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Zoomorphology

Morphology of spines and spine joint in the crown-of-thorns starfish *Acanthaster planci* (Echinodermata, Asteroida)

Tatsuo Motokawa
Department of Biology, University of the Ryukyus, Nishihara, Okinawa, 903-01 Japan

Summary. Morphology and movement of the spines of *Acanthaster planci* were studied. All surfaces of the animal are covered with spines. The spines on the aboral surface are cylindrical with sharp tips. The spines on the oral surface are flat; they bend over to cover the mouth and the ambulacral grooves when these soft parts are stimulated. Those on the side of the animal make a barrier of crossed spines. Thus the structure and movement of the spines are well-adapted for defense.

The junction between the primary aboral spine and its pedicel makes a movable joint. The ultrastructure of the connective tissue at the joint was studied. The connective tissue is mainly composed of collagen fibers. Presumed neurosecretory cells with processes which are filled with electron-dense granules of 0.2 μm diameter were found between collagen fibers. Muscle fibers are mainly found in the connective tissue at the central holes. These observations support the view that the joint connective tissue has catch properties.

A. Introduction

Acanthaster planci is a large multi-armed starfish which feeds on corals (Fig. 1). The animal is notorious for population outbreaks which have caused serious depletion to corals on reefs in the Indo-Pacific region (Endean 1973), including Okinawa where the present study was carried out (Nishihira and Yamazato 1972; Sakai 1985). It everts its stomach onto the corals and digests and absorbs their soft parts, leaving the skeleton intact (Endean 1973). This chemical feeding method seems to have advantages over mechanical ones. The chemical digestion of soft parts is probably the most efficient method of eating animals with hard defensive structure such as corals.

One drawback is slowness: the digestion and absorption take time. *Acanthaster* is motionless for hours when feeding on corals, which grow in open places because they need light. In other words, *Acanthaster* remains exposed in the tropical shallow water where predation pressure is very high.

Acanthaster has both chemical and mechanical devices which are probably for defense. The former is saponin and the latter is spines (Hashimoto 1977; Halstead 1978). The aboral surface is covered with pointed and toxic spines, hence the common name of this starfish. Although the spines seem to play vital roles in the life of this starfish, only a short note has appeared on spine morphology (Madsen 1955). In this report I describe the structure and movement of spines. The ultrastructure of the connective tissue at the spine joint is also described. Motokawa (1982a) suggested that this connective tissue has catch properties, i.e., it changes its mechanical properties by a non-muscular mechanism (see reviews by Motokawa 1984; Wilkie 1984). No ultrasturctural study has appeared before on the catch connective tissues of asteroids.

Materials and methods

Specimens of *A. planci* (Linnaeus, 1758) were collected from the lagoon in front of the Sesoko Marine Science Center, University of the Ryukyus. The animals studied were 20–30 cm in total diameter, measured from arm tip to arm tip. They were kept at the Center in an aquarium with flowing sea water.

Gross morphology of the spines was studied in both live specimens and ones which were fixed in formalin and then dried. Paraffin sections were prepared as follows: spines were fixed in 10% neutral formalin, decalcified in 5% trichloracetic acid, cut, and stained with Masson's trichrome stain. For electronmicroscopy, the joint region of primary aboral spines was fixed for 2 h by cold 2% glutalaldehyde in 0.1 *M* cacodylate with 6% sucrose (pH 7.4). Then it was washed by the same buffer, post fixed for 2 h by cold 1% osmium tetroxide in 0.2 *M* s-collidine with 6% sucrose (pH 7.4), washed by the same buffer as in the postfixation, dehydrated in ethanol, and embedded in Epon 812 via a propylene oxide step. Ultrathin sections were made and stained with uranyl acetate and lead citrate, and observed under a Hitachi HS-9 electron microscope.

