

Adaptive evolution in spatangoid echinoids living in the shallow sublittoral zone

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General introduction

Spatangoid echinoids appeared in the Early Cretaceous and made dynamic diversification during the Eocene. Today, they live in a variety of substrate and there are a lot of fossil records. Spatangoid echinoids, therefore, are good materials suitable for studying long-term, continuous evolution. However, surprisingly little is known about their ecology; though some species have been intensively studied, each study dealt with one species, and the ecological data were taken only from the area in which the target echinoid lived and not from the surrounding area. There has been no comprehensive ecological study on several spatangoids, which live in an area, and thus it is still difficult to judge the factors that define the inhabitation of the spatangoids. In this study, several spatangoid species living in an area are investigated, and the ecological knowledge obtained from the Recent spatangoids enables to study the adaptive evolution in spatangoid echinoids. In geologic time spatangoid echinoids are known to have suffered high levels of predation from cassid gastropods because there are many fossils of echinoid tests with predatory holes presumably produced by the gastropods. McNamara (1994) demonstrated that from late Oligocene to Early Miocene in Australia many spatangoids suffered quite high levels of predation from cassid gastropods, and thereby the successive species migrated into the regions of lower predation pressure. Kanazawa (2004) indicated that the morphological diversification which occurred in spatangoids in the Eocene was presumably brought about by cassid predation because the new types of morphology apparently enable the spatangoids to escape from the predators. These studies imply that cassid predation was an important factor which controlled the adaptation of spatangoids. There is, however, no other comparable study that showed the impact of gastropod predation on evolution of spatangoids. To be able to assess the significance of cassid predation, it is necessary to know the mode of cassid predation on spatangoids. With the information obtained from these different sources a possible adaptive significance can be ascribed to the evolution of spatangoid echinoids in the Cenozoic.

Material and methods

Field investigations for 6 spatangoid species, *Lovenia elongata* (Gray), *Nacosptangus alta* (A. Agassiz), *Metalia spatagus* (Linnaeus), *Brissus agassizii* Döderlein, *Echinocardium cordatum* (Pennant) and *Moira lachesinella* Mortensen, were carried out in the Oki-Islands in the Japan Sea between November 2007 and July 2013. The helmet snail, *Cassid cornuta*, was observed in its habitat on sea floor at depths of 3-22 m in Oura Bay, Okinawa, Japan in May 2009. The animals

used for aquarium experiments were transported to the laboratory of Kanagawa University with a cooler-box and immediately placed in a marine aquarium with circulating sea water.

Adaptation for living in the shallow sublittoral zone in spatangoid echinoids

Adaptive morphologies to the shallow sublittoral zone: The shallow sublittoral zone is very unstable environment, the sea floor being often disturbed by water currents. *L. elongata* has specific morphologies for quick burrowing and rapid righting, with which it probably burrows deeper before it is washed-out by currents, and even if washed out, it could rapidly right and re-burrow in storm disturbance. The animal, thus, would survive, though it burrows just below the unstable sand surface. *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. Since *M. spatangoid* and *B. agassizii* burrow 10-15 cm deep below the sediment surface, they can usually avoid being washed out to death in storm disturbance. *N. alta* has no specific morphology against water disturbance in spite of its burrowing in the unstable surface layer of sediment.

Life history corresponding to habitat-stability: In the shallow sublittoral zone the spatangoid echinoids apparently have different kinds of life histories corresponding to the condition of the respective habitats (Fig.1). In *N. alta* that lives in unstable surface sediment, it grows rapidly and reaches sexual maturity early, but the life span is short. In contrast, *M. spatagus* and *B. agassizii* that live deep in the sediment in relatively stable condition grow slowly and reach sexual maturity late, and the life span is long. Accordingly, the spatangoids living in unstable environments have

