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Abstract

Edrioasteroids are extinct sessile marine suspension feeders, which passively use the water current to obtain food particles. Discocystinid edrioasteroids have the ability to extend and contract and it has been suggested that this mechanism functions as a device for respiration. The objective of this analysis was to determine whether extension could have also provided a feeding advantage to the animal. Model edrioasteroids were made, which exhibited contracted, extended and bent extended positions. These models were put into a flume and the behavior of the water around the models gave insight on whether a certain position would be advantageous. It was determined that the bent extended model with its oral surface facing into the current, was ideal for catching food. Flow was accelerated along the thecal regions and the boundary layer was minimized.

Introduction

Edrioasteroids are an extinct group of organisms that belong to the animal kingdom and are a part of the phylum Echinodermata. This phylum includes organisms such as sea urchins, sand dollars and starfish. Edrioasteroids represent a distinct class within the phylum Echinodermata and more than 200 species have been described. The range of edrioasteroids within the fossil record covers a time span from the Early Cambrian to the Late Pennsylvanian (Sumrall, 1994).

Edrioasteroids are sessile marine organisms that require a hard substrate for attachment. They either attach to the hard sea floor or to other organisms such as brachiopods. Like all other echinoderms, the body of an edrioasteroid is composed of numerous small plates and the internal organs are enclosed in a series of magnesium calcite plates called the theca (Figure 1). Unlike

most other echinoderm groups edrioasteroids lack appendages. Furthermore, edrioasteroids have five ambulacra, which radiate from a centrally-located peristome or mouth and are used to feed. The peripheral rim, which is a ring shaped feature around the theca, functions as an attachment device, with which edrioasteroids could affix themselves to the substrate.

Edrioasteroids are suspension feeding organisms that passively capture food suspended in the water column. Paleobiologists assume that

Ambulacrum

Mouth

Peripheral Rim

Figure 1: Theca of an edrioasteroid showing the mouth, ambulacra and peripheral rim.

