

## Research Article

# Locomotion and Functional Spine Morphology of the Heart Urchin *Brisaster fragilis*, with Comparisons to *B. latifrons*

Danielle E. Walker<sup>1</sup> and Jean-Marc Gagnon<sup>2</sup>

<sup>1</sup> Interdisciplinary Office/Biomedical Science Program, Faculty of Science, University of Ottawa, Gendron Hall, 30 Marie Curie, Room 081, Ottawa, ON, Canada K1N 6N5

<sup>2</sup> Research & Collections, Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, ON, Canada K1P 6P4

Correspondence should be addressed to Jean-Marc Gagnon; [jmgagnon@mus-nature.ca](mailto:jmgagnon@mus-nature.ca)

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The heart urchin *Brisaster fragilis* is an important bioturbator found in the Estuary and Gulf of St. Lawrence. Several adaptations allow it to move within fine sediments (e.g., test shape, spine morphology, and distribution), which are compared here to those of its Pacific sibling species *B. latifrons*. While ventral spatulate spines and dorsal and anterolateral curvilinear spines are similar between the two species, anterior spines differ significantly: sigmoid-shaped for *B. fragilis* and curvilinear for *B. latifrons*. This morphological difference, in addition to a narrower plastron for *B. fragilis*, suggests a different digging strategy. *In situ* video observations of *B. fragilis* show a “dig and move” strategy: anterior spines “dig” forward at the sediment while the plastron spines “move” the urchin into the newly created space. *B. latifrons* on the other hand uses an oblique rocking motion. This suggests that generalizations derived from one or few species displaying similar body shapes may not be possible. Factors such as sediment depth (i.e., the amount of sediment above the urchin) are likely to affect movement and force the animal to employ a different digging strategy, even within a single species. The role of spines for locomotion is further discussed, with additional reference to tubercle morphology.

## 1. Introduction

The heart urchin *Brisaster fragilis* is an irregular sea urchin belonging to the Echinodermata order Spatangoida; a group that is adapted to dig or burrow within the ocean bottom sediments. *Brisaster fragilis* is the only species of this group commonly found in the Estuary and Gulf of St. Lawrence, living in soft fine mud from relatively shallow to deep water [1]. It is also found in the Northwest Atlantic Ocean and the Barents Sea-Faroe Channel (10–1700 m depth range [2, 3]). In the North Pacific Ocean, its sibling species, *Brisaster latifrons*, is found at the type locality (Gulf of Panama) and from the Gulf of California north to Alaska and west to Japan, at a depth ranging from 11 to 1820 m [4].

The ability to move within a semisolid environment such as marine mud requires certain adaptations that allow efficient displacement of sediment particles and access to oxygen via interstitial water. Like most spatangoid urchins, adaptations that allow *Brisaster fragilis* to move unidirectionally

within the sediments include test shape (i.e., bilateral body plan, low test profile) and the morphology and distribution of their spines (e.g., division of labour with functionally and structurally distinct areas of spines and tubercles [5]).

While many test shapes are observed amongst the irregular urchins, Kanazawa [6] classified them primarily into four categories: globular, domed, flat, or wedge-shaped. These shapes have been applied to other species of irregular urchins to make predictions about their movements within sediment [7]. *Brisaster fragilis* falls within the wedge-shaped category and can therefore be compared to other wedge-shaped urchins (e.g., *Brisaster latifrons*, *Brissopsis lyrifera*, and *Schizaster lacunosus*) in terms of their movement. The shape of the test plays a large role in how the urchin moves through the sediment; for these wedge-shaped species, the test itself is used to push through the sediment [6]. This also influences how the spines are positioned relative to the surrounding sediment [8].

