with wide striations on both radial halves. One or two arms of the traces corresponding to the arms lifted were shorter than the others (Figure 5L–U). The traces had various shapes of grooves by sharply curved (Figure 5M, R), slightly curved (Figure 5N, U), long and straight (Figure 5L, T).

When asteroids were covered with even thicker layer of sand equalling 136 % and 266 % of R in thickness, they did not appear on the sand after 74 and 281 minutes, respectively (Table 1, Observation Nos. 22, 23). When the sand was removed, the asteroids remained upside down in the sand (Figure 4F2, G2; "inverted" in Table 1). In both observations, the traces left on the substratum had five irregular indistinct arms with wide striations. The traces had grooves similar to those in relatively thick sand cover (Figure 5V, W).

In situ* observations of *Astropecten scoparius

When asteroids were covered with coarse sand of about 50 % of arm length (R) in thickness, they escaped onto the sand slightly tilting their bodies in about 20 seconds (Figure 6). Their behavior is similar to that of asteroids covered with thin sand in laboratory observations (Figure 6).

Discussion

The ichnospecies *Asteriacites quinquefolius* from the Shirahama Formation is described for the first time from Japan in this study although another ichnospecies *A. lumbricalis* of the star-shaped trace fossil ichnogenus *Asteriacites* has been reported from the Triassic Hiraiso Formation, Miyagi Prefecture (Ishida *et al*, 2013, 2017) and from the Cretaceous Himenoura Group, Kumamoto Prefecture (Ishida *et al.*, 2017). *Asteriacites quinquefolius* has been previously reported from older strata: the Upper Carboniferous of the U.S.A. (Hakes, 1977), the Middle Jurassic of Germany (Seilacher, 1953), the Upper Jurassic of Germany (Röper and Rothgaenger, 1998; Ishida *et al.*, 2013), the Lower Cretaceous of India (Patel *et al*. 2008) and the Lower Triassic of Italy (Twitchett and Wignall, 1996). This fossil from the Miocene Shirahama Formation is the youngest record. The detailed morphology of the fossil from the Shirahama

Formation is similar to that reported in the previous papers on *A. quinquefolius* from the Middle Jurassic of Germany (Seilacher, 1953, Table 10, fig. 1a), and the Lower Cretaceous of India (Patel *et al*. 2008, Fig. 1c, d, e, g).

In this study, burial observations using an extant asteroid in aquariums and *in situ* (Figures 4, 6) revealed the producing process of the present fossil. This paper mentioned for the first time that *Asteriacites quinquefolius* is produced by asteroids' escaping behavior after being covered by sand. The ophiuroid-related trace fossil *Asteriacites lumbricalis* is also inferred to have been made by escaping behavior from sand cover on the basis of the mode of occurrence of fossils (Seilacher, 1953, 2007). Escape movements of extant ophiuroids from the smothering sediments in aquariums and *in situ* were reported by Ishida (1999), Ishida and Fujita (2001) and Ishida *et al.* (2004).

In aquarium observations, if the thickness of sand cover does not exceed 136 % of the major radius (R), the asteroids successfully escaped from the sand cover (Table 1). The asteroids moved obliquely upwards when the sand cover was thin (Figure 4A, B), while they moved mostly vertical (Figure 4C, D, E) when they were covered with a thick layer of sand. However, when the thickness exceeded 136% of R, they failed to escape from the sand cover and were found in the sand in upside-down posture (Figure 4F, G). The behavior on the sea floor in *in situ* observations (Figure 6) was similar to that from thin cover sand in the laboratory observations (Figure 4A, B). The results of these observations suggest that escape behavior from the sand cover produces star-shaped traces. The star-shaped trace of the extant asteroids has five distinct arms with wide striations on both lateral sides when it escapes from the sand cover. The morphology of the traces, however, varied slightly depending on the thickness of sand. In thick sand, the arms are not uniform in length, the central disc has various irregularly shaped grooves and the shape was not bilateral (Figure 5L–W). *Asteriacites quinquefolius* from the Shirahama Formation had distinct five arms, bilaterally symmetrical body and wide striations on both sides of each arm (Figure 3). Their morphologies are strikingly similar to the traces when the asteroid is covered with thin sand (Figure 5B, D–J). Our results suggest that the Shirahama specimen represents the trace produced by an asteroid that escaped after being covered by thin sand (Figure 7). The sand cover may have been caused by a storm or tidal current event (Tanabe Research Group, 1992).