C. Results

I. Aboral surface spines

The body surface of *A. planci* is covered with thousands of spines (Fig. 1). They can be grouped into six types (Fig. 2). The number and length of the spines on an animal with a 26.0 cm diameter are as follows: primary aboral spine, 816, 16–28 mm; secondary aboral spine, 160, 7–11 mm; latero-oral spine, 256, 9–20 mm; oral spine, 2,304, 5–7 mm; circumoral spine, 224, 7–11 mm; subambulacral spine, 4,320, 1–4 mm. The spine length was measured

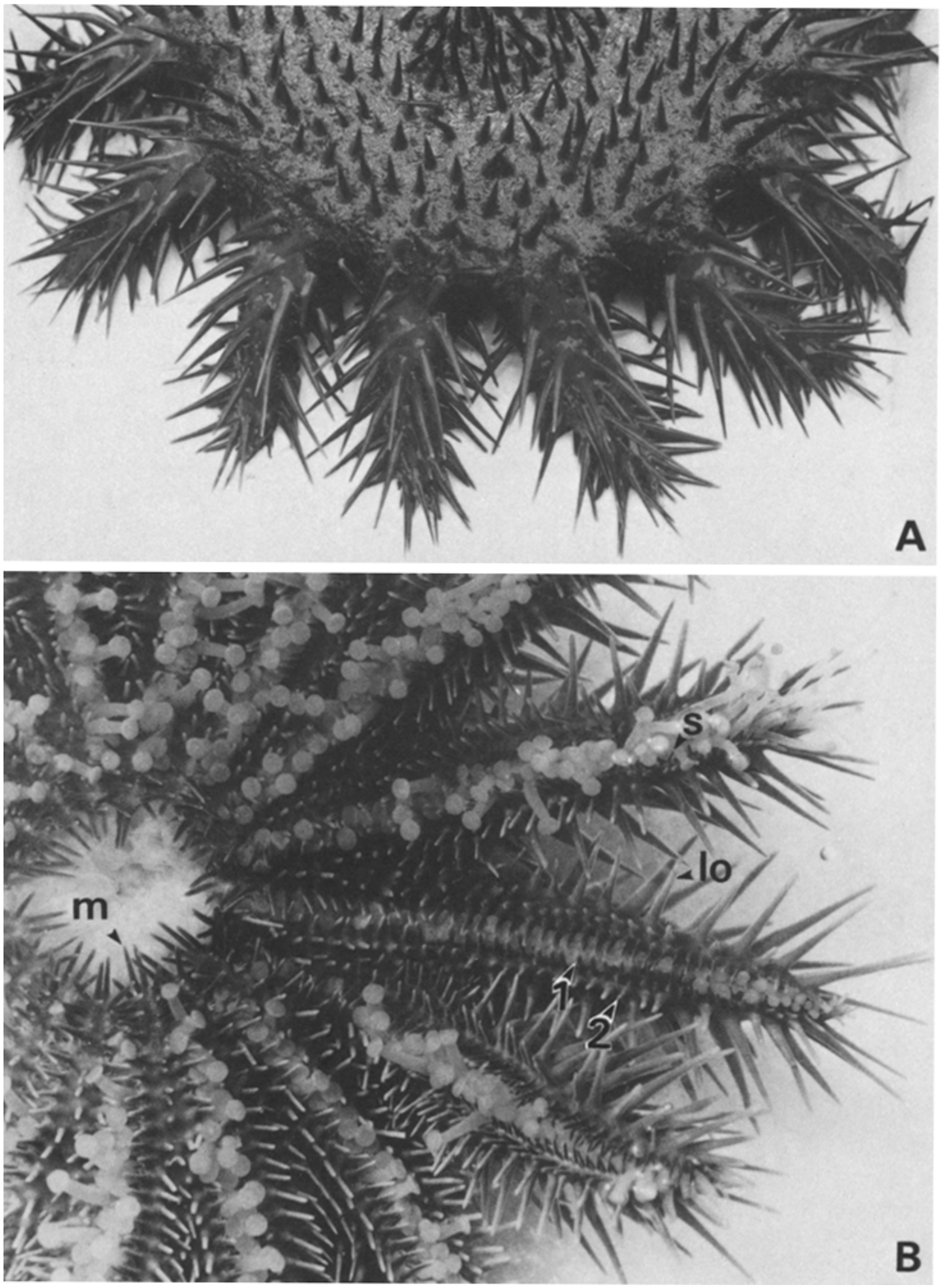

Fig. 1 A, B. Aboral view (**A**) and oral view (**B**) of *Acanthaster planci*. Aboral survace is covered with sharp-tipped spines. Notice that some are bent at the joint. Oral surface is covered with four types of spines. Mouth (*m*) is surrounded by circumoral spines (*arrowhead* beside *m*). Ambulacral groove fringed with rows of subambulacral spines (*s*), oral spines of arm (first row) (*1*), oral spines of arm (second row) (*2*) and latero-oral spines (*lo*). Notice the latero-oral spines of two adjacent arms make a barrier of crossed spines. Ambulacral groove at the 3 o'clock position partially closed; in other arms the grooves are open and tube feet extended