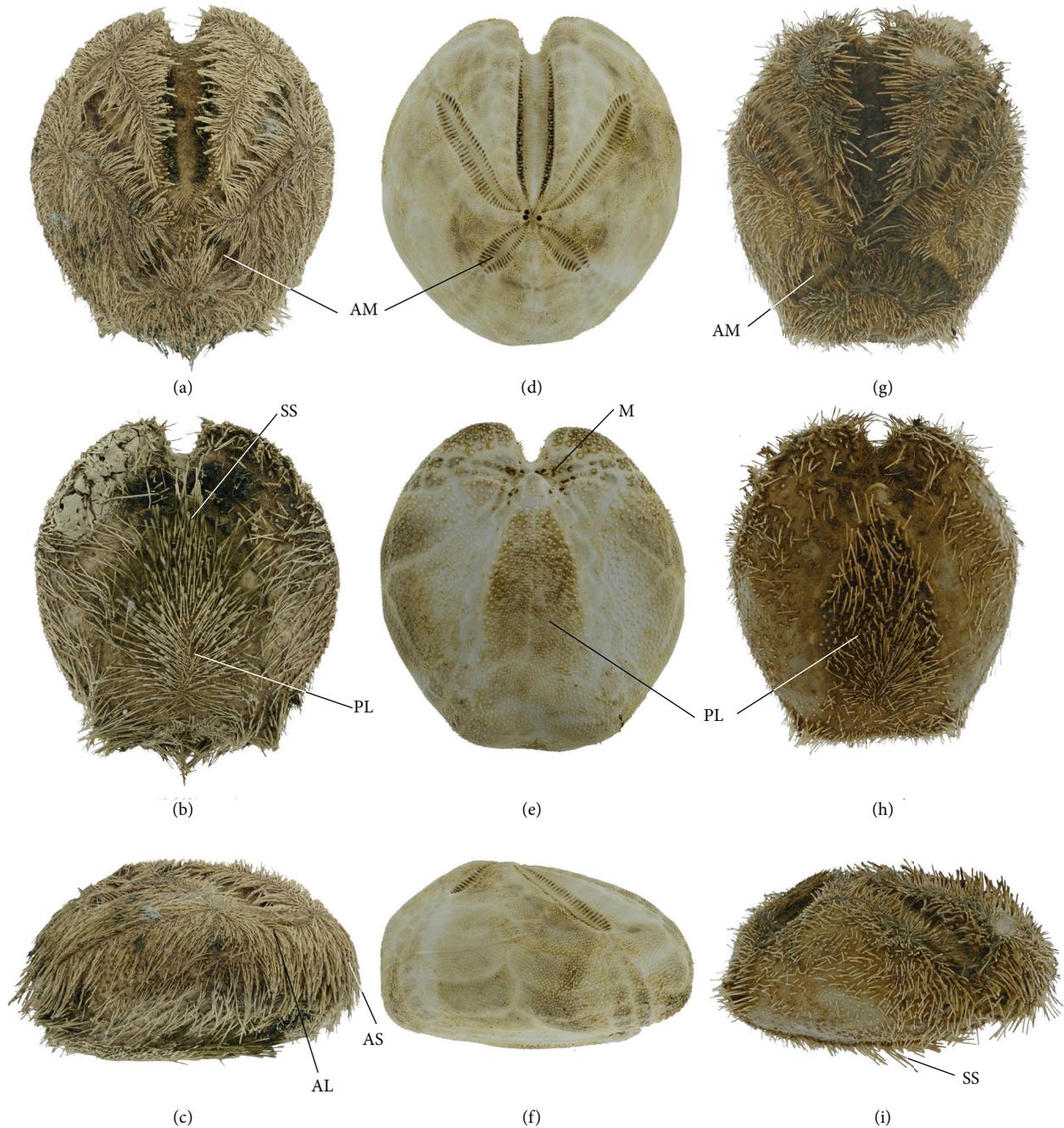


FIGURE 1: ((a) to (f)) *Brisaster fragilis*; ((g) to (i)) *Brisaster latifrons*; ((a), (d), and (g)) dorsal view; ((b), (e), and (h)) ventral view; ((c), (f), and (i)) lateral view. AL: anterolateral spines; AM: ambulacra; AS: anterior spines; M: mouth; PL: plastron; SS: spatulate spines.

To facilitate the comparison of the different regions of spatangoid tests and because of their very strong bilateral symmetry, we opted to deviate from the traditional urchin test nomenclature and use the terms “ventral” (instead of “oral”) and “dorsal” (instead of “aboral”). In this fashion we believe it is easier for the reader to relate to the orientation of the animal in relation to its locomotion.

Irregular urchins have several morphologically distinct spine types, depending on where those spines are located on the urchin test. On the ventral side of these urchins,

the structure called “plastron” (Figure 1) bears a large number of spatulate-shaped spines, parted in the middle and slightly splayed out sideways [9]. It has often been stated that the plastron and the large spatulate spines are the main locomotory structure [5, 9]. The exact motion of these spines, however, is difficult to observe since these urchins live in the sediment. Other spine types provide protective [4], supportive [6], or excavating functions.

Gibbs [4] studied *Brisaster latifrons* in detail, with emphasis on its general biology, test and tube feet morphology,

and the respiratory current. Very little has been published, however, on the functional morphology of spatangoid urchin spines as it pertains to within-sediment locomotion. Consequently, for *B. fragilis*, there is no published information on the specific morphology, motion, and function of spines involved in locomotion. Yet, this is one of the top bioturbating species in the sediments of the St. Lawrence deep-water maritime ecosystem (J.-M. Gagnon, personal observation). Therefore, the aim of the present study is to describe the morphology of spines for *B. fragilis* in the context of locomotion within fine sediments. In particular, we examine the specific function of the spatulate spines found on the plastron and those located in the anterolateral portion of the test, which appear to be specifically involved with digging. Earlier laboratory observations (J.-M. Gagnon, personal observation) suggested that the spatulate spines of *B. fragilis* serve a largely supportive role while the anterior spines play more of an excavatory function. The structure of spine tubercles also plays a role in the movement of spines [10]. In the present study, we specifically compare the tubercles of the plastron and the anterior and anterolateral regions between the two *Brisaster* species. We hypothesize that the latter spines dislodge the sediment away from the front of the animal and that the plastron spines support (i.e., lift) and help move the urchin forward to fill the excavated space. Test and spine morphology are also compared between *B. fragilis* and *B. latifrons*, with reference to Gibbs [4].