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Explanation of figures and table

Figure 1. Localities of *Asteriacites quinquefolius* from the Shirahama Formation, Wakayama Prefecture (Site A) and of extant *Astropecten scoparius* in Moroiso Bay, Kanagawa Prefecture (Site B).

Figure 2. Experimental design for observations of behavior of the extant asteroid covered by sand and the trace produced on the substratum. 1, Substratum and sea water were filled in a plastic bowl. 2, An asteroid was put on the substratum. It buried itself in the substratum. 3, The asteroid was covered with sand. 4, The asteroid escaped onto the sand. 5, The bowl was cut and the sand was removed. 6, The trace was left on the substratum.

Figure 3. *Asteriacites quinquefolius* from the Shirahama Formation. A, synthetic resin mold; B, sketch showing striations. The arrow shows the estimated moving direction, and bold lines show the axis of bilateral symmetry of the trace. Abbreviations: Mo, mound of substratum; Stw, wide striation. Scale bars equal 1 cm.

Figure 4. Behavior of *Astropecten scoparius* in aquarium observations. Asteroids buried themselves when they were put on the substratum (1 in A–G). After they were covered with sand, they escaped (2–4 in A–E) or failed to escape (2 in F–G). Bold lines in B3 show the axis of bilateral symmetry of the trace. Abbreviations: La, lateral arm; Mo, mound of substratum; Poa, posterior arm; Pra, preceding arm; Tu, tube-foot. Scale bars equal 1 cm.

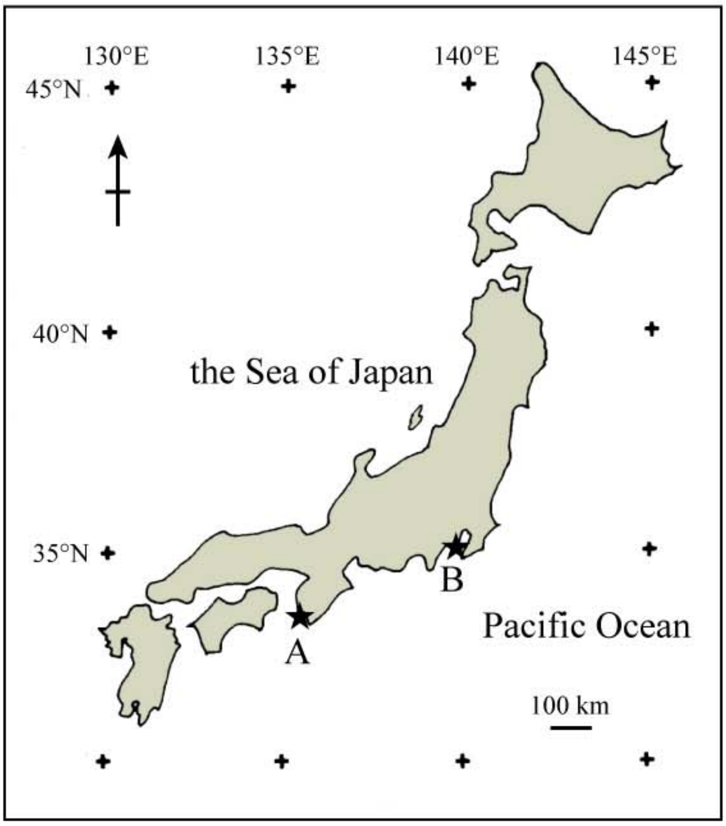
Figure 5. Traces of *Astropecten scoparius* left on the substratum in aquarium observations. In sketches, arrows show the moving direction, and bold lines show the axis of bilateral symmetry of the trace. Bilateral symmetry (B, D–J), completely radial symmetry (A, C, K), and irregular form (L–W) were observed. Abbreviations: La, lateral arm; Mo, mound of substratum; Poa, posterior arm; Pra, preceding arm; Stw, wide striation. Scale bars equal 1 cm.