edrioasteroids are suspension feeders because there is no evidence for a filter feeding device. The ambulacra are the feeding devices, with which the animals caught food from the water column by using small structures called tube feet or podia, which extend from the ambulacra. Through the arrangement of trough-shaped plates a channel is formed in the ambalacrum, which served to transport food to the mouth. Additionally, smaller plates cover the channel and most likely functioned as an opening a closing mechanism (Figure 2) (Sumrall, 1994).
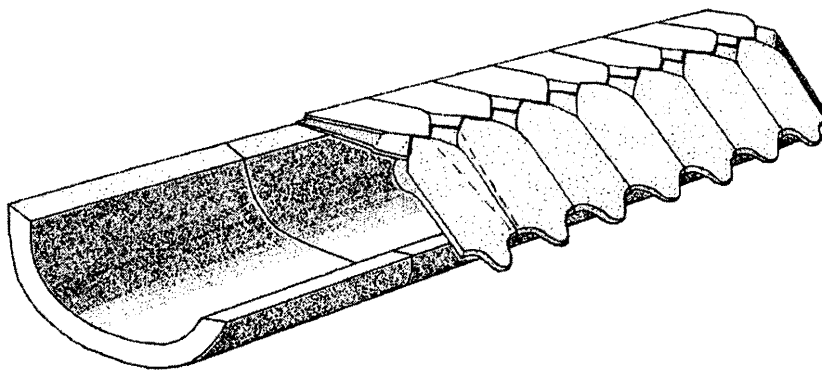
Figure 2: Depiction of the plate arrangement in an ambulacrum segment (Bell, 1977).
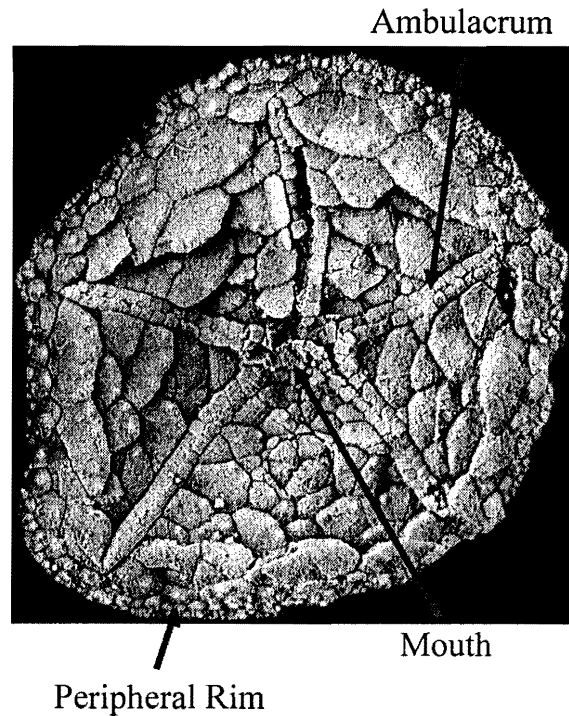
Discocystinid edrioasteroids, which are the focus of this analysis, are a subfamily of the family Agelacrinitidae (Sumrall, 1996). Fossilized discocystinids have only been found in North America and Europe and are best known for their occurrences from the Carboniferous of North America (Sumrall, 1996). Sumrall (1994) suggested that late Paleozoic edrioasteroids can be separated into three groups based on the shape of their theca. These edrioasteroids either have a pyrgate thecal design, domal thecal design or a clavate thecal design. Discocystinids exhibit a clavate thecal design, which is mushroom-shaped. One distinctive feature of a clavate theca is that the diameter of the peripheral rim is much smaller than the diameter of the theca. The approximate diameter of the theca is confined between 14 and 90mm, whereas the peripheral rim commonly has a diameter of less than 12mm (Figure 3) (Sumrall, 1996). Another feature of clavate discocystinids, which is also shared by edrioasteroids with pyrgate theca, is the ability of extension and contraction of their body. The mechanism of extension and contraction in clavate theca appears to be more evolved than in pyrgate forms (Sumrall, 1993). The ability to extend and contract is evident in the fossilization of discocystinids in extended and contracted positions (Figure 4).
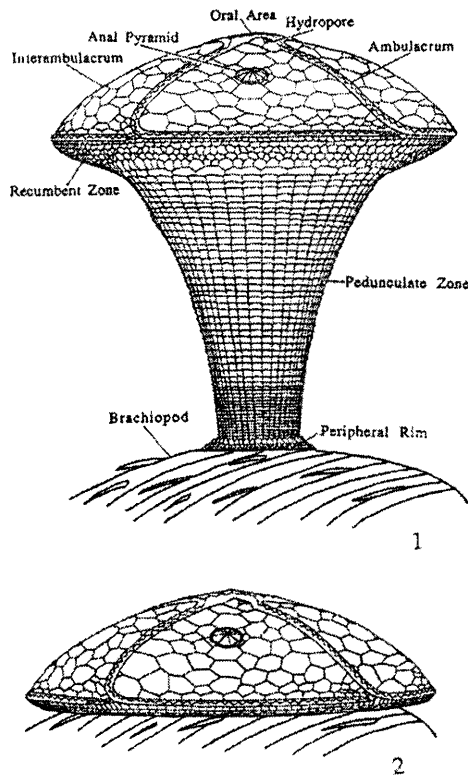
Figure 3: Morphology of discocystinid edrioasteroid in extended (1) and contracted (2) position (Sumrall, 1992).

The purpose of this extension has been extensively discussed in the literature. Bell (1977) suggested that extension and contraction could serve a respiratory function. It is assumed

that most edrioasteroids used a hydrovascular system for

respiration, in which podia extended from the food

groove within the ambulacra to capture food and absorb

oxygen from the sea water. Because podia seem to be

absent in discocystinids Bell (1977) proposed that

extension and contraction could function as a respiratory

mechanism. The organism would extend when taking

up water, extract oxygen from it, and then contract when

releasing excess water and carbon dioxide.