## 2. Materials and Methods

Specimens of *Brisaster fragilis* were obtained from the Invertebrate Collection at the Canadian Museum of Nature (CMN; 466–700 m depth on the Labrador Shelf, 620 m depth off south Nova Scotia Shelf, and 146 m depth in southwest Bay of Fundy), from Dr. Pierre Brunel's Marine Invertebrate Collection (Université de Montréal; 329–355 m depth in Lower St. Lawrence Estuary), and from a 2013 benthic survey conducted by Fisheries and Oceans Canada in the northern part of the Gulf of St. Lawrence (148–343 m depth range). Specimens of *B. latifrons*, also from the CMN Collection, were collected on La Pérouse Bank and Barkley Sound (90–100 m depth off Vancouver Island) and off north Queen Charlotte Islands. With few exceptions, specimens were preserved in 70% ethanol. Seven specimens of *B. fragilis* and one specimen of *B. latifrons* were examined and photographed for this study.

Fluid-preserved specimens were observed under an Olympus SZX12 dissecting microscope equipped with a PixeLINK camera. Images were captured and stacked using the PixeLINK  $\mu$ Scope Professional Software. Spines from the different regions of the urchin tests were compared for both species to assess differences in morphology. Dry specimens were used for high magnification images of spines and tubercles in the anterior, anterolateral, dorsal, and plastron regions. These images were obtained using a Philips XL30ESEM Scanning Electron Microscope (SEM). No coating was applied to the specimens prior to SEM; in one instance, soft tissues were removed using a low-concentration peroxide/HCl treatment.

A time-lapsed video of one individual *Brisaster fragilis* (length = 3.75 cm, width = 3.4 cm, and height = 2.0 cm) burrowing at 10 cm depth near the glass wall of an aquarium during mesocosm experiments [11] was analysed; it showed *in situ* movement of the spines in the anterolateral portion of the urchin during a period of 12 hours (1 frame per second). Images were captured at 3-minute intervals in order to quantify and characterise the movement of the specimen through the sediment. These stills were used to estimate the speed and angle of movement of the specimen. They were then compared with corresponding video segments to describe *in situ* spine motion. Stills were also related to spine morphology to describe how they affect locomotion through the sediment. Finally, sediment displacement rate ( $R$ ) was estimated by calculating the surface-area ( $A$ ) of the urchin's cross-section at its widest point, considered here as an ellipsoid ( $A = \pi wh/4$ , where  $w$  is the width and  $h$  is the height), multiplied by the net horizontal movement of the urchin ( $H$ ), and divided by duration in time ( $T$ ) for that horizontal movement; that is,  $R = \pi whH/4T$ .

## 3. Results

**3.1. Preserved Specimen Observations.** Some important differences were found between *Brisaster fragilis* and *B. latifrons* in terms of test shape, plastron size, and the curvature of anterior spines. The lateral profile of *Brisaster fragilis* shows a more truncated posterior end (Figure 1(f)) than for *B. latifrons* (Figure 1(i)). On the dorsal side, the two posterior ambulacra (I and V) of *B. fragilis* are shorter (Figures 1(a) and 1(d)), not reaching as far back as those of *B. latifrons* (Figure 1(g)). On the ventral side of the latter species, the plastron is also wider (Figures 1(b), 1(e), and 1(h)). The ratio of plastron width in the midsection against the maximum specimen width shows little overlap (Figure 2), with only one specimen of *B. fragilis* from the Gulf of St. Lawrence displaying a relatively broad plastron. While the plastron width is significantly different, the average number of spines across the midsection of the plastron is only slightly lower in *B. fragilis* (Figure 2) and not significantly different (one-tail  $t$ -test,  $t = -1.46$ ,  $N = 38$ ,  $df = 30$ , and  $P > 0.077$ ).

Spatulate spines point mostly towards the anterior end, almost resting flat on the plastron when the animal is in the preserved state (Figures 1(b) and 1(h)). Some of the longest spines actually extend well beyond the mouth and can almost reach the anterior end of the test. Near the posterior end of the plastron, however, the spatulate spines are much shorter and radiate out in all directions (Figure 1(b)). The shape of spatulate spines is very similar for both species, with a nearly straight shaft and a broad, paddle-like distal end (Figure 3), which is often bent slightly toward the animal (Figures 3(b) and 3(d)). Some of the largest spatulate spines also display a spoon-like concavity in the broad distal end, hence their resemblance to a wooden spatula.