Figure 6. *In-situ* observations of escape behavior of *Astropecten scoparius*. A and B show different specimens. Asteroids were covered with thin sand (1 in A–B). The asteroids escaped from the sand cover (2 in A–B). In sketches, arrows show the moving direction, and bold lines show the axis of bilateral symmetry of the trace. Scale bars

equal 1 cm.

Figure 7. Schematic diagram of the producing process of *Asteriacites quinquefolius* from the Shirahama Formation. A, Horizontal and vertical view of producing process by asteroid; B, Trace fossil left on the substratum. Thin and thick arrows show the movement of tube-feet and the escape direction of the asteroid, respectively. 1, asteroid burying itself in the substratum. 2, asteroid covered with thin sand. 3, asteroid escaping from the sand cover. Abbreviations: Ar, arm; Mo, mound of substratum; Stw, wide striation; Tu, tube-foot. Figure 1 in A is modified from Ishida *et al.* (2017).

Table 1. Laboratory observation of *Astropecten scoparius* covered with sand in aquariums. The same individual was repeatedly used in observations 18, 21, 22 and 19, 20, respectively, shown by asterisks. Abbreviations: abr, aluminous abrasive; as, artificial sea water; ns, natural sea water.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135°E
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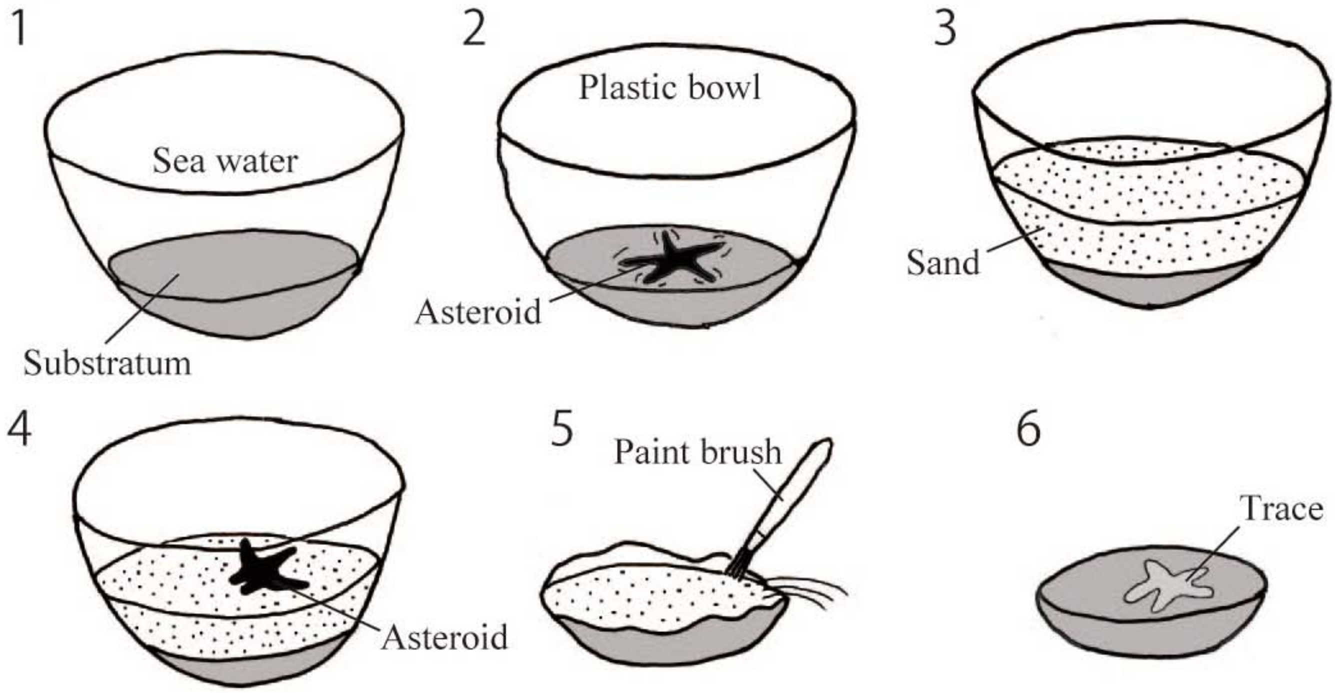
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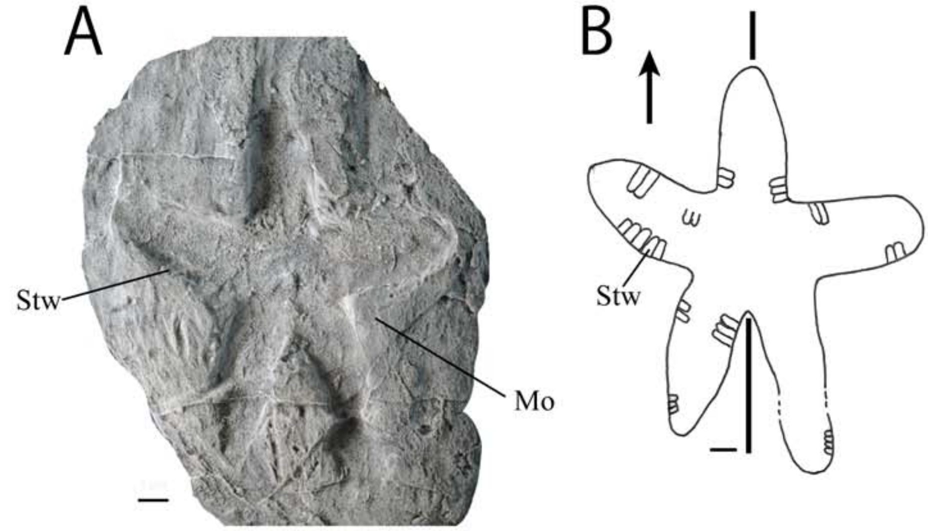
3
Sand
4
Asteroid
5
Paint brush
6
Trace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Mo
