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Adaptative morphology for living in shallow water environments in spatangoid echinoids*

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Abstract

Six spatangoid species living in an area about 1 km^2 at depths of 5–18 m were investigated in the Oki-Islands in the Japan Sea. The spatangoids capable of burrowing deeply principally adapt to unstable environment where the sediment surface is disturbed by storms. They are confined to the respective habitats depending on their functional morphology; apical tuft spines and fascioles for respiration, inflated plastron and stern-like postero-ventral shape for deep-burrowing. An exceptional spatangoid, *Lovenia elongata*, has specific morphologies for quick burrowing and rapid righting against disturbance of superficial sediment, which make it possible for it to live in fine- to coarse-grained sand at various water depths in spite of its burrowing just below the sediment surface.

Key words: Echinoidea, Spatangoida, morphology, distribution, burrowing depth

Introduction

Spatangoid echinoids live in littoral to bathyal zones, burrowing to various depths in different types of sediments. They have a wide variety of test shapes with a complex arrangement of functionally and morphologically distinct spines, and their morphologies with respect to function, ontogeny, phylogeny, *etc.* have been studied in detail (*e.g.*, Nichols 1959; Smith 1980; McNamara 1987; Kanazawa 1992; Nérauderau *et al.* 1998; Eble 2000; Villier *et al.* 2004; Smith & Stockley 2005; Saucède *et al.* 2006; Kroh & Smith 2010). In contrast to extensive morphological knowledge, little is known about ecological aspects of spatangoids, and only some species have been intensively studied: Moore (1936), Nichols (1959), Buchanan (1966), Beukema (1985), De Ridder & Jangoux (1987, 1993), Nakamura (2001), Nunes & Jangoux (2004, 2007) for *Echinocardium cordatum* (Pennant); Brattström (1946), Hollertz & Duchene (2001) for *Brissopsis lyrifera* (Forbes); Chesher (1963), Moore & López (1966) for *Moira atropos* (Lamarck); Kier & Grant (1965), Chesher (1968) for *Meoma ventricosa* (Lamarck), Ferber & Lawrence (1976) for *Lovenia elongata* (Gray); Schinner (1993) for *Schizaster canaliferus* (Lamarck); Thompson & Riddle (2005) for *Abatus ingens* (Koehler). These studies have shown that each spatangoid species has a specific ecology in relation to the environment it is adapted to, such as substratum and water depth. However, a comprehensive ecological study on several spatangoids that live in a region where they are confined to their respective habitats has not been made so far. For such

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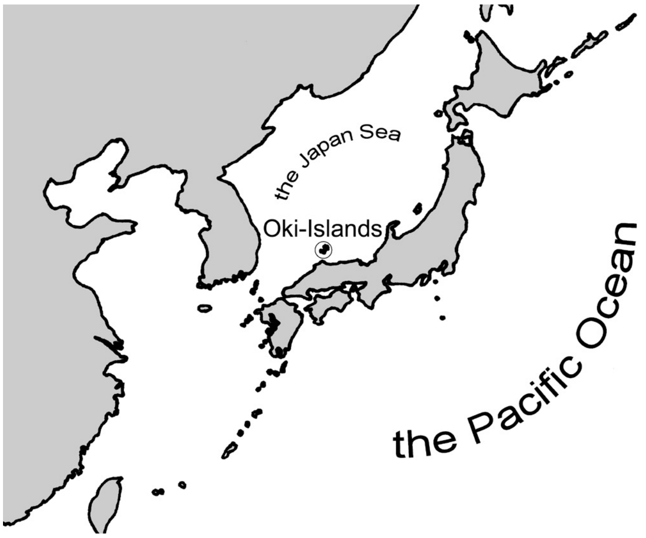

FIGURE 1. Map of Japan and adjacent regions. The study area (Oki-Islands) is located in the Japan Sea.

ecological study the Oki-Islands in the Japan Sea are excellent. Here six spatangoid species live in an area about 1 km^2 at water depths of 5–18 m, where there are different kinds of environments that apparently enable the six different spatangoids to inhabit such a small area. In this paper, based on field investigations and aquarium experiments, the factors that control the spatangoid distribution in shallow water environment are studied from the viewpoint of adaptive morphology.