Plastron tubercles are also similar for both species of *Brisaster*. They are slightly tilted forward in position, with the areole enlarged in the direction opposite to the orientation of the spine (Figures 4(a) and 4(b)), where the bulk of spine

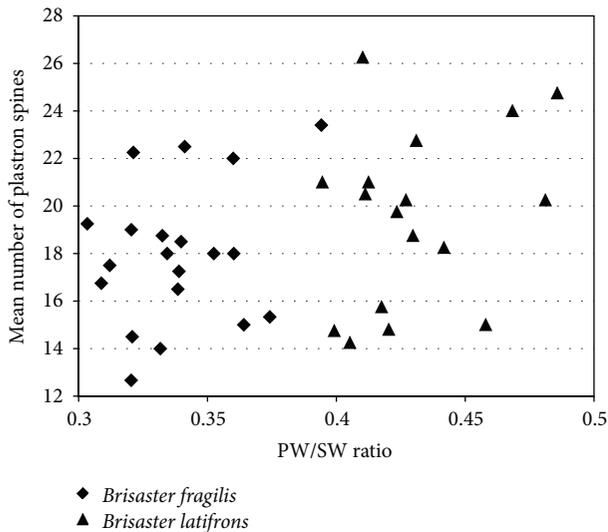


FIGURE 2: Comparison of the mean number of plastron spines (across midsection of plastron) against the ratio of plastron width (PW, at midsection) over the maximum specimen width (SW).

muscle fibres attach. The crenulated area of the platform (Figures 4(a) and 4(b)) is also more developed on the side opposite to the orientation of the spine, with a smoother or sometimes reduced area under the spine. The tubercle mamelon is raised above the platform, with a slightly eccentric, elongated (oval) perforation. The major axis of the latter is oriented in the direction of the spine (Figures 4(a) and 4(b)). A ligament located in the mamelon perforation and attached to the base of the spine prevents the latter from becoming dislocated, especially in oblique position [10].

Anterior and anterolateral tubercles do not have an areole as distinctly enlarged as those associated with plastron spines (Figures 4(c) and 4(d)). The mamelon is also raised with a perforation, but the latter is almost circular (Figure 4(d)). The crenulation is more symmetrically distributed around the platform and slightly more developed than that of the plastron tubercles, with some of the nodules enlarged and forming small ridges (Figure 4(d)).

The anterior spines in *Brisaster fragilis* have a distinctive sigmoid curvature (Figure 5) while spines located on the anterolateral and dorsal regions are curvilinear (Figure 6). In *B. latifrons*, however, anterior spines are curvilinear in shape, similar to its anterolateral and dorsal spines and those of *B. fragilis*. The shaft of the curvilinear spines is not completely round in cross-section but somewhat oval and usually tapers into a slightly flattened tip (see Figure 6 for *B. fragilis*). Many of the curvilinear spines on the dorsal side, except those covering the anterior ambulacrum (III), gradually broaden and flatten distally (Figure 7). In extreme cases, these resemble the spatulate spines of the plastron, albeit never as long or as broad at the tip.

**3.2. Video Observations.** The time-lapse video of *Brisaster fragilis* traveling along the glass wall of an aquarium (Figure 8, see insert) displayed only the anterolateral region

of the specimen. No respiratory or sanitary funnels were visible. For the most part, the urchin moved horizontally, with some vertical movements, forming a slight “dip” that levels out halfway along its path (Figure 8). Occasionally, the specimen moved backwards. A speed of  $0.22 \text{ cm hr}^{-1}$  is estimated based on the overall forward movement of the specimen over a period of 8.75 hours. Sediment displacement rate ( $R$ ), based on specimen size (width = 3.4 cm, height = 2.0 cm) and observed movement, is estimated at  $1.1 \text{ cm}^3$  of sediment per hour.

The anterolateral spines were observed to be actively digging away at the sediment in front of and beside the urchin, moving back and forth while displacing sediment (Figure 8, see insert). These spines specifically moved sediment around the anterolateral region of the urchin by scraping sediment particles (or lumps of sediment) from the front of the burrow and pushing them laterally and under the urchin. This front to back movement of individual spines is also accompanied by sideways movement, which seemingly assists in dislodging sediments.

The plastron spines were not observable on the video. Their general movement, however, was assessed based on the fact that there was a visible space created under the urchin as a result of the specimen being lifted upward by those spatulate spines (see insert in Figure 8). No other spines serve such a function. The maximum observed vertical displacements during the 3-minute and 6-minute intervals were 2.2 mm and 3.0 mm, respectively. The specimen maintained its horizontal position, never orienting itself obliquely.

## 4. Discussion

Locomotion of spatangoid urchins in unconsolidated sediments is achieved through the division of labour amongst different groups of spines [5]. In the genus *Brisaster*, spines from several distinct areas are involved in locomotion: the spatulate spines of the plastron, which lift the test; the “spatulated” curvilinear spines of the dorsal region, which support the surrounding sediment; the curvilinear (for *B. latifrons*) or sigmoid (for *B. fragilis*) spines of the anterior region, which are used for excavating; and the curvilinear spines of anterolateral regions, which also assist in dislodging the sediment and moving it laterally and ventrally.