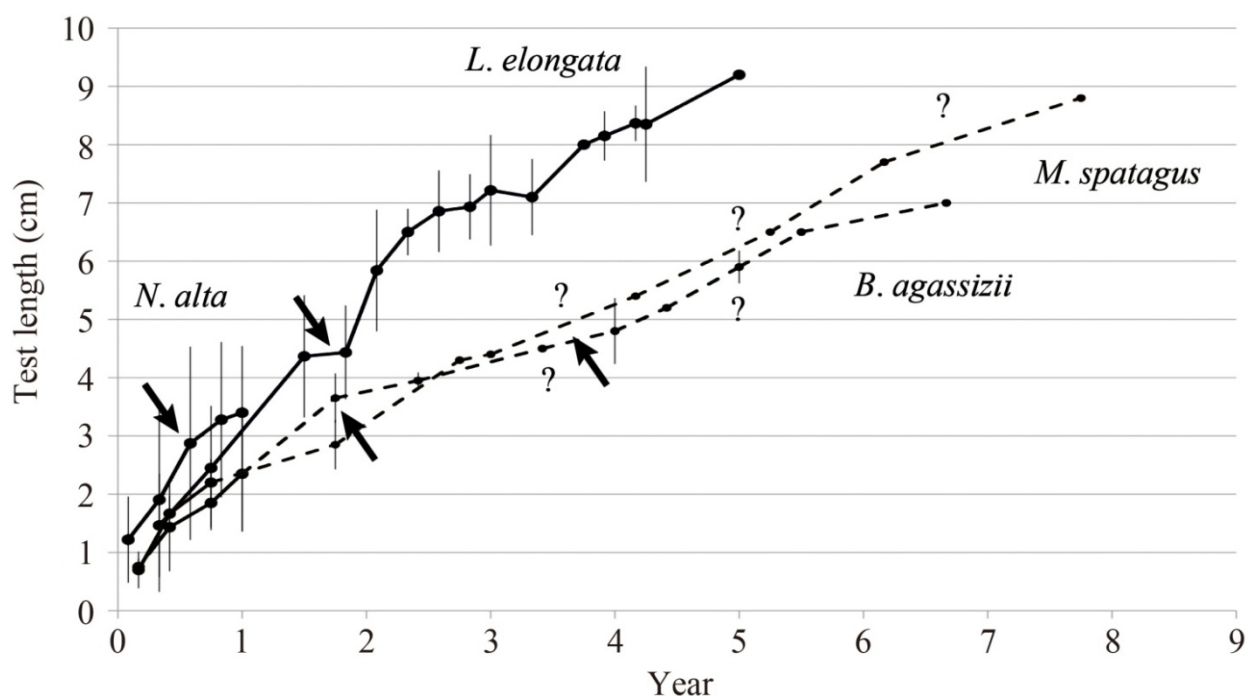


Fig. 1. Growth rate, sexual maturity and life span of four spatangoid species. A solid line shows the growth curves based on an identical cohort, a dotted line shows the growth curves based on some mixed cohorts and an arrow indicates the timing of first sexual maturity.

rapid alternation of generations, and those living in stable environments have slow alternation of generations. This principle, however, is not applicable to *L. elongata*. In unstable environment, the animal grows rapidly, but its sexual maturity is not early and the life span is long. The contradiction is explainable from its surprising ability of survive in water disturbance by virtue of the specific morphologies for quick burrowing and rapid righting.

Trade-off and life history: It is quite interesting that *N. alta* reaches sexual maturity earliest at one year in addition to the fastest growth rate of test length among the four spatangoid echinoids. Its habitat, nutrient-rich surface sediment, probably enables the echinoid to have the life style. It should be, however, noted that *N. alta* construct the test with very thin plates, whereby the echinoid can reduce the cost of test construction and allocates more energy to the development of the gonads. It must be essential for *N. alta* to reach sexual maturity earlier to spawn within 1 year, because it has no specific morphology against storm disturbance. This is understandable by contrast with *L. elongata*, another spatangoid living near the nutrient-rich sediment surface with a similar fast growth rate of test length. *L. elongata* constructs the test with thicker plates on which stout, longer spines supported by thicker muscles occur, and it reaches sexual maturity at two years. In this sea urchin, the energies derived from nutrients should be first allocated to the construction of the rigid test with the stout long spines by which it can survive in storm disturbance. In *L. elongata* the gonad develops in accordance with a marked decrease in growth rate of the test. It seems, therefore, inevitable that the energies are not allocated to the gonad until the second year when the sea urchin possesses the specific morphology against storm disturbance. Owing to the specific morphology, *L. elongata* is able to live several years, resulting in several times of spawning in a life span. In *M. spatagus* and *B. agassizii* living in nutrient-poor environment, the growth rates of the test length are low and the gonads need more than 2 years to begin to develop. They, however, possess more phyllodal tube feet which enable them to obtain more nutrients, and they form more rigid tests with thicker plates than *N. alta*. They undoubtedly allocate the energies not to the gonad development but to the test growth first. This is possible because these spatangoids burrow deeply in sediment where they can avoid storm disturbance and have the long life span as a result. In the safe place deep in sediment, on the other hand, the pressure from surrounding sand is relatively high, so that the spatangoids must resist the high pressure under which they excavate and transport sediment to move. Therefore, the deep-burrowing spatangoids should allocate the energies first to forming the rigid tests with the thick plates on which the spines playing those roles under high pressure.