Materials and Methods

Field work. Field investigations were carried out around Takugi village of the Oki-Islands in the Japan Sea (Fig. 1). Observations and specimen collection were made by scuba diving at five stations at depths from 5 to 18 m (Fig. 2, Table 1). An area of about 80 square meters at each station was investigated. Six spatangoid species; *Lovenia elongata* (Gray), *Pseudomaretia alta* (A. Agassiz), *Metalia spatagus* (Linnaeus), *Brissus agassizii* Döderlein, *Echinocardium cordatum* (Pennant), and *Moira lachesinella* Mortensen were found (Table 1). The echinoids were collected by digging in the sand manually, and their burrowing depths were measured. The number of collected specimens was counted for each species in their respective stations. The conditions of sediment surfaces at the stations were examined through ripple marks made by water disturbance on the sea floor. The field investigations were carried out 11 times (November 2007; April and October 2008; January, May, August and November 2009; February, May, July and November 2010). All the heart urchins collected were transported to the laboratory of Kanagawa University and deposited there for further investigations.

Laboratory work. Taking into account respiration and burrowing, morphology and behavior of the spatangoids were examined because burrowing in sediment to gather food and obtaining fresh water for respiration are essential for infaunal spatangoids.

In spatangoids fascioles that are densely packed bands of small ciliated spines have a specific function to create water currents to draw fresh water (Nichols 1959; Chesher 1968). The placement of fascioles on the test and the current produced around a buried echinoid were examined. Red food dye was used for tracing the course of currents. Also, apical tuft spines that form an apical funnel to