It is also possible that the ability to extend and

contract serves feeding purposes. Suspension feeding

becomes most effective when more water, which

Figure 4: Fossils of discocystinids in extended and contracted positions (Sumrall, 1996).

contains suspended food particles, passes by the ambulacra. Suspension feeding causes

difficulties for the organism feeding in currents. If the animal stays within the boundary layer,

where the water velocity is effectively zero, little food capture is possible. However, if the

animal extends into the current, the higher flow rates allow it to catch more food, even though it

has to contend with increased drag and turbulent flow. Since discocystinids can extend into the

active water column it is possible that extension provides a feeding advantage. Sumrall and

Parsley (2003) suggested that because the ambulacra extend along the edges of the theca, the

flow rate is increased there, which allows feeding to be more effective. They also suggested that

discocystinids bent in the direction of current flow, which would accelerate water along the

ambitus where the ambulacra are located.

This study tested the hypothesis that extension and contraction in discocystinid edrioasteroids provided a feeding advantage. Models of these organisms were constructed and put into a flume to see how the water behaved around the body of the animals.

Methodology:

For the conducted experiments, model edrioasteroids were constructed to exhibit different postures. Models were necessary, because fossilized discocystinids are not preserved three dimensionally. The models were made of modeling clay and the models exhibited contracted, upright extended and bent extended postures (Figure 5). The dimensions of the models were taken from estimated dimensions from fossilized edrioasteroids. The thecal diameter of all models was roughly 40mm and the vertical length of the theca, without the stalk, was about 10mm. The stalk of the extended models was approximately 42.5mm and the diameter of the bottom of the stalk was 12.5mm. The ambulacra were made of different colored clay so that they could be seen easily. The relief of the ambulacra was less than a millimeter.
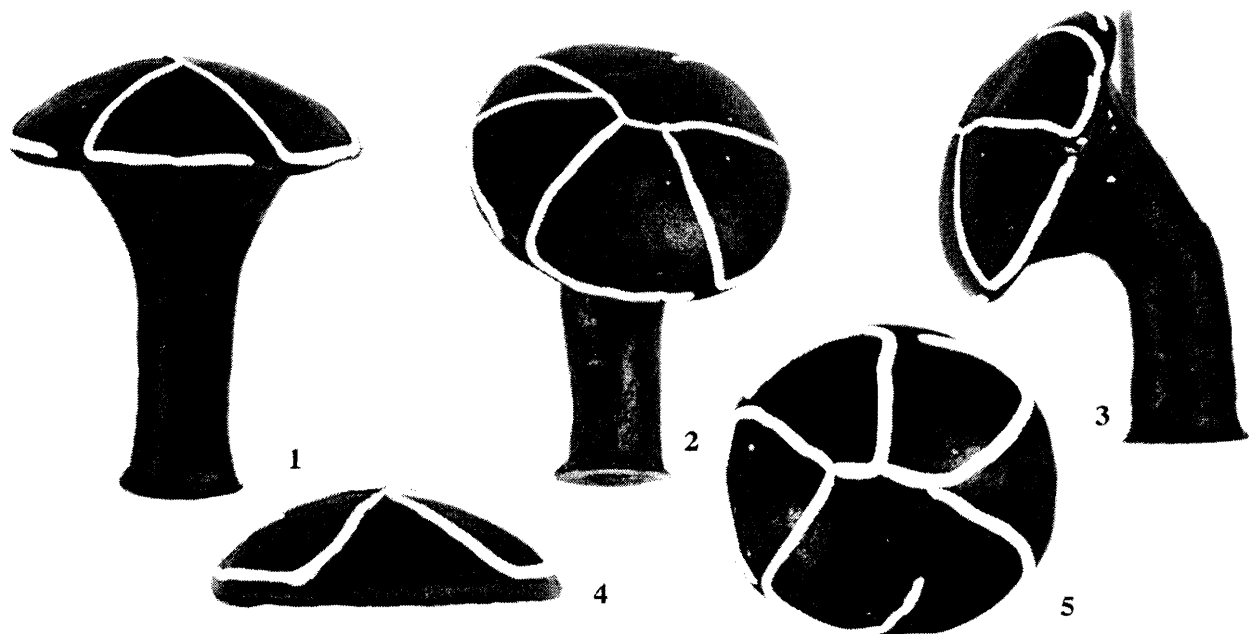

Figure 5: Pictures of models. **1**, upright extended posture. **2**, bent extended posture viewed from the front. **3**, bent extended postures viewed from side. **4**, contracted posture viewed from side. **5**, contracted posture viewed from the top.