Based on preserved specimens and the video examined in this study, differences in the anterior spine morphology suggest distinct spine functions between *Brisaster fragilis* and *B. latifrons*. Kanazawa [6] describes anterior spines of *B. latifrons* as morphologically indistinct from the dorsal spines. However, *B. fragilis* has sigmoid-shaped anterior spines (Figure 5) whereas its dorsal and lateral spines are curvilinear. These anterior spines, along with the anterolateral spines, appear to be mostly responsible for digging forward. These sigmoid-shaped spines may be more efficient in digging forward, although there are no observations from this study to confirm it. In the video, curvilinear spines of the anterolateral region were seen actively digging away at the sediment but also moving dislodged sediment from the front to the side and under the animal. The shape of spine

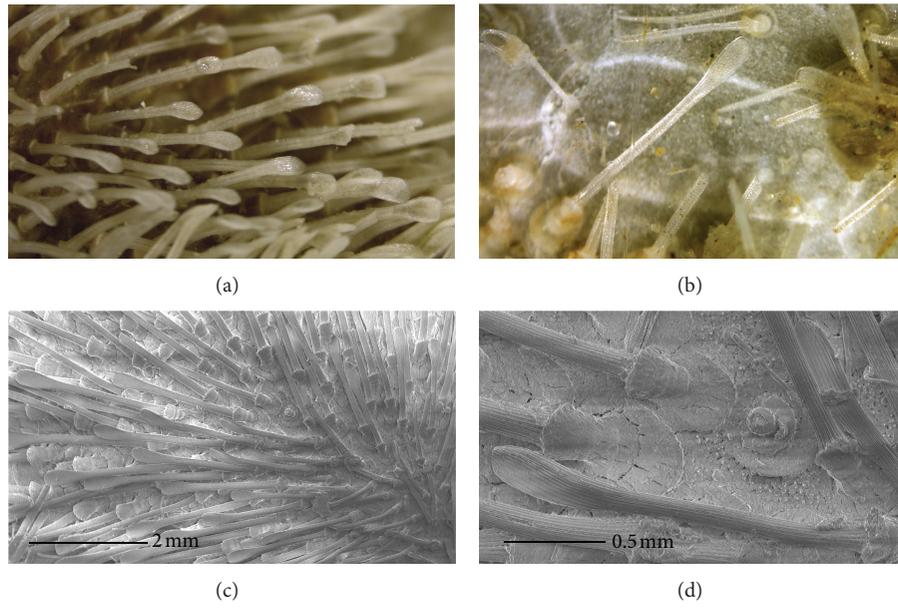


FIGURE 3: Plastron spines of *Brisaster fragilis*. ((a) and (b)) Stereomicroscope images; ((c) and (d)) SEM micrographs; ((a) and (c)) mid-section view showing the fan-like arrangement of spines; ((b) and (d)) close-up view of spatulate spines and tubercles.

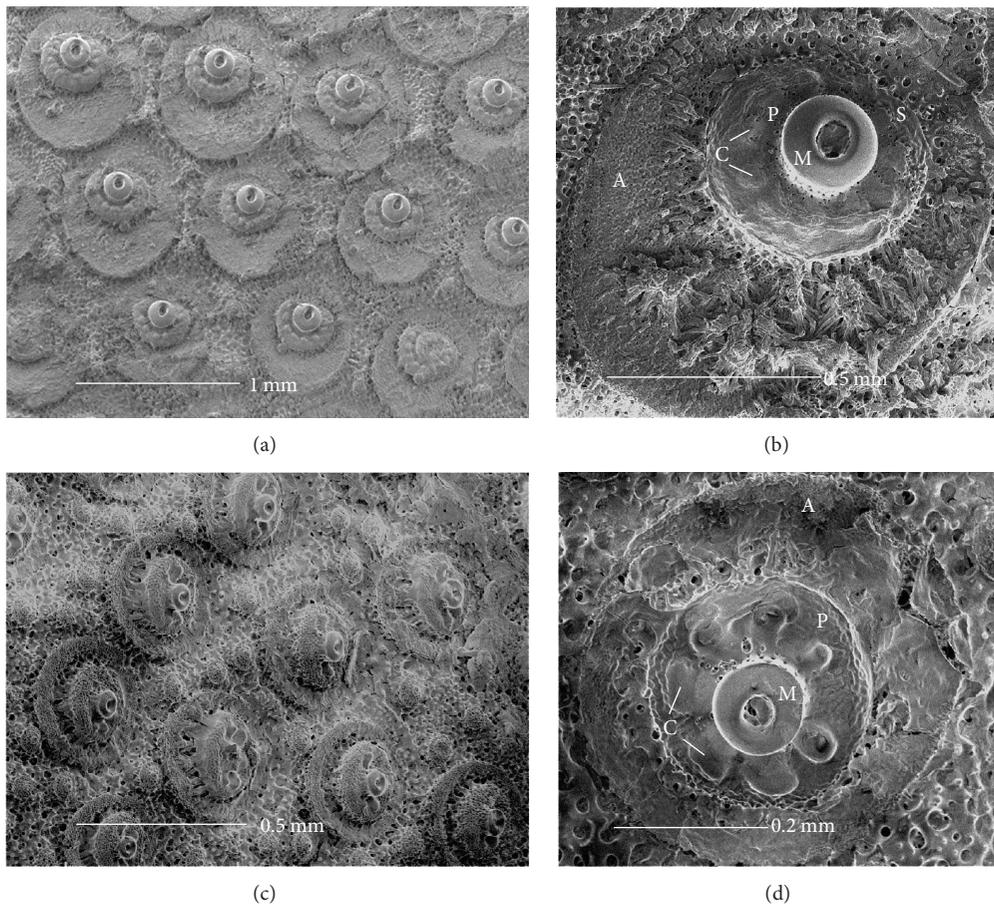


FIGURE 4: Scanning electron micrographs of spine tubercles of *Brisaster fragilis*. ((a) and (b)) Plastron tubercles; ((c) and (d)) anterior tubercles. A: areole; C: nodules of the crenulation; M: mamelon; P: platform; S: smooth area of platform.