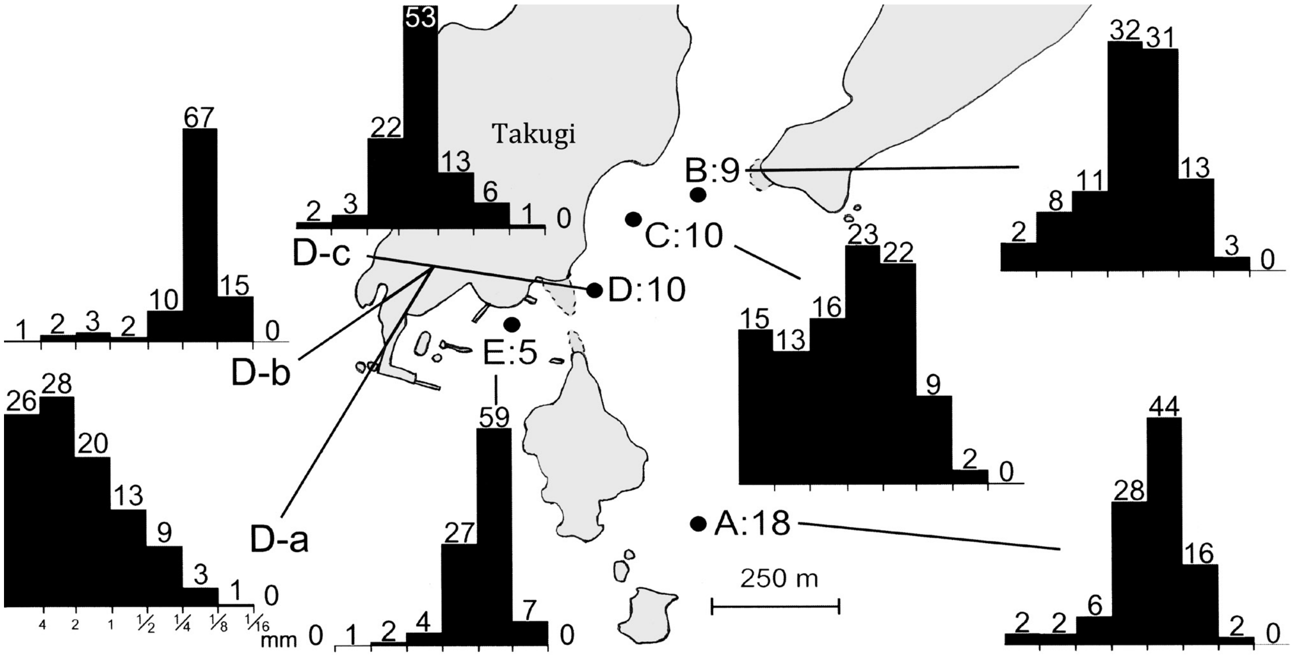

FIGURE 2. Map of the Dogo region of the Oki-Islands, showing stations studied (●) with water depth, and histograms of the substratum particle size distribution; numbers in histograms indicate percent dry weight (see also Table 1).

draw fresh water from sediment surface were observed. In order to check the effectiveness of an apical funnel, a spatangoid whose apical tuft spines were cut off was allowed to burrow in fine-grained sand in an aquarium and its behavior was observed.

Mode of burrowing is closely related to test shape, particularly the shape of plastron and postero-ventral part (Kanazawa 1992). Focusing on this test morphology and related function of spines, burrowing behavior of the spatangoids was examined in aquaria. The activity in the sediment was observed when the urchin appeared at a side wall of an aquarium. The sediments taken from their habitats were used for the experiments, and each echinoid was allowed to burrow not only in the native sediment but also in non-native sediment in different grain size.

The behaviors of the spatangoids under water disturbance were examined in an aquarium. The currents were produced manually by waving a hand in the aquarium, and sediment overlying a burrowing echinoid was washed away at a rate of 6–10 cm per minute. The behavior of the urchin was recorded by a video camera. Righting and re-burrowing behaviors on the sediment were observed in an aquarium. Each animal was placed in an upside-down position on the sediment surface and its speed of righting and re-burrowing was measured.

Results

Habitat condition. The investigated area is located in a protected bay surrounded by capes and islands and is usually calm except at times of storm. In the Oki-Islands as well as other coastal regions of the Japan Sea, strong storms come in winter: ripple marks about 5 cm high and 20–30 cm wave length formed by storm disturbance were frequently observed on the sea floors at depths shallower than 10 m and sometimes at depths from 10 to 18 m during winter and early spring. Dead tests of *P. alta* were often found on sediment surfaces at depths shallower than 10 m in spring and numerous dead tests of *M. spatagus* were observed once at the station B at a depth of 9 m in April 2008. In other seasons ripple marks were rarely observed on the bottoms at depths deeper than 5 m except after a typhoon.

Spatangoids in their habitats. Only *Lovenia elongata* was observed in a variety of habitats in different conditions, while the other five species were found in distinct habitats, depending on substratum and water depth (Table 1).

Lovenia elongata (Fig. 5A) was found at water depths of 5 to 18 m (stations A, B, C, D-b, E). The animals burrowed in various kinds of sediments from fine- to coarse-grained sand with the apex 2 to 3 cm below the sediment surface. Many individuals were observed in fine-grained sand of the station E where other sea urchins were rarely found. The burrowing depths of small and large individuals did not differ. In the winter storm seasons from November 2007 to April 2008 and from January 2009 to May 2009 no decrease in number of individuals was observed for any station (Fig. 3).

Pseudomaretia alta (Fig. 5B) was found at water depths of 9 to 18 m (stations A, B, C, D-c). It burrows in medium- to coarse-grained sand with the apex 2 to 3 cm below the sediment surface. The burrowing depth for small and large individuals did not differ. In the winter storm seasons from November 2007 to April 2008 and from January 2009 to May 2009, a remarkable decrease in number of individuals was observed at station C at a depth of 10 m, while no such decrease occurred at station A at a depth of 18 m (Fig. 4).

Metalia spatagus (Fig. 5C) and ***Brissus agassizii*** (Fig. 5D). These spatangoids lived in gravely coarse-grained sand at water depths of 9 to 18 m (stations A, B, C, D-a). Large individuals more than 5 cm test length burrowed 10 to 15 cm deep below the sediment surface, while small ones burrowed only about 5 cm deep. Although the number of observed individuals was few, in these species, a decrease in number of individuals was found in winter storm seasons.