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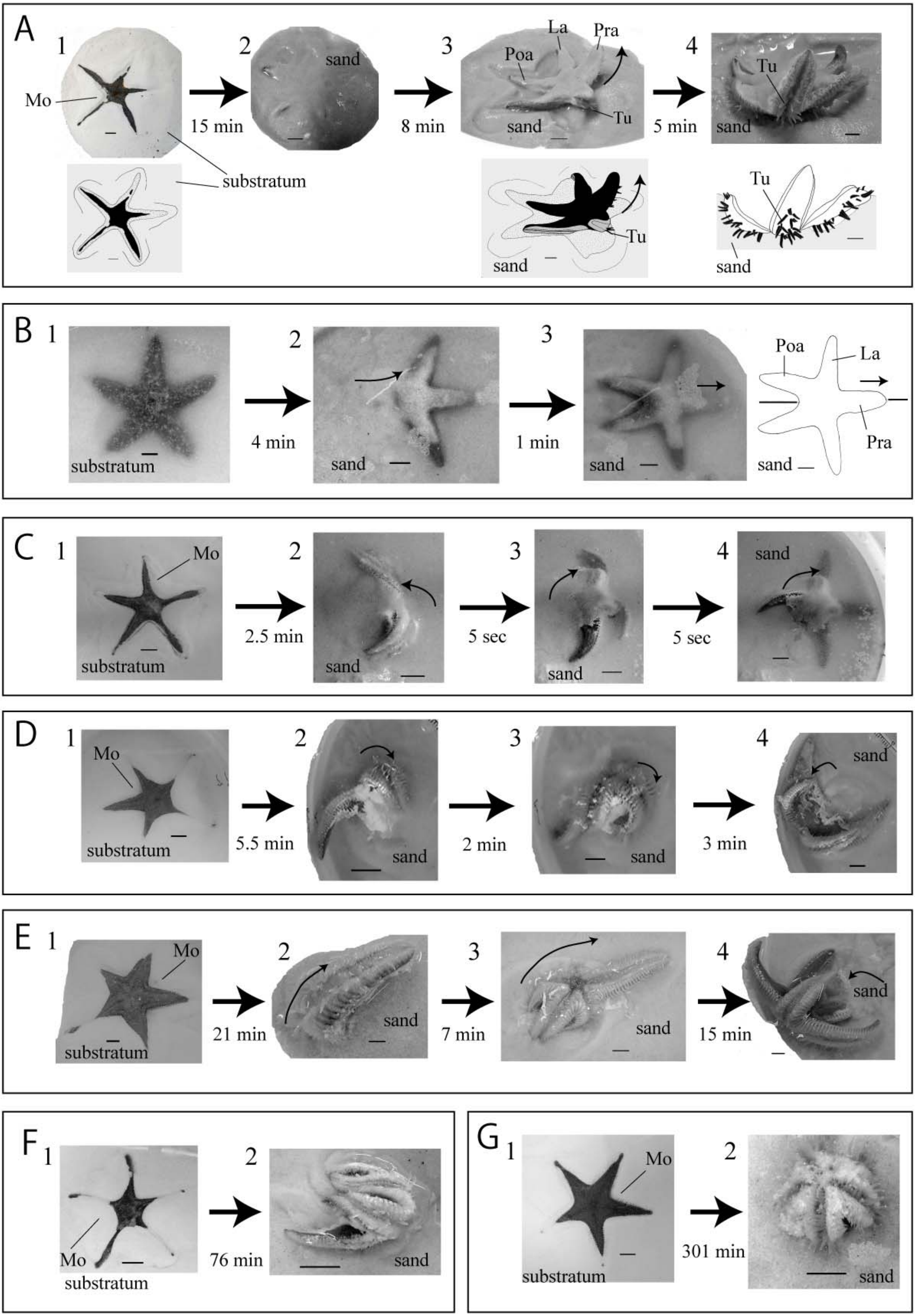
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sand
B
1
substratum
4 min
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3
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substratum
2.5 min
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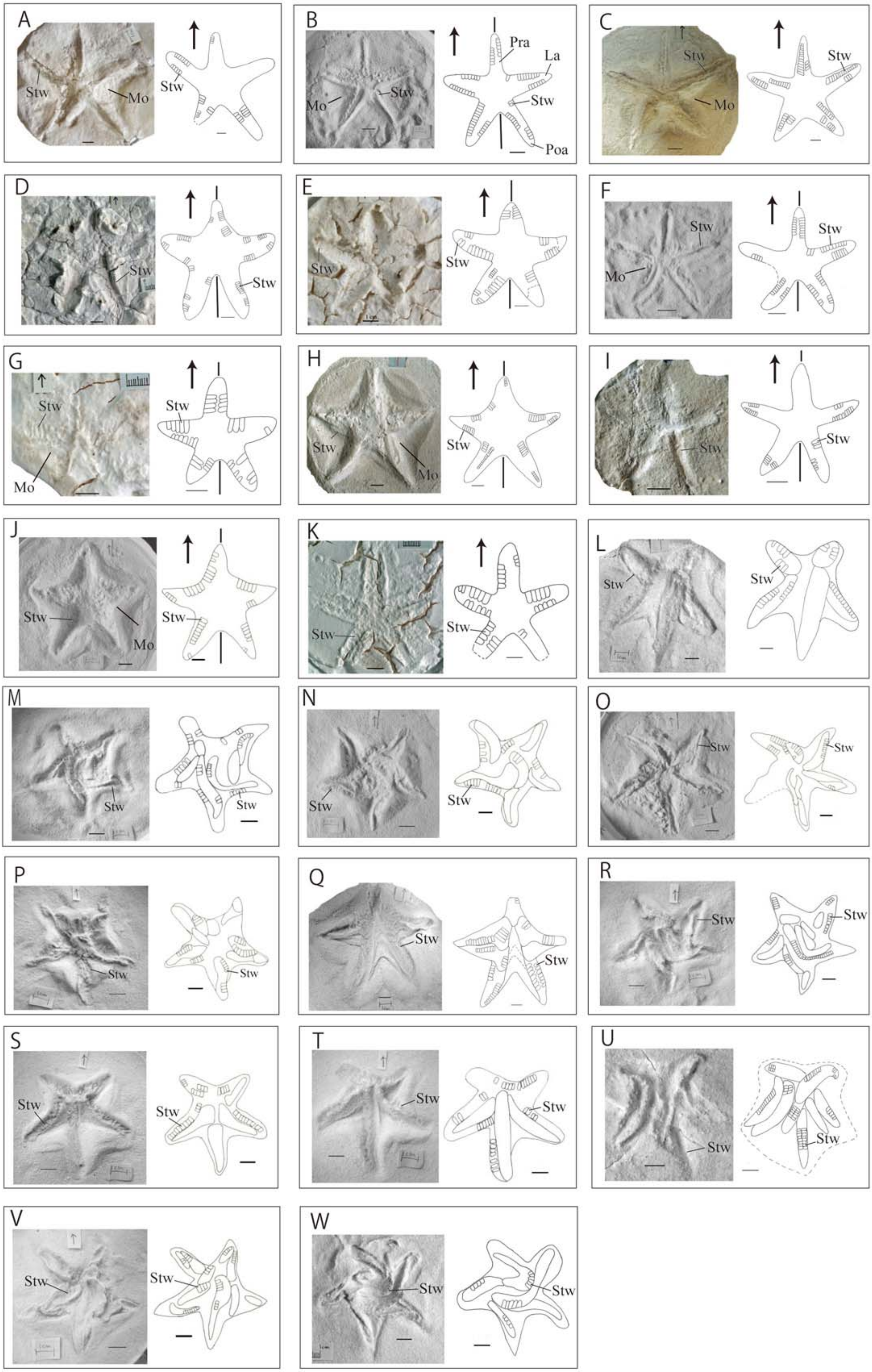
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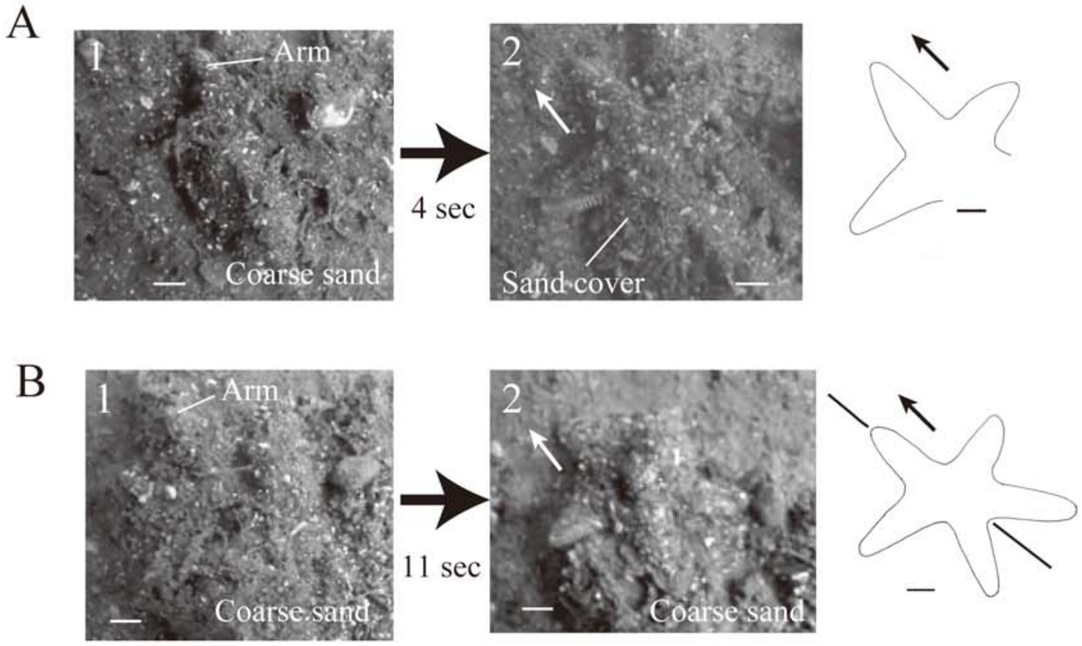