A flume made of Plexiglas with a length of 541cm, a height of 30 cm and a width of 20.2 cm was used to conduct each experiment. Even though a flow straightener was already present as part of the flume, an additional flow straightener was made to ensure laminar flow. This flow straightener was assembled by gluing regular drinking straws together with a glue gun. The width and height of this straightener matched those of the flume, so that all water would be forced through it to create laminar flow, which was important to observe the behavior of the water around the models.

To observe and record the interaction between the models and fluid flow, dye was injected into the stream. A dye injector was made out of Pyrex tubing, which had been heated and stretched into a very fine point so that minimal amounts of dye where injected at a time. A platform to which the injector was attached was constructed out of wood. This gave vertical and horizontal control over the position of the injector, so that dye streams could be observed at any point of the model without having to adjust its position.

The water depth in the flume was about 13cm during the experiments. The water velocities were kept between 3 and 5 cm/s. The water velocities were kept low, so that the flow would not become turbulent. The Reynold's Number, which is an indicator of whether flow is turbulent or laminar, was calculated to be less than 500 with these average velocities. If the Reynold's Number is less than 500, flow is laminar. The Froude Number, which gives an indication of whether flow is tranquil or shooting, was calculated to be less than 1, which indicates tranquil flow. Dye streams were run along different parts of the models and pictures were taken to record fluid behavior.

Experiment 1:

Experiment 1 was conducted on the extended upright model. The water velocity was 4.76 cm/s. The dye injector was aimed 1) at the center of the oral surface and at the area where the ambulacra run along the edge of the oral surface (Figure 6 A, C), 2) at the distal ambulacra and to one side of the center of the oral surface (Figure 6 B, C), 3) at the center of the oral surface and below the ambitus (Figure 6 A, D).

Experiment 2:

For experiment 2, the bent model was positioned so that the oral surface was on the lee side. The water velocity was 3.33 cm/s. The dye stream was directed towards 1) the center of the oral surface and area where stem is bent (Figure 6 A, E), 2) one side of the oral surface at the same height (Figure 6 B, E), 3) area below bend in the stem (Figure 6 F).

Experiment 3:

During experiment 3 the water velocity was 3.33 cm/s and the bent position was tested, but this time the oral surface was facing into the flow. The dye stream was first aimed 1) towards the center of the oral surface (Figure 6 G), 2) towards center of oral surface at varying heights.

Experiment 4:

For this experiment the bent model was positioned so that the oral surface was at a right angle to the direction of water flow and the flow velocity was held at 3.33 cm/s. The dye stream was aimed at 1) the distal ambulacra at the center of the oral surface (Figure 6 H), 2) the distal ambulacra above and below the center of the oral surface.

Experiment 5:

In the last experiment the contracted model was used to show how the water flow would interact with this posture. The velocity of the water was 3.33 cm/s. The dye injector was only aimed at the center of the model (Figure 6 A, I).
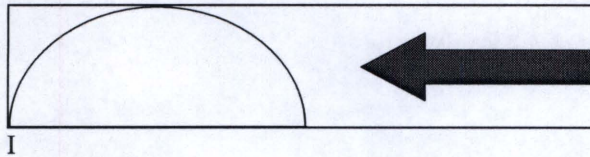