Echinocardium cordatum and ***Moira lachesinella*** These echinoids were rarely found in the investigated area. They were observed only at station E, burrowing 10 to 15 cm deep in fine-grained sand. Changes in number of individuals could not be studied due to the scarcity of these species (4 speci-

TABLE 1. Habitats of the spatangoids studied. Abbreviations: m-c, medium- to coarse-grained; g, gravelly; c, coarse-grained; m, medium-grained; f, fine-grained. In each species the number and percentage of individuals show the cumulative figure for three-year investigation.

Station	Depth	Substratum	Sea grass	Species observed					
	(m)			*L. elongata*	*P. alta*	*M. spatagus*	*B. agassizii*	*E. cordatum*	*Moira lachesinella*
A	18	m-c sand	scarcely	17 (4%)	161 (50%)	33 (22%)	4 (5%)	0	0
B	9	g m-c sand	patchily	91 (20%)	23 (8%)	36 (25%)	27 (36%)	0	0
C	10	g m-c sand	all around	62 (14%)	101 (33%)	40 (27%)	14 (19%)	0	0
D-a	10	g c sand	scarcely	0 (0%)	0 (0%)	36 (25%)	29 (39%)	0	0
D-b	10	f sand	patchily	83 (19%)	0 (0%)	0 (0%)	0 (0%)	0	0
D-c	10	m sand	patchily	0 (0%)	19 (7%)	0 (0%)	0 (0%)	0	0
E	5	f sand	patchily	193 (43%)	6 (2%)	1 (1%)	1 (1%)	4	4

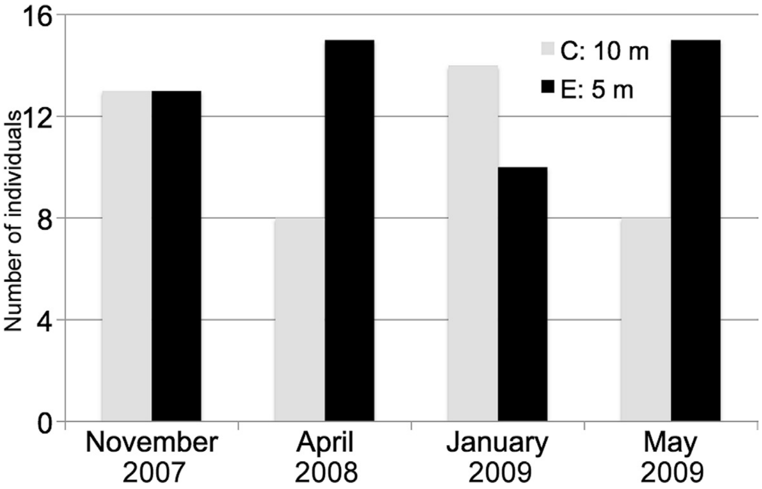

FIGURE 3. Changes in number of individuals for *Lovenia elongata* in winter storm seasons. Cumulative figures for all stations are shown.

mens collected in total during all sampling campaigns).

Morphology and behavior in relation to respiration. *L. elongata* has an internal fasciole and an apical tuft on the dorsal side. In an aquarium, the sea urchin burrowed in fine-grained sand with the apex 1 to 2 cm below the sediment surface, constructing an apical funnel to the sediment surface. There was a water current drawn from the sediment surface into the apical funnel. No other current into the burrow was observed. When the apical tuft spines were cut off, the animal was not completely buried with the apex exposed on the sediment surface. *P. alta* has neither fasciole nor apical tuft on the dorsal side. In an aquarium, the sea urchin was entirely buried in medium- to coarse-grained sand with the apex 1 to 2 cm below the surface. On the sediment surface above the animal no water current filtering through the sediment onto the dorsal area was observed. In fine-grained sand it burrowed exposing the apex on the sediment surface. *M. spatagus* and *B. agassizii* have peripetalous fascioles and no apical tuft on the dorsal sides. In an aquarium, *M. spatagus* and *B. agassizii* burrowed about 10 to 15 cm deep below the sediment surface in coarse-grained sand. In fine-grained sand, the sea urchins burrowed exposing the petalodium on the sediment surface. When the urchins burrowed about 1 to 2 cm deep below the sediment surface, a water current filtering from the sediment surface approximately above the petal region into the burrow was observed.