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1
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Coarse sand
4 sec
2
Sand cover
B
1
Arm
Coarse sand
11 sec
2
Coarse sand

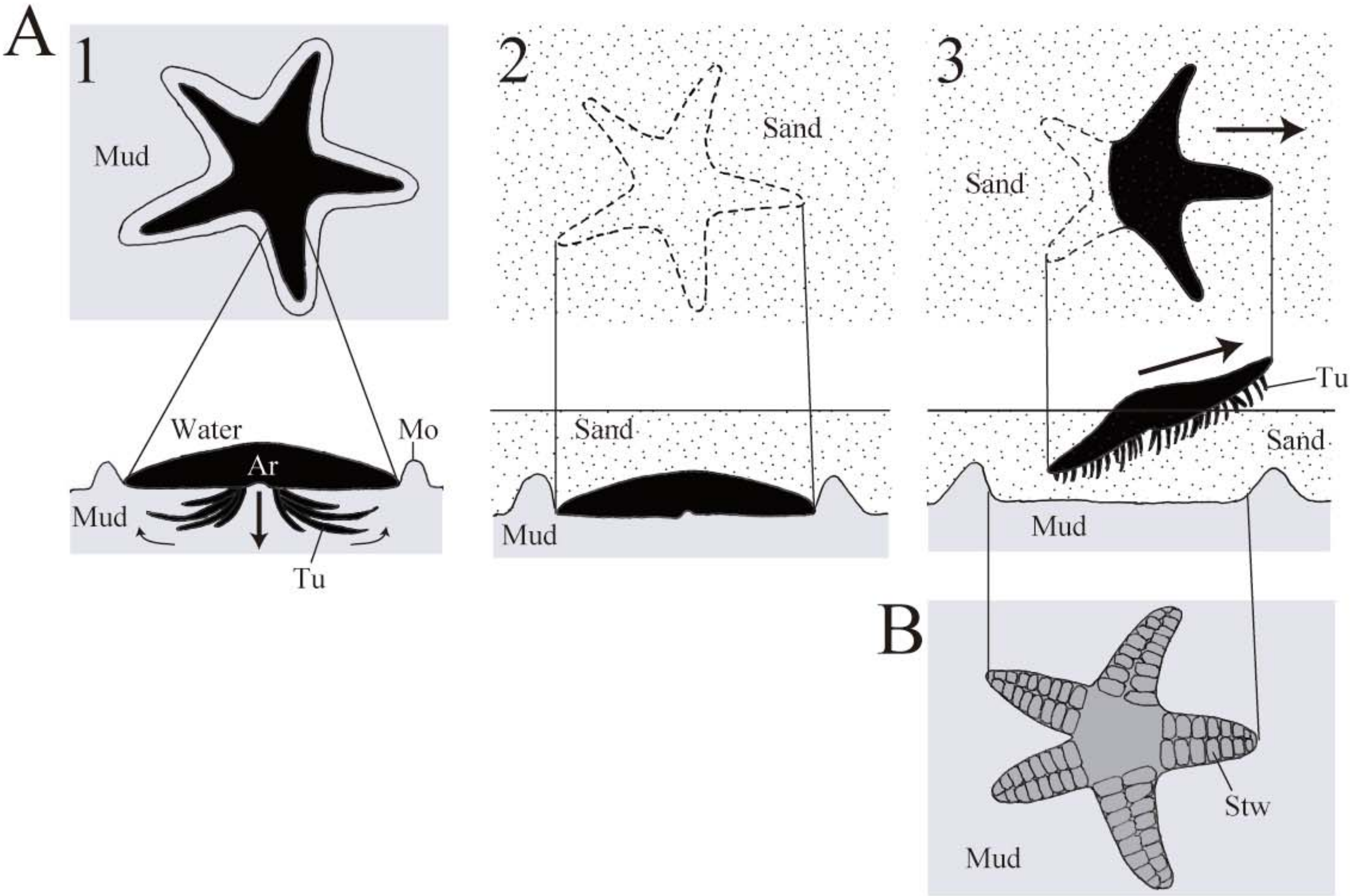
A
1
Mud
Water
Mo
Ar
Mud
Tu
2
Sand
Sand
Mud
3
Sand
Tu
Sand
Mud
B
Stw
Mud