Prey-predator relationship between spatangoids and cassids

The aquarium observation on *Cassid cornuta* suggests that the large helmet snail must be a lethal predator for most spatangoid echinoids, because the predator can seek out the echinoids burrowing in sediment and prey on them. Surprisingly, even *L. elongata* which can probably move most

powerfully and rapidly among spatangoids was easily preyed by the predator. It should be noted that the individuals of *L. elongata* preyed by the cassid were all smaller than 7 cm in test length, suggesting that they cannot escape from the predation if the cassid is more than 2.5 times larger than them. The cassid preys on the urchins by mounting and clasping it with the foot, so that the

Table 1. The result of the feeding behavior of *C. cornuta* to *L. elongata*

Individual number (Test length)	Result	Behavior of <i>C. cornuta</i>
1. (5.3 cm)	Preyed	Toward the posterior of the prey and covered it completely
2. (5.4 cm)	Preyed	Toward the left side of the prey and covered it completely
3. (5.5 cm)	Preyed	Toward the right side of the prey and covered it completely
4. (5.8 cm)	Preyed	Toward the right side of the prey and covered it completely
5. (6.0 cm)	Preyed	Toward the posterior of the prey and covered it completely
6. (6.5 cm)	Preyed	Toward the right side of the prey and covered it completely
7. (7.1 cm)	Run away by escaping to sediment surface	Toward the right side of the prey and just touched it
8. (7.5 cm)	Preyed	Toward the posterior of the prey and covered it completely
9. (8.5 cm)	Run away by escaping to sediment surface	Toward the posterior of the prey and just touched it

body size, especially the shell weight and the foot size must be important to make a success of the predation. In the case that *L. elongata* survived the cassid predation, it showed the amazing escape owing to the specific morphologies; while the long, stout dorsal spines pushed up the overlying foot of the gastropod to avoid its clasp, the long, stout latero-ventral spines thrust the echinoid powerfully and quickly onto the sediment surface. These morphologies are, therefore, undoubtedly essential to escape from the cassid predation. In the experiments on burrowing depth in search of prey, the cassid could not find out the prey in the case that the prey was buried 18 cm deep in fine-grained sand. Since most spatangoids cannot burrow to such a depth, it seems difficult for them to survive the cassid predation. However, to burrow deeply to escape from the predation might be a possible strategy, if the cassid would be much smaller in size and could not burrow deeply. According to fossil records the first certain cassid gastropod appeared in the tropical region in Eocene, and interestingly, in the same epoch *Lovenia* and *Brissus* also appeared for the first time in the same region (Fischer 1966). It is noteworthy that *Lovenia*, *Brissus* and cassids had almost the same small size 3-4 cm in length in Eocene. With the small difference in body size *Lovenia* could easily survive the cassid predation because the anti-predatory behavior brought about by the specific morphologies must have been effective enough to escape from the predator, as indicated by the aquarium experiments. This implies that the specific morphologies of *L. elongata* would originally have developed as an anti-predation device. The same could be said for the oval test with specific ventral morphology for efficient burrowing in *Brissus*. It should be paid attention that in the Eocene the specific morphologies convergently appeared in different spatangoid lineages, which fact indicates that a common functional significance can be ascribed to the appearance of the morphologies. Like many other large species of Genus *Cassis*, the oldest fossil of *Cassis cornuta* is known from the Miocene, and the shell was about 20 cm in length. In *Lovenia elongata*, the oldest fossil is also known from the Miocene, and the test was about 5 cm in length (Kier 1972), which