Morphology and behavior in relation to burrowing. *L. elongata* has a completely flat oral side, *i.e.* an entirely flat plastron and not stern-like postero-ventral shape. The flat oral side brings the latero-ventral spines into contact with the bottom of the burrow. Their backward-directed power strokes propel the urchin forwards. The latero-ventral spines also transport the sand excavated in front to the latero-posterior end and push it into the surrounding sand because the flat ventral surface leaves no space below the test for accumulating the transported sand. This burrowing mechanism appears to be useful only in the superficial layer of sediment. In *P. alta* the posterior part of the plastron is slightly projecting, forming a somewhat stern-like shape. In this sea urchin, the plastron spines as well as the latero-ventral spines provide the principal thrust for forward locomotion. The slightly stern-shaped postero-ventral region produces a small space below the latero-ventral area of the test for accumulating the sand excavated in front and transported to the posterior, though the sand is rejected to some extent into the surrounding sediment. *M. spatagus* and *B. agassizii* have inflated plastrons and a

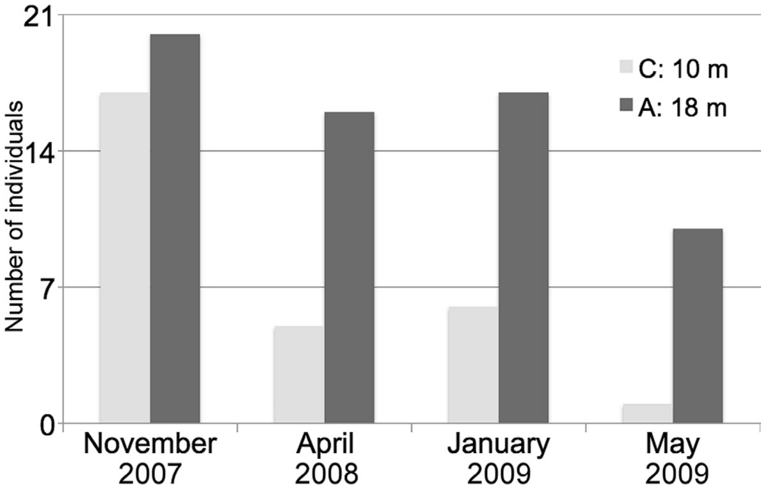

FIGURE 4. Changes in number of individuals for *Pseudomaretia alta* in winter storm seasons. Cumulative figures for all stations are shown.

remarkable stern-like postero-ventral shape. They also have a much more tuberculated plastron and larger sternal plates in comparison to *L. elongata* and *P. alta*. The elevated plastron brings the plastron spines into contact with the floor of the burrow, whereby the spines support the test. Their backward-directed power strokes provide the principal thrust for forward locomotion. The elevated plastron also provides the latero-ventral spines with a convenient space under the test to transport excavated sediment posteriorly. The stern-shaped latero-ventral region produces a large space adequate to accumulate the posteriorly transported sand below the latero-posterior area of the test without pushing it into the surrounding sediment. This morphology presumably enables the spatangoids to burrow deeply in sediment where the pressure of surrounding sediment is expected to be much greater than near the sediment surface.

Behavior under water disturbance. In aquarium experiments with *P. alta*, *M. spatagus* and *B. agassizii*, the urchin was washed out onto the sediment surface and rolled over when the sediment overlying a burrowing urchin was washed away by currents, having no chance to re-burrow. In *L. elongata*, when the dorsal side was partly exposed as overlying sediment was washed away, this urchin started to burrow more deeply and was not washed out. However, after it reached the bottom of aquarium and was no longer able to burrow deeply, the urchin was washed out and overturned. But *L. elongata* soon righted quickly and was not rolled over the sediment surface. The flat test shape with the completely flat ventral side provides the animal with significant stability in currents on the sediment surface.