Table 1. Laboratory observation of *Astropecten scoparius* covered with sand in aquariums. The same individual was repeatedly used in observations 18, 21, 22 and 19, 20, respectively, shown by asterisks. Abbreviations: abr, aluminous abrasive; as, artificial sea water; ns, natural sea water.

Observation no.	Type of aquarium	Material of substratum and type of sea water	Major radius (R) of asteroid (mm)	Thickness of sand cover (mm) and % of R in parentheses	Start and end time of escape behavior (minutes after covered)	Behavior pattern	Trace form	Figure
1	small bowl	abr (#2000), ns	46.0	5.0 (11)	6－14	slanting	radidal	4A, 5A
2	small bowl	abr (#1500), as	37.7	7.0 (19)	4－4.5	slanting	bilateral	5B
3	small bowl	abr (#2000), as	49.9	10.0 (20)	29－31	slanting	radidal	5C
4	large bowl	gypsum, ns	43.9	15.0 (34)	1－20	slanting	bilateral	5D
5	small bowl	gypsum, ns	41.9	15.0 (36)	6－9	slanting	bilateral	5E
6	small bowl	abr (#1500), as	34.5	15.0 (44)	0.8－1.5	slanting	bilateral	5F
7	small bowl	gypsum, ns	38.5	20.0 (52)	1－3	slanting	bilateral	4B, 5G
8	small bowl	abr (#2000), as	49.0	30.0 (61)	2－7	slanting	bilateral	5H
9	small bowl	abr (#2000), ns	28.5	20.0 (70)	1－4	slanting	bilateral	5I
10	small bowl	abr (#2000), as	44.0	32.0 (73)	4.6－8.5	slanting	bilateral	5J
11	small bowl	gypsum, ns	40.3	30.0 (74)	9－12	slanting	radidal	5K
12	small bowl	abr (#2000), as	53.0	40.0 (75)	10－15	vertical	irregular (two short arms)	4D, 5L
13	small bowl	abr (#2000), as	33.0	25.0 (76)	6.5－11	vertical	irregular (two short arms)	5M
14	small bowl	abr (#2000), as	41.5	34.0 (82)	1.5－6.5	vertical	irregular (two short arms)	5N
15	small bowl	abr (#2000), as	48.0	40.0 (83)	4－26	vertical	irregular (two short arms)	5O
16	small bowl	abr (#2000), as	43.5	38.0 (87)	9－11.2	vertical	irregular (two short arms)	5P
17	small bowl	abr (#2000), as	55.5	50.0 (90)	21－48	vertical	irregular (one short arm)	4E, 5Q
18	small bowl	abr (#2000), as	33.0*	30.0 (91)	9.7－12.5	vertical	irregular (two short arms)	5R
19	small bowl	abr (#2000), as	36.0**	35.0 (97)	2－3	vertical	irregular (two short arms)	4C, 5S
20	small bowl	abr (#2000), as	36.0**	35.0 (97)	1.8－2.8	vertical	irregular (two short arms)	5T
21	small bowl	abr (#2000), ns	33.0*	45.0 (136)	50－77	vertical	irregular (two short arms)	5U
22	small bowl	abr (#2000), as	33.0*	45.0 (136)	74－ no escape	inverted	irregular	4F, 5V
23	Box	abr (#2000), ns	37.6	100.0 (266)	281－ no escape	inverted	irregular	4G, 5W