was the largest size in *Lovenia* lineage since its appearance in Eocene. *Brissus* also had attained to the largest size in the Miocene since its appearance, but still about 5 cm in length (Kier 1972). The 4 times difference in body size indicates that it was most likely difficult for *Lovenia* and *Brissus* to live together with the cassid. In the Recent *C. cornuta* is the largest helmet snail and attains 36 cm in length. *L. elongata* also reaches the largest size about 12 cm in the Recent. If the urchin would be attacked by the cassid, it probably has no chance to escape. In the Recent sea, therefore, these animals could not live together in the same region. McNamara (1994) demonstrated that in *Lovenia* lineage high levels of predation from cassid gastropods resulted in evolution of the successive species from shallow to deep water habitats. It, therefore, seems possible that the descendant species also evolved into the very shallow sublittoral zone and temperate zone which were region of no predation pressure.

Conclusions

According to fossil records, the first spatangoid echinoid appeared in the Early Cretaceous. During the time of Cretaceous spatangids had small tests with less diversified morphology (Fischer 1966) and seems to have lived only in stable environments below the extent of water turbulence, burrowing shallowly in the sediment or crawling on the surface. In the Eocene, however, new types of test morphology related to new modes of life suddenly and convergently appeared in the spatangoids which inhabited sandy bottoms in the shallow sublittoral zone in tropical and subtropical regions. This morphological change was probably induced by predation of cassid gastropods which also appeared in the same regions in the same epoch with their prey spatangoids. Flat tests with long, stout spines on the dorsal and ventral sides, as in *Lovenia*, probably enabled the urchins to escape from gastropod attack and emerge onto sediment surface. Oval tests with the specific ventral morphology for efficient burrowing, as in *Brissus*, allowed the spatangoids to burrow deeply in sand to avoid the gastropod predation. From Eocene to Miocene, these spatangoids with the new modes of life apparently struggled along with the co-existing gastropods by virtue of the attainment of large size which resulted from the co-evolution between the predator and the prey. In the Miocene, however, many of the spatangoids appear to have left their habitats so as to avoid the predators which had attained to the shell size about 4 times larger than their prey spatangoids. Accordingly, many spatangoids evolved not only into deep water environment, as McNamara (1994) suggested, but probably also into the very shallow sublittoral zone and/or into the temperate zone where the predatory cassid gastropods did not live. The morphologies for anti-predation probably enabled the sea urchins to inhabit the unstable environments of the very shallow sublittoral zone. The spatangoids, like *Brissus* and *Metalia*, with the ability for burrowing deep in sand can avoid being washed out to death in storm disturbance. In the safe habitat they could probably evolve the life history in which they grow slowly and reach sexual maturity late

with the long life span and slow alternation of generations. On the other hand, the spatangoid like *Lovenia elongata*, living near the turbulent sediment surface has specific morphologies for quick burrowing and rapid righting. In a disturbance, this urchin can burrow deeper than usual before it is washed out by currents. Even if washed out, it can rapidly right and re-burrow. In the unstable environment, the animal grows rapidly, but its sexual maturity is not early and the life span is long, because in this sea urchin, the energies derived from nutrients should be first allocated to the construction of the rigid test with the stout long spines by which it can survive in storm disturbance. In contrast to these spatangoids, *N. alta* has no specific morphology against either predation or storm disturbance, indicating that its ancestors would not have suffered cassid predation. This spatangoid, instead, adapts to the unstable environments with a specific trade-off between test growth and sexual maturity in its life history; it reduces the cost of test construction with very thin plates and allocates more energy to the development of the gonads. Consequently, *N. alta* can reach sexual maturity earlier at one year in addition to the faster rate of test growth than other spatangoids, resulting in certain alternation of generations in the unstable environment. Thus, spatangoids adapt to the shallow sublittoral zone in different ways depending on their respective evolutionary histories. The outstanding success in adaptation to the unstable environment in the extent of water turbulence would not have been achieved without predation pressure. For deposit-feeding spatangoids that inhabited calm safety environments, like those in the Cretaceous, it was presumably no use to burrow deep in sediment, where fewer nutrients are contained than near the surface, or to move rapidly, which needs much more energy than to do slowly. This is strongly suggested by the fact that the specific morphologies for these behaviors had never evolved before the Eocene while spatangoids had suffered almost no predation pressure and had stayed in the calm sublittoral zone for about 100 million years.

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