from the body surface to the spine tip, including the length of the pedicel. This particular animal has a total of 8,080 spines.

The primary aboral spine is the longest. It gradually tapers towards the tip, which is shaped like a triangular spear. At one corner of the triangle, the ossicle has a sharp edge like a scalpel (Fig. 3). The spine is mounted on a prominence of the body wall, called a pedicel (Fig. 4), which acts in a similar way to the tubercle of other echinoderm spines. The aboral body wall of the starfish has a reticulate endoskeleton. The pedicels are found on this framework, usually at the crossings of the framework ossicles. Both the pedicel and the polygonal plates of the framework on-which the pedicels are mounted have a flowershaped relief with a depression on each petal (Fig. 5). The pedicels on the disk stand upright whereas those on the arms incline toward the arm tip; the degree of inclination of the pedicel, and thus of the spine, increases towards the distal end. The spines on the arms are a little longer than those of the disk.

The secondary aboral spines are similar in shape to the primary aboral spines. However, their length is only about one third that of the primary spine. They are distributed only on the disk. The number of secondary spines is far smaller than that of primary ones.

II. Oral surface spines

The oral surface is covered with spines whose shape is different from that of aboral spines: the tip of an oral spine is blunt and the cross-sectional shape is flattened (Figs. 1 B, 2, 8). Spines that cover the general oral surface have a furrow on their tip; those fringing the mouth and ambulacra have no furrows.

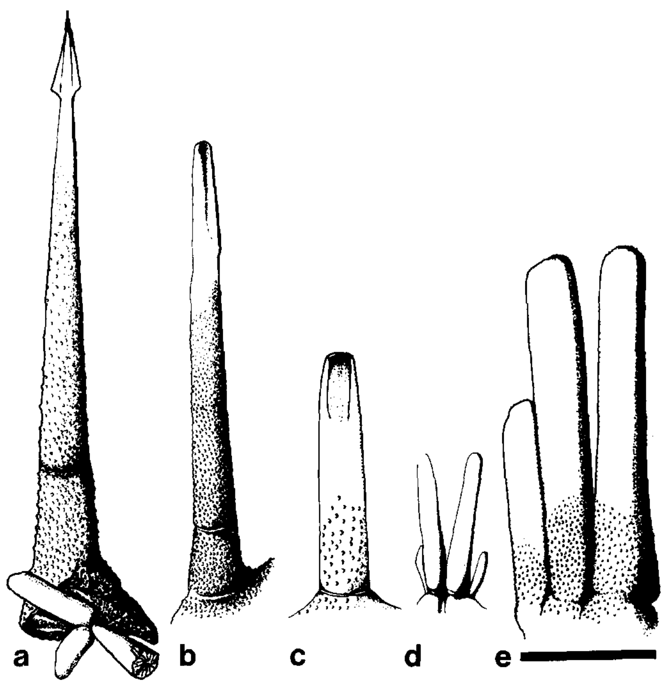

Fig. 2a–e. Spines of *Acanthaster planci*. **a** primary aboral spine with frame ossicles attached; **b** latero-oral spine; **c** oral spine; **d** subambulacral spine; **e** circumoral spine. A dried specimen was drawn because joint positions and grains in the skin covering the spines were more apparent in dried than in fresh samples. The scale bar is 5 mm