Righting and re-burrowing on the sediment. In aquarium experiments, *L. elongata* can right much more quickly than the other spatangoids (Table 2): on average 10 seconds, which was about 35 times faster than the other urchins. On the dorsal side, *L. elongata* has very long and stout spines for righting. The tubercles of the spines possess deeply sunken areoles that form large bulges on the inside of the test (camellate tubercles) and provide support for the extremely long and thick muscles. The other echinoids in this study lack such spines.

In re-burrowing experiments it took on average 1 minute for *L. elongata* to disappear under the sediment, which was about 8 times faster than the others. All the spatangoids use the latero-ventral spines for burrowing into sediment, but only *L. elongata* has particularly long, stout spines with

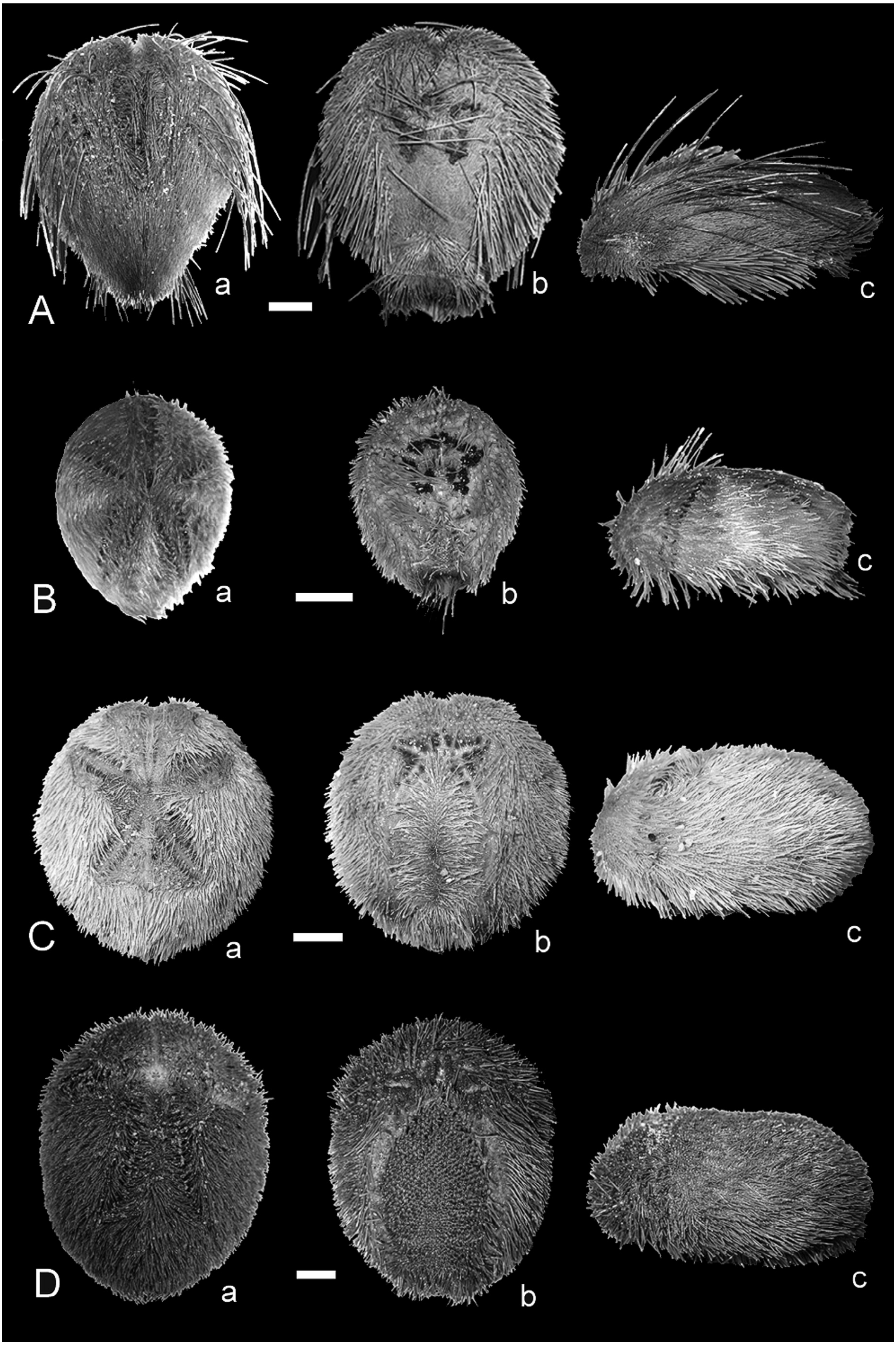

FIGURE 5. Spatangoids examined in this study. A, *Lovenia elongata* (64 mm long); B, *Pseudomaretia alta* (44 mm long); C, *Metalia spatagus* (70 mm long); D, *Brissus agassizii* (76 mm long): a, dorsal side; b, ventral side; c, lateral side. Scale bars equal 10 mm.

deeply sunken tubercles like its long dorsal spines. In the other echinoids, the latero-ventral spines are much smaller and their tubercles are not sunken, providing no support for long thick muscles. The completely flat ventral side of *L. elongata* also facilitates the movement of the latero-venral spines to excavate the sediment beneath the test rapidly because all the spines are in contact with the sediment surface. Additionally, the ventro-lateral areas in *Lovenia* are enlarged compared to the other echinoids studied here and also bear more muscular spine attachments.

Discussion

The study area is located in a calm protected bay, where different kinds of substrate are distributed in a narrow area. This exceptional situation basically enables six spatangoid species to live there. The bottom surfaces are disturbed at the time of storms in accordance with water depths, whereby the spatangoids are confined to their specific habitats.