A

B

C

D

E

F

G

H

I
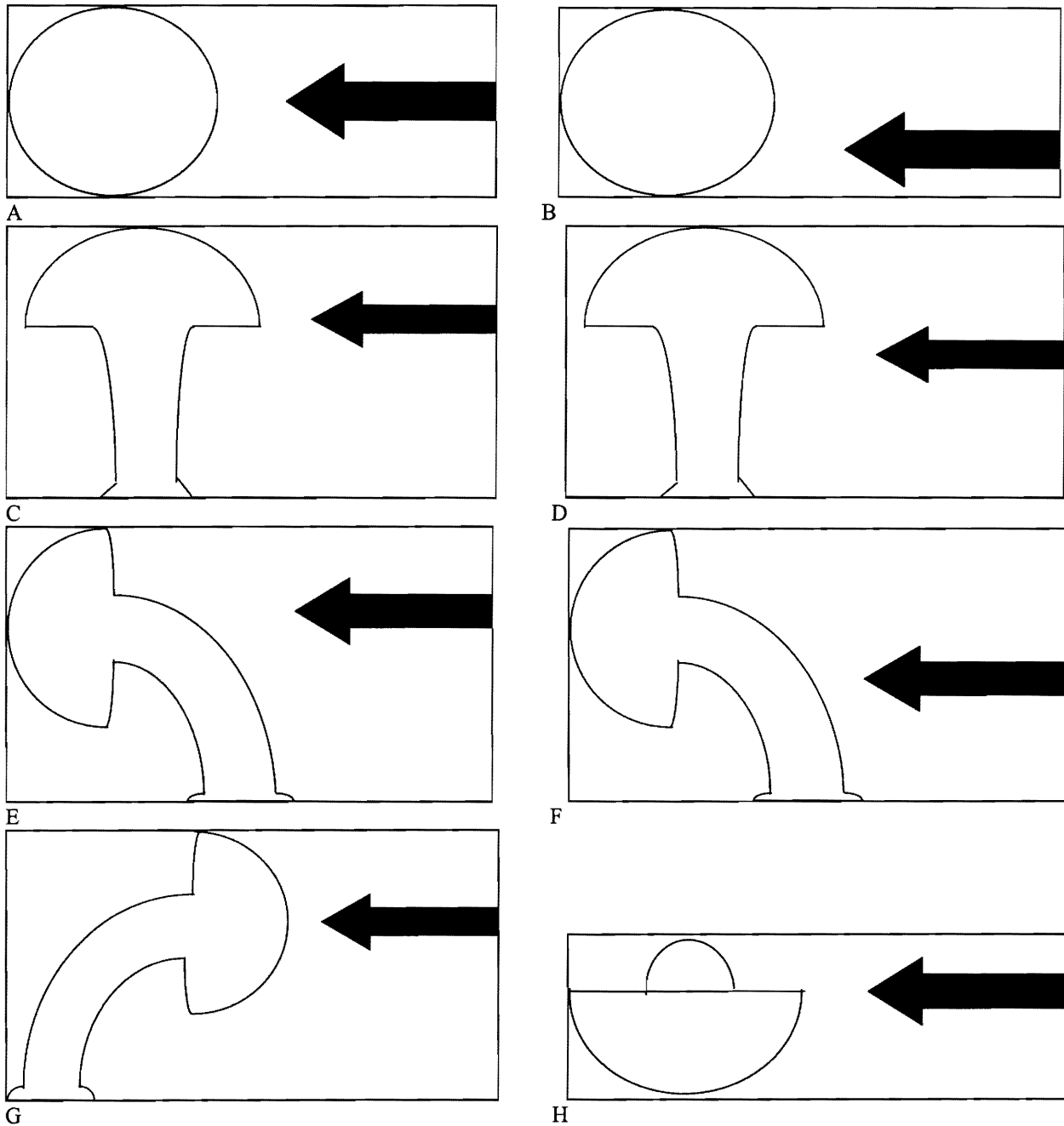
Figure 6: Position of dye stream injector relative to models. Arrows show position of dye stream. **A**, center of oral surface viewed from the top. **B**, ~2cm to one side of oral surface viewed from the top. **C**, region where stem attaches to theca with lateral view of extended position. **D**, three quarters up stem with lateral view of extended position. **E**, bend in stem with lateral view of bent extended position. **F**, below bend in stem with lateral view of bent extended position. **G**, center of oral surface with lateral view of bent extended position pointed in the opposite direction of current flow. **H**, region where stem attaches to oral surface viewed from top of bent extended position facing at a right angle to current direction. **I**, center of oral surface with lateral view of contracted position.

Results

Experiment 1:

Water was accelerated over the top of the upright extended model when the dye stream was directed towards the center of the oral surface (Figure 7 A). Accelerated flow was evident through the observation of the dye stream. Increased water velocities were present only on the stoss side of the model. Acceleration took place in the ambulacral region of the stoss side. However, flow was not accelerated on the lee side of the model and the formation of an eddy was observed there.