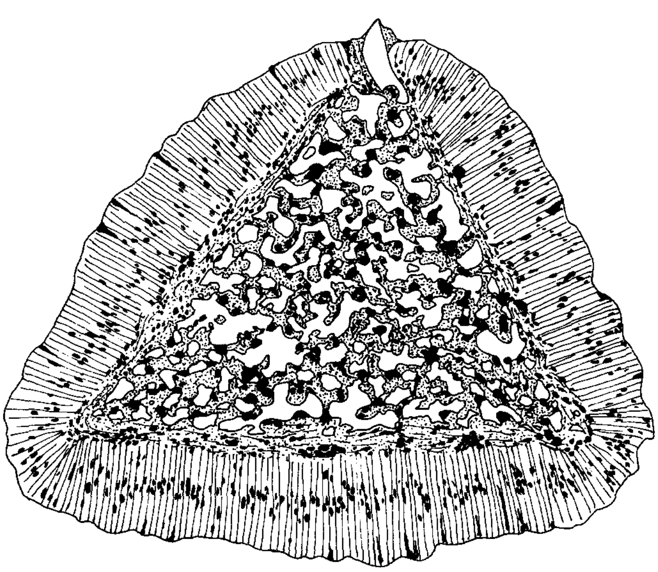

Fig. 3. Cross section of the tip of a primary aboral spine. Note the sharp edge of the ossicle at the top corner

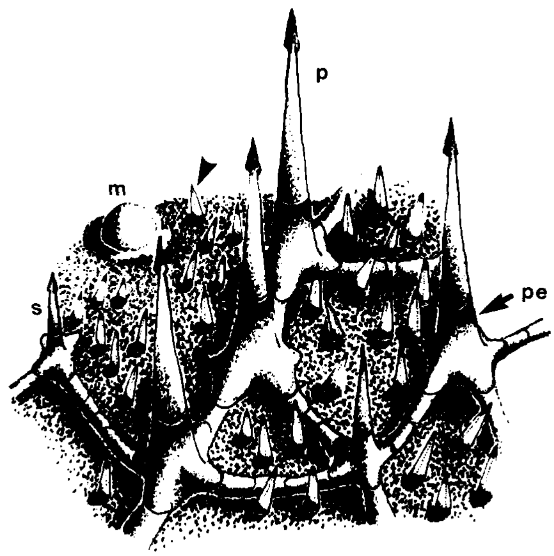

Fig. 4. Aboral surface of disk. The drawing is of a dried specimen in which framework ossicles are more apparent than in live specimens. *m* madreporite; *p* primary aboral spine; *pe* pedicel of primary aboral spine; *s* secondary aboral spine; *arrowhead* pedicellaria

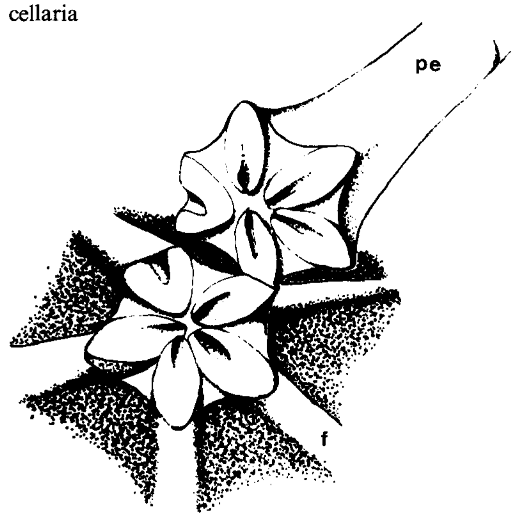

Fig. 5. The frame-end of a pedicel (*pe*) of a primary aboral spine and the frame ossicles (*f*) on which the pedicel is mounted

Subambulacral spines fringe the margin of ambulacral grooves (Figs. 1 B, 8). Three spines, two long and one short, stand on one ossicle. The flat and thus wider surface of the spine faces the ambulacral groove. Pedicellariae are sometimes associated with these spines. A single row of circumoral spines surrounds the mouth, their flat surface facing it (Fig. 1 B).

Oral spines cover the general oral surface (Fig. 1 B). Their cross-sectional shape resembles a somewhat flattened cylinder. One flattened surface, opposite the mouth, bears a furrow at the tip (Fig. 2c). These spines form two rows on the arms (Figs. 1 B, 8). The first row is just adjacent to the row of subambulacral spines and thus fringes the ambulacral groove. The second is located between the first row and the row of latero-oral spines. Pedicellariae are usually associated with the spine of the first row.