Adaptation to fine-grained sand bottom in very shallow water. In field investigations, *L. elongata* exclusively lives in fine-grained sand within the study area. In aquarium observations, only *L. elongata* was completely buried in fine-grained sand, constructing a respiratory funnel formed by the apical tuft spines. However, if the apical tuft spines were cut off, the animal was no longer able to disappear under the sediment. Considering that in fine-grained sand *P. alta*, *B. agassizii* and *M. spatagus* that have no apical tuft spine burrowed exposing the petal areas on the sediment surface, the respiratory funnel must be essential for spatangoids to be buried under fine-grained sand, which has already repeatedly noted by many authors (*e.g.*, Nichols 1959; Chesher 1963; Smith 1984). However, unlike *Echinocardium cordatum* and *Moira atropos* observed by those authors, *L. elongata* has no funnel-building tube feet, so that it constructs only a short respiratory funnel about 1 to 2 cm that is slightly longer than the apical tuft spines. It is probable that this constraint allows the animal only to burrow just below the surface of fine-grained sediment.

In the field observations, the fine-grained sand bottom at a depth of 5 m where *L. elongata* lives was often disturbed by water currents. *L. elongata* has specific morphologies for quick burrowing and rapid righting. In a disturbance, this urchin presumably burrows deeper than usual before it is washed-out by currents. Even if washed out, it could rapidly right and re-burrow. *L. elongata*, thus, would survive, though it burrows just below the unstable sand surface in very shallow water environment. No decrease in number of individuals was observed for *L. elongata* in storm seasons.

Other spatangoids (*E. cordatum* and *Moira lachesinella*) found together with *L. elongata* in fine-grained sand burrow 10–15 cm deep below the sediment surface, constructing long respiratory funnels by the funnel-building tube feet. Owing to their deep-burrowing mode of life, these spatangoids would survive in storm disturbance.

	Righting	Re-burrowing
L. elongata	10 sec	1 min
P. alta	5 min	10 min
M. spatagus	10 min	11 min
B. agassizii	7 min	17 min

TABLE 2. Elapsed time for righting and re-burrowing; the average time is shown: 3 individuals for *L. elongata*, 6 for *P. alta*, 2 for *M. spatagus*, 4 for *B. agassizii*.