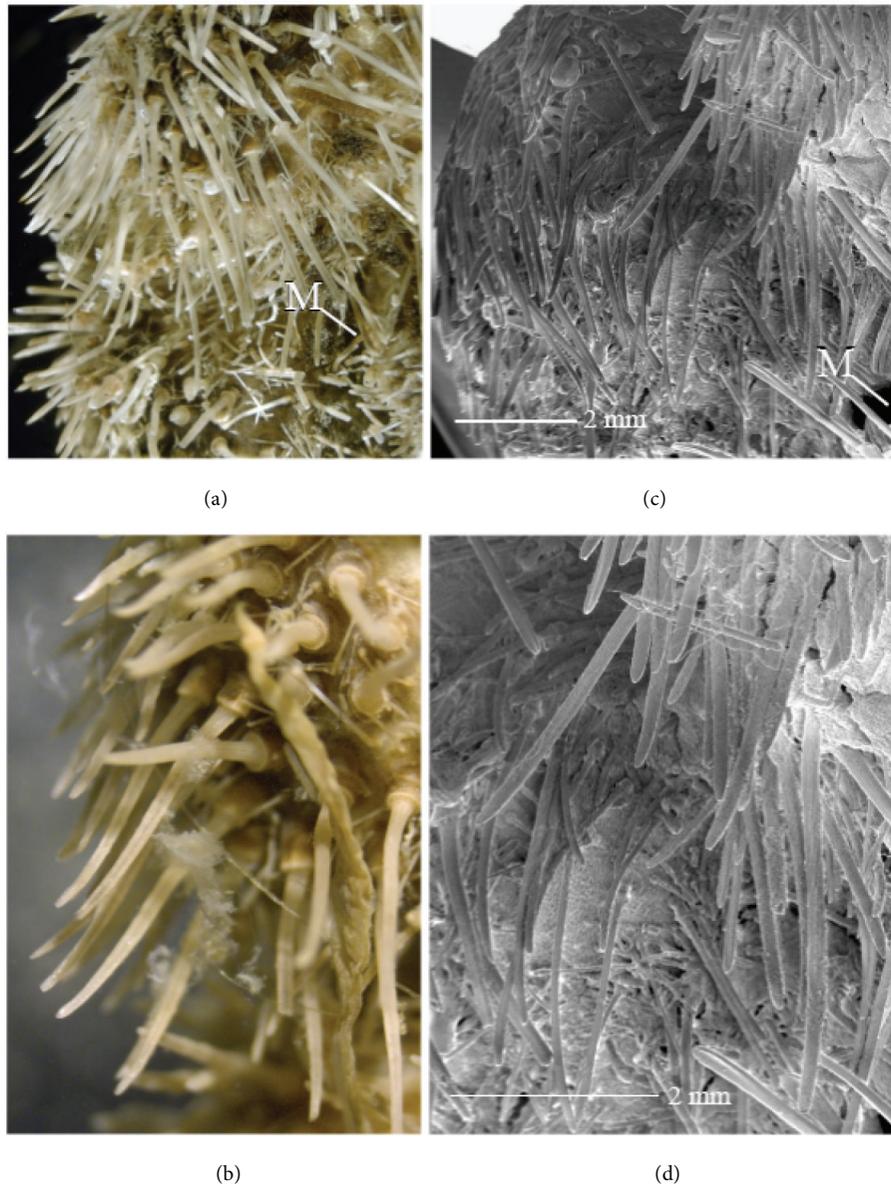


FIGURE 5: Anterior spines of *B. fragilis*. ((a) and (b)) Stereomicroscope photographs; ((c) and (d)) SEM micrographs. M: mouth.

tubercles in the anterior and anterolateral regions is similar and mostly symmetrical (Figures 4(c) and 4(d)), supporting the observations that while these spines are typically oriented downward, their motion tends to be in all directions when digging.

Gibbs [4] indicates that the dorsal spines are small and flattened in *Brisaster latifrons*. Smith [10] refers to these as spatulate, although they are still curvilinear and do not have as distinctive a tip as the plastron spines. Kanazawa [8] describes these as supportive spines which serve to maintain the ceiling of the burrow for the globular type urchins. Kanazawa [6] states that “The dense dorsal spines provide a canopy which supports and maintains the ceiling and walls of the burrow. The dorsal side always bears the load of the overlying sediment, so that this function is probably

significant. The backwards inclination of the dorsal spines is significant to support the burrow without interfering with forward locomotion.” These supportive spines appear to be similar between *Brisaster fragilis* and *B. latifrons* and probably play a similar role as that described for the globular type urchins.