Along the lateral edge of the arms, there are latero-oral spines (Figs. 1 B, 8). Their cross-sectional shape is round in the proximal part, but in the distal part it is oval with a furrow (Fig. 2b). The length of the latero-oral spines increases towards the distal end (Fig. 1 B).

III. Primary aboral spine joint

There is a joint between the primary aboral spine and the pedicel. Both the spine and the pedicel have shallow holes at their centers (Fig. 6). Histological section revealed that the joint is surrounded by an epidermis and an underlying dermis. The main component of the dermis is collagen fibers (Fig. 7), which have muscle fibers scattered among them.

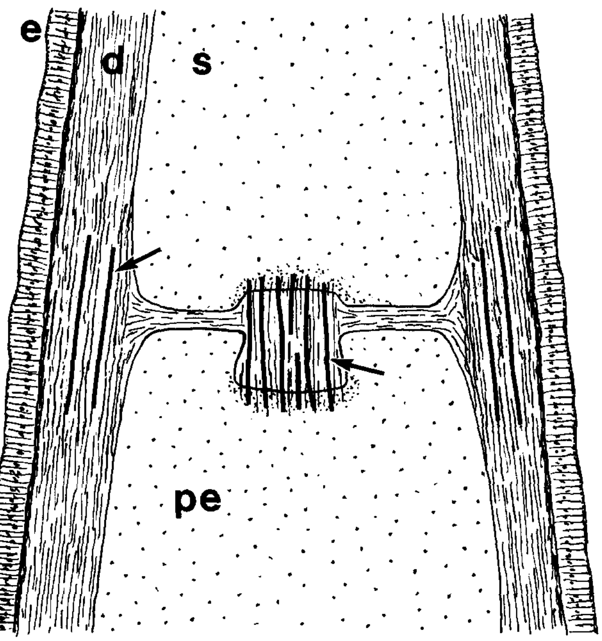

Fig. 6. Schematic drawing of a longitudinal section of the joint region of the primary aboral spine. Notice the holes at the center of the joint. Muscles (*arrows*) are more densely packed inside the hole than outside. *d* dermis; *e* epidermis; *s* spine ossicle; *pe* pedicel ossicle

The holes in the ossicles are also filled with collagen and muscle fibers. The fibers penetrate into the ossicles at the bottom of the holes. The fibers are oriented along the long axis of the spine in the dermis around the joint and in the holes, but are oriented radially in the space between the spine ossicle and the pedicel.

The collagen fibers are round or oval in cross section and 2.5 ± 1.5 μm in diameter (average ± S.D., $N = 79$, range: 0.4–12.3 μm; Fig. 7A). They are made of parallel collagen fibrils which are round in cross section and 40–200 nm in diameter. The fibrils have an axial band pattern whose periodicity is 54.9 ± 3.2 nm (average ± S.D., $N = 65$; Fig. 7B).

Muscle fibers are smooth (Fig. 7C) and have a diameter of 1.2 ± 0.6 μm (average ± S.D., $N = 90$, range: 0.2–3.5 μm). The diameter of the thick filament is 34 ± 7 nm (average ± S.D., $N = 48$, range: 19–63 nm), which suggests that the filament is paramyosin (Smith et al. 1981). The density of muscle fibers is not high in the dermis surrounding the spine joint. When measured in the electronmicrographs at ×1,000 magnification, the cross sectional area of the muscle occupies less than 2% of the total area in most photographs. It never exceeded 10%. In the connective tissue in the central holes, however, the density of muscles is 30% or more (Fig. 6).

Three kinds of cells with electron-dense granules are found in the connective tissue. The first is an oval cell with large spherules (L in Fig. 7A). The diameter of the spherule is 1.1 ± 0.3 μm (average ± S.D., $N = 40$). The second is the presumed neurosecretory cell with slender processes (N in Fig. 7C, D). Both the cell body and the processes are filled with granules which are usually round in cross section but sometimes drug capsule shaped. The diameter of the granules is 0.20 ± 0.04 μm (average ±S.D., $N = 65$). Some drug capsule shaped granules are up to 0.4 μm in their long axis. The processes of these cells are the most frequently found cellular elements in the connective tissue. The third cellular element is a nerve-like cell process with small, round, and electron-dense granules (S in Fig. 7A, C). The diameter of the granule is 0.10 ± 0.02 μm (average ± S.D., $N = 21$). This process often closely associates with muscle fibers and presumed neurosecretory cells (Fig. 7C).