Although in aquaria *P. alta*, *B. agassizii* and *M. spatagus* apparently have no problem of living in fine-grained sand by exposing their apices on the sediment surface, in the natural environment these spatangoids would be undoubtedly washed out by water disturbance and die. Also, the spatangoids exposed on the sediment surface would easily become prey of many predators like fishes living in shallow waters.

Adaptation to coarse-grained sand bottom in very shallow water. In the field investigations, four spatangoids, *L. elongata*, *P. alta*, *M. spatagus* and *B.agassizii* were found from coarse-grained sand, but their respective distributions are strongly controlled by water depth except *L. elongata*. *P. alta* has no specific morphology to draw water from the sediment surface and the ventral morphology is not appropriate for deep burrowing. These morphological constraints probably confine this sea urchin just below the surface of coarse-grained sand, as observed in the habitat and the aquarium. *P. alta* was found at depths from 9–18 m, but in winter storm seasons a remarkable decrease in number of individuals was observed at depths shallower than 10 m, where dead tests of *P. alta* were frequently found in spring. No such decrease in number occurred at a depth of 18 m. *P. alta* living just below the sediment surface in unstable environment without specific morphology for righting and re-burrowing could be subject to death by storm disturbance. In the other regions in Japan, *P. alta* was usually found in habitats deeper than 20 m (Shigei 1986; Kanazawa 1992). *M. spatagus* and *B. agassizii* have morphologies appropriate to burrow deeply in sand: an inflated plastron and a stern-like postero-ventral shape for transport and accumulating sand in great pressure of surrounding sand. They, however, have neither apical tuft spines nor funnel-building tube feet to construct a respiratory funnel, though they possess peripetalous fascioles to draw water through the sediment above. Owing to these functional morphologies, *M. spatagus* and *B. agassizii* burrow deeply only in coarse-grained sand. In their habitats, large individuals were found in gravelly coarse-grained sand 10–15 cm deep below the sediment surface, where they can usually avoid being washed out to death in storm disturbance. However, numerous dead tests of *M. spatagus* were once observed during our three-year investigation, which indicates that it seems still difficult for *M. spatagus* to survive in severe disturbance caused by a very strong storm. In Toyama Bay *B. agassizii* was found burrowing 20 cm deep in gravelly coarse-grained sand in high-energy environment near the tidal zone (Kanazawa 1992). *B. agassizii* may be capable of burrowing more deeply than *M. spatagus*, which makes it possible for it to inhabit more unstable environment.

L. elongata lives in also fine-grained sand, and it seems easy for it to inhabit coarse-grained sand, where the specific morphologies for quick burrowing and rapid righting makes it possible for it to survive storm disturbance. It is, however, uncertain why *L. elongata* prefers fine-grained sand to coarse-graind sand.

Conclusions

Spatangoids capable of burrowing deeply in sediment can principally adapt to unstable shallow water environments and are confined to specific habitats depending on their functional morphology.

The spatangoids that have fascioles and apical tuft spines with funnel-building tube feet on the dorsal sides, an inflated plastron and a stern-like postero-ventral shape, like *E. cordatum* and *Moira lachesinella*, are capable of burrowing deeply in fine-grained sand.

Spatangoids that have no apical tuft spines but peripetalous fascioles on the dorsal sides and inflated plastron and stern-like postero-ventral shape, like *M. spatagus* and *B. agassizii*, can burrow deeply in coarse-grained sand.

Spatangoids that have neither dorsal fasciole nor apical tuft spines, like *P. alta*, burrow just below the surface of coarse-grained sand. They are thus confined to somewhat deeper calm environment where the sediment surface is scarcely disturbed in a storm.

Specialized spatangoids like *L. elongata*, which has an internal fasciole and apical tuft spines on the dorsal side and the specific morphologies for quick burrowing and rapid righting (*i.e.*, large, stout dorsal spines on camellate tubercles) against disturbance of superficial sediment, can live in fine- to coarse-grained sand in unstable environment in spite of burrowing close to the sediment surface.

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