In addition to the difference in spine morphology observed for the anterior region of *Brisaster fragilis*, this species has a reduced plastron size. However, the spatulate spines and their tubercles are morphologically similar and their numbers appear to be comparable for both species of *Brisaster* (at least in the middle and anterior portions of the plastron). The narrower plastron surface of *B. fragilis* suggests a different role in locomotion, perhaps due to reduced leverage.

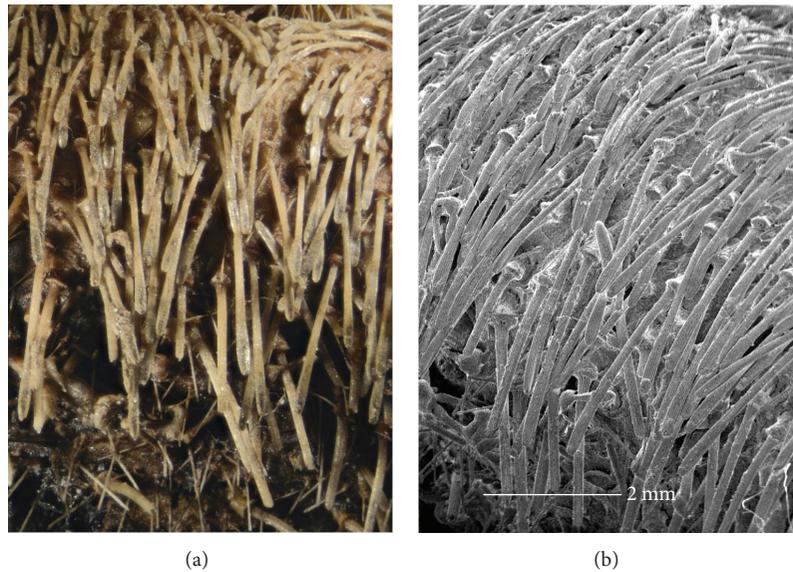


FIGURE 6: Anterolateral spines of *Brisaster fragilis*. (a) Stereomicroscope photograph; (b) SEM micrograph of the same area.

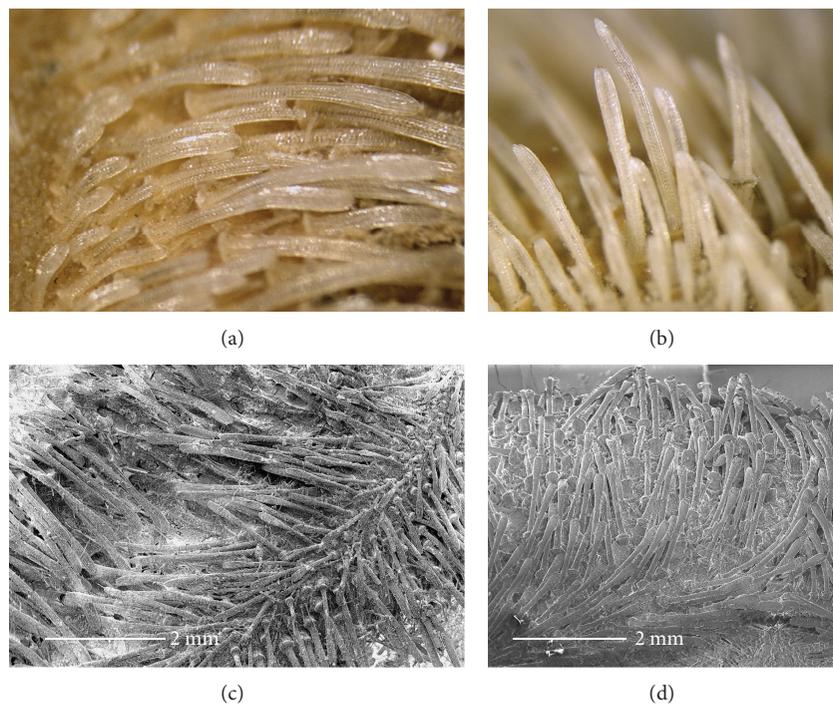


FIGURE 7: Dorsal supportive spines of *Brisaster fragilis*. ((a) and (b)) Stereomicroscope photograph; ((c) and (d)) SEM micrographs.

Nichols [9] and Smith [5] describe the plastron as the main locomotory organ. This does not appear to be the case for *B. fragilis*. In the video, the spatulate spines could not be observed directly but their actions can be inferred based on the space created beneath the urchin and the actual observed movement. It appears that these spines serve more of a supportive role, keeping a relatively constant space under the urchin, rather than the “ramming” role described by Kanazawa [6, 8] for *B. latifrons*.