The spaces between the cells and collagen fibers are filled with a felt-like meshwork of fine filaments (Fig. 7A, B, C). The diameter of the filament varies: the maximum is 32 nm and the minimum is less than 4 nm.

IV. Spine movement

Aboral spines were usually maintained straight at the joint. The mobility of the joint was confirmed when the animal passed through a narrow space. An animal with a body height of ca. 2.5 cm and dorsal spines ca. 2.5 cm in length, making a total height of 5 cm, was put in an aquarium. The tank contained a partition which stopped 3 cm from the bottom. The animal was illuminated with a 350 W floodlight lamp. This caused it to move to the other side of the partition through the 3 cm space. When the animal touched the partition, it decreased its total height by flattening its body and bending the aboral spines backwards at the joints. I could not determine, however, whether the spines actively bent or were passively bent by the shear forces between the partition and the animal. After the spines had cleared the partition, they straightened again. The time taken to straighten the spines varied. Some were straight several seconds after being freed from the partition but some remained bent at various angles for several minutes or more. This suggests that the straightening is not a simple elastic recovery but an active straightening.

The active movement of aboral spines in response to stimulation was observed in the animal, which was taken from sea water into the air. This caused many spines to bend at the joint. All the stimulation applied on the body surface adjacent to the the spine caused straightening of the bent spine. No movement was observed in the straight spines. The stimulation employed was as follows. Mechanical stimulation: prodding with a blunt needle; electrical stimulation: 3V repetitive square pulses through a pair of chlorided silver electrodes; chemical stimulation: blotting paper soaked in saturated NaCl; photic stimulation: flashlight from a photographic xenon flashtube.

The spines on the oral surface also moved at the joint. In undisturbed animals, the ambulacral grooves were open and the tube feet, which extended out from the grooves, supported the body of the animal. The oral spines of the arm (first row) pointed downward (Fig. 8A). Mechanical stimulus applied to the tip of an extending tube foot caused rapid retraction of that tube foot and also the adjacent ones, followed by closing of the ambulacral groove. Closing was accomplished by the narrowing of the arch formed by the ambulacral plates and by covering the opening of the groove with subambulacral spines and the oral spines of the arm (first row) (Figs. 1B, 8B). The spines of both sides of the groove bent over the groove, which then looked as if closed with a zipper. The body was supported at this point by oral spines of the arm (second row) and those on the disk (Fig. 8B). Chemical stimulation of the tube feet and photic stimulation of the oral surface of the arm also caused closing of the groove.

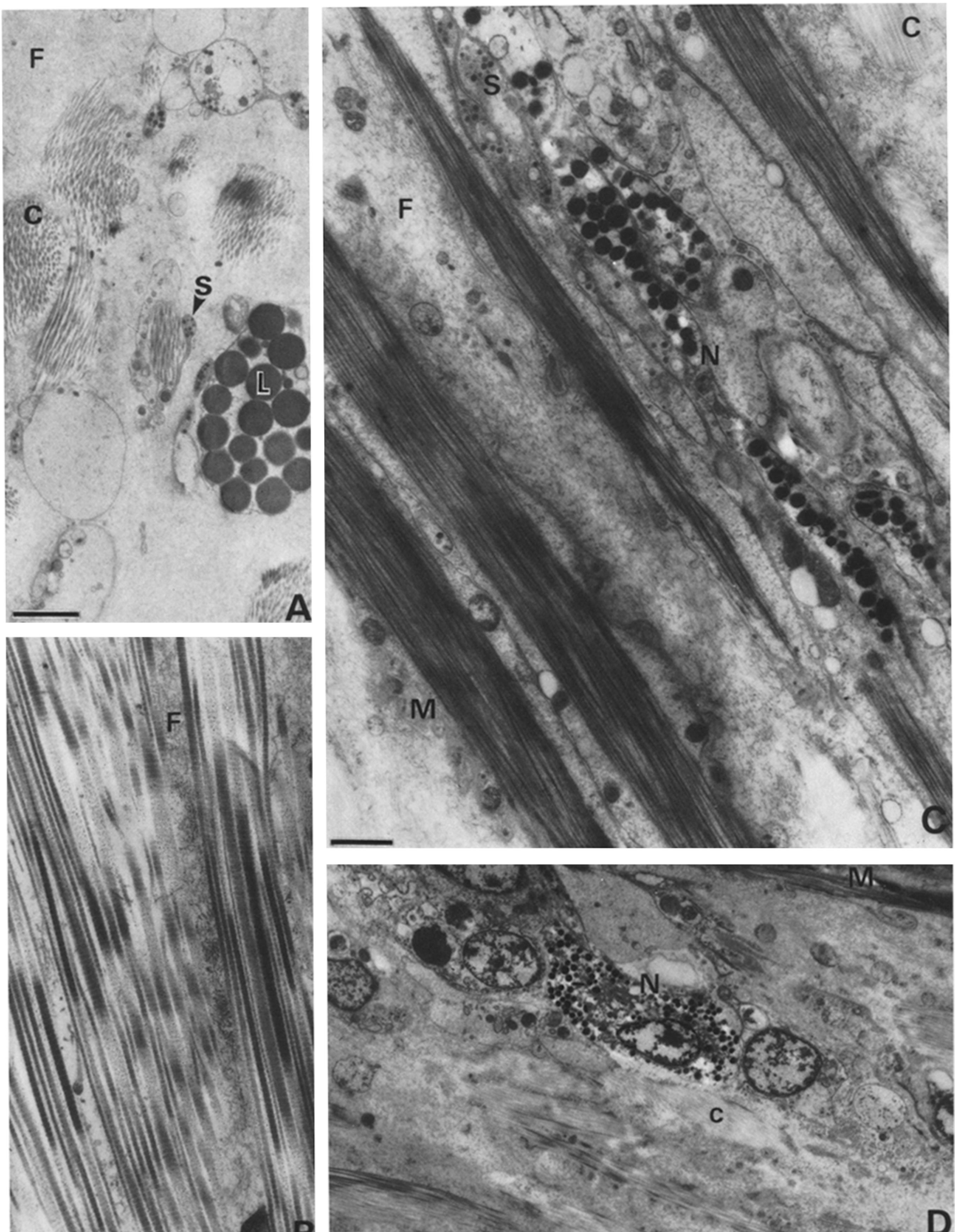

Fig. 7A–D. The dermis surrounding the joint of the primary aboral spine. **A** shows collagen fibers (*C*), a cell with large spherules (*L*), and nerve-like cell process with small granules (*S*). **B** is the longitudinal section of collagen fibers. Notice the meshwork of fine filament (*F*) fills the space between collagen fibers. **C** shows a longitudinal section of muscle fibers (*M*). The presumed neurosecretory cell (*N*) and nerve-like cell process with small granules (*S*) are also shown. A meshwork of fine filaments (*F*) fills the space between muscle fibers and that between muscles and collagen fibers (*C*). **D** shows the cell body of the presumed neurosecretory cell (*N*). Scale bar is 2 μm for **A** and **D** and 1 μm for **B** and **C**