Kanazawa [6, 8] describes the oblique movement of *Brisaster latifrons*, allowing it to ram through the sediment; it is referred to as the rocking motion. However, the forward movement of *B. fragilis* observed in the video was noticeably different from the up and down rocking motion reported for *B. latifrons*. As indicated earlier, this may be due to the reduced plastron leverage in the former species. Instead, *B. fragilis* uses more of a “dig and move” technique: it scrapes sediment from the front of the burrow with its anterior and

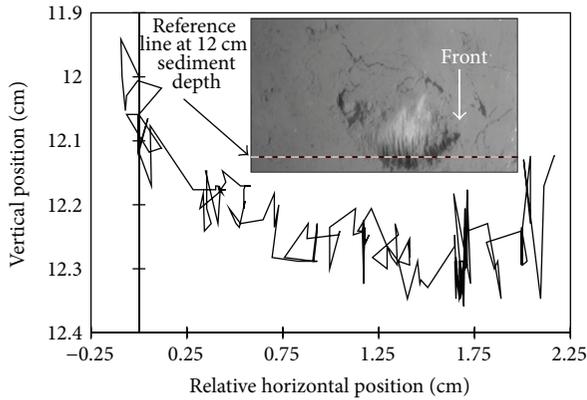


FIGURE 8: Movements of *Brisaster fragilis* during 8.75 hours of video observations against the side glass of an aquarium. Insert shows an example of captured video image.

anterolateral spines and moves it around and under itself before being able to move forward by the limited thrust of the plastron spines.

When analysing the video (Figure 8), the specimen travelled primarily horizontally, with some limited vertical movement (about an order of magnitude smaller than horizontally), but rarely shifted obliquely. These relatively small movements suggest that, unlike *Brisaster latifrons*, *B. fragilis* does not assume the 30° oblique posture described by Kanazawa [6, 8]. Also, that oblique motion in *B. latifrons* repeats itself every 3–5 minutes; such a motion was not observed in the 12 hr video for *B. fragilis*. This suggests that the generalization proposed by Kanazawa [6, 8] based on wedge-shaped tests does not apply to *B. fragilis*. Instead, the latter moves in a fashion similar to what Kanazawa describes for globular type urchins.

The average speed of the specimen ( $0.22 \text{ cm hr}^{-1}$  under 10 cm of mud) is much slower than that observed for *Brisaster latifrons* (a few centimetres per hour [6, 8]) and only slightly slower than that of *Brissopsis lyrifera* ( $0.3\text{--}0.4 \text{ cm hr}^{-1}$  [7]). However, the specimens observed by Kanazawa [6, 8] and Hollertz and Duchêne [7] were under much less sediment (2–5 cm and 2 cm, resp.), although depths reaching 15 cm have been reported for *B. latifrons* [12]. The calculated sediment displacement rate ( $R = 1.1 \text{ cm}^3 \text{ hr}^{-1}$ ) for the specimen observed in the video is also much less than the range of values reported by Hollertz and Duchêne [7] for *Brissopsis* ( $14\text{--}22 \text{ cm}^3 \text{ hr}^{-1}$ ,  $N = 24$ ; mean specimen width = 4.2 cm, mean specimen height = 2.8 cm).

The difference in depth and consequently the greater weight of sediment over *B. fragilis* could contribute to the more horizontal “dig and move” motion as opposed to the “ramming” mechanism described for *B. latifrons*. This increased sediment weight may make it more difficult for the plastron spines to lift the urchin repeatedly, which would be required to achieve Kanazawa’s rocking motion. Here, it is possible that the smaller plastron of *B. fragilis* significantly reduces the ability to lift the test with enough force to achieve the rocking motion. Smith [5] states that the wedge-shaped

profile is more effective in soft mud than coarser sediments. However, the rocking motion associated with that shape by Kanazawa [6, 8] may not apply to all species with that profile or may vary depending on the burrowing depth. Admittedly, a sample size of one specimen for video observation, which is comparable to what Kanazawa based his conclusions on for *B. latifrons*, is limiting. However, in the case of *B. fragilis*, the morphological features observed on preserved specimens, particularly the shape of the anterior spines and the size of the plastron, appear to support the conclusions drawn from the video, at least for specimens buried below 10 cm of sediment.

## 5. Conclusion

The sigmoid curvature of the anterior spines in *Brisaster fragilis*, compared to the curvilinear shape of those of *B. latifrons*, may have a significant impact on how these species of urchins dig in fine sediments. While the oblique rocking motion reported for the latter species requires a substantial contribution of the spatulate spines of the plastron in lifting the animal obliquely, the “dig and move” technique observed for *B. fragilis* appears to shift more of the digging effort to the anterior spines. The difference in plastron size (while seemingly maintaining a similar number of spatulate spines) is thought to contribute to this variation in locomotion; while *B. latifrons* uses its broader plastron to push itself up and forward and then uses its anterior spines to excavate downwards, *B. fragilis* uses its anterior spines to “dig” forward at the sediment and then uses its plastron spines to “move” into the newly created space.

The structure of the tubercles for both species is consistent with the rotational movement of the anterior and anterolateral spines and the up-down movement and forward orientation of the plastron spines. The lower sediment displacement and speed for *B. fragilis*, when compared to other irregular urchins, may be due in part to the greater burrowing depth. This study suggests that generalizations derived from observations based on one or few species displaying similar body shapes may not be entirely sound. In fact, factors such as sediment depth (i.e., the amount of sediment above the urchin) are likely to affect movement and force the animal to employ a different digging strategy, even within a single species. Further observation and experimentation are required to confirm the digging strategy and biomechanical advantage of anterior sigmoid spines in the locomotion of *B. fragilis*.

## Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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