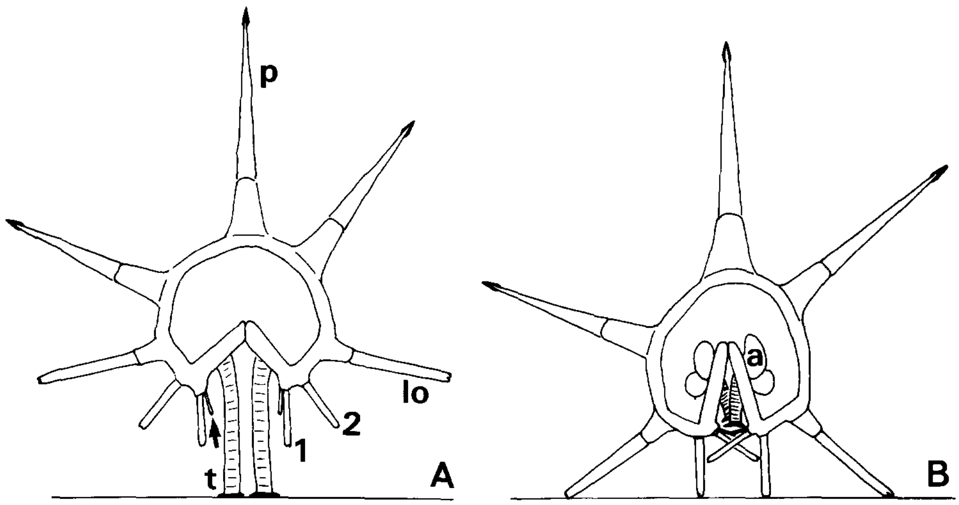

Fig. 8 A, B. Cross sections of arm with ambulacral groove opened (**A**) and closed (**B**).
A tube feet (*t*) support the body, subambulacral spines (*arrow*) and oral spines of arm (first row) (*1*) point downward.
B tube feet retracted and ampullae (*a*) bulged. The opening of the groove is covered with subambulacral spines and oral spines of the arm (first row). The body is supported by the oral spines of the arm (second row) (*2*) and by latero-oral spines (*lo*).
p primary aboral spine

Mechanical stimulation applied to the mouth or photic stimulation to the oral surface of the body caused covering of the mouth by the circumoral spines.

In conclusion, the morphology and movement of *Acanthaster* spines are well adapted for defense. The aboral spines, which have a pointed tip with a sharp side edge, stood upright. They may well be effective armature against potential predators. The spines on the oral surface protect the soft parts (ambulacra and mouth) by covering them. Their flattened shape increases in area they can cover. The latero-oral spines and the primary aboral spines on the lateral side of an arm, together with those on the facing side of the adjacent arm, make a barrier of crossed spines (Fig. 1 B). The increased length of the latero-oral spines in the distal region makes the barrier more effective because the distance between the adjacent arms becomes greater in this region. Therefore all the surfaces, top, bottom, and side of the animal, are protected by the spines.

D. Discussion

The shape and movement of *Acanthaster* spines strongly suggest that the animal is well-protected by spines. The toxin in the aboral spines no doubt makes the defense more effective (Taira et al. 1975). We do not know, however, how effective these spines are for defense. Very little is known about the extent of predation on *Acanthaster* (Potts 1981).

The joint of primary aboral spines had holes at the center. Similar central holes are observed in the spine joint of several echinoids such as *Diadema setosum* (Motokawa 1983). The central ligament, which fills the holes and connects the spine of *Diadema* to the test, is a collagenous connective tissue with no muscles in it. Muscles form a discrete layer which surrounds the spine joint of *Diadema*. This is in contrast to the observation that the muscle content is high in the connective tissue in the central holes and very low in the dermis surrounding the joint of *Acanthaster*. The distribution of muscle fibers suggests that the joints of the primary spines of *Acanthaster* are designed not for active bending but for passive bending and active straightening. The muscles at the center cannot contribute to the bending movement. Bent spines became erect when stimulated but straight spines did not move, which may support the suggestion.

Motokawa (1982a) showed that the dermis surrounding the joint of the primary spine of *Acanthaster* changes the joint's stiffness on application of celomic factors, which also cause a stiffness change in other catch connective tissues. Although the stiffness change may be caused by muscle contraction in the dermis of *Acanthaster*, the very small number of muscle fibers suggests that the connective tissue has catch properties. The presence of the presumed neurosecretory cells supports this suggestion, because they are a common component of the echinoderm catch connective tissues and may control the catch and relaxation of the tissues (Wilkie 1979; Holland and Grimmer 1981; Smith et al. 1981; Byrne 1982; Motokawa 1982b, 1983; Hidaka and Takahashi 1983; Wilkie et al. 1984). The connective tissue is perhaps normally stiff, to hold the spine upright. This would guard the animal from predators. It probably becomes soft to allow passive bending of the spine when the animal passes through narrow spaces, for example, when hiding under the corals during the day.

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