When the dye stream was aimed about 1-1.5 cm from the center of the model,

A

B
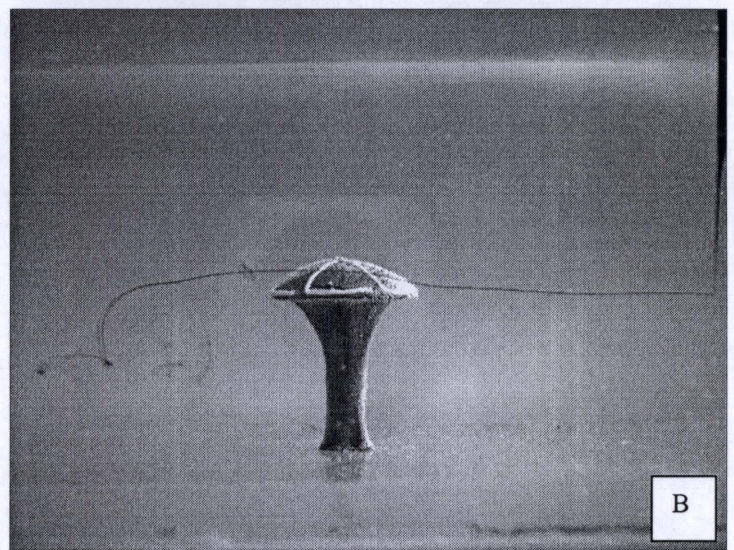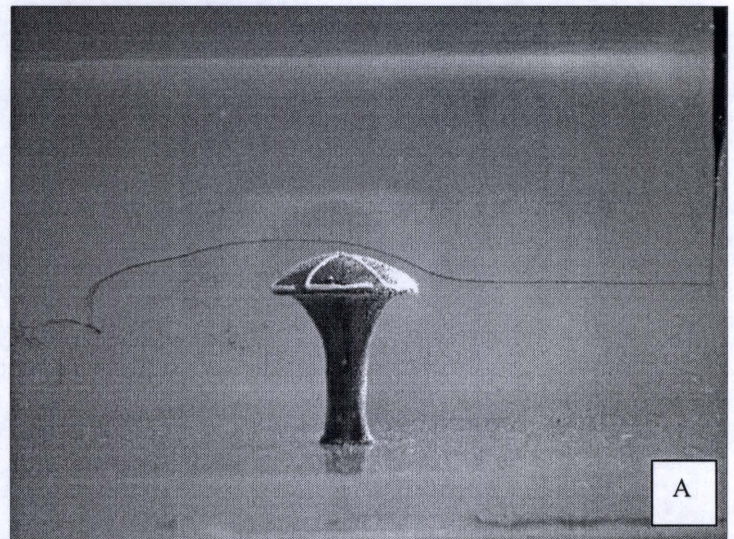
the water was deflected to the side and again accelerated over the top of the organism (Figure 7 B). This shows a similar behavior in that acceleration took place on the stoss side, but not on the lee side of the model.

Water was diverted to either side of the stem when the dye stream was directed towards the area where the stem attaches to the oral surface (Figure 7 C). The flow rate was

Figure 7: Fluid behavior around upright extended model. **A**, dye stream directed towards center of oral surface. **B**, dye stream pointed to one side of oral surface. **C**, dye stream directed below oral surface.

increased around the top of the stem. Additionally, turbulence was formed on the lee side below the thecal area.

Experiment 2:

Flow is accelerated at the ambitus when oral surface of the bent extended model was on the lee side. The flow rate increased around the distal ambulacra when the dye stream was aimed above the bend in the stem (Figure 8 A). Some turbulence was generated on the lee side of the model.

When the dye stream is dropped slightly lower, the water is diverted to either side of the stem and flow velocity is increased around the sides of the theca (Figure 8 B). This posture appears to be effective in channeling most flow around the theca to the ambulacral regions. As the dye injector is dropped even lower, the flow is increased around the distal ambulacra on the bottom of the oral surface (Figure 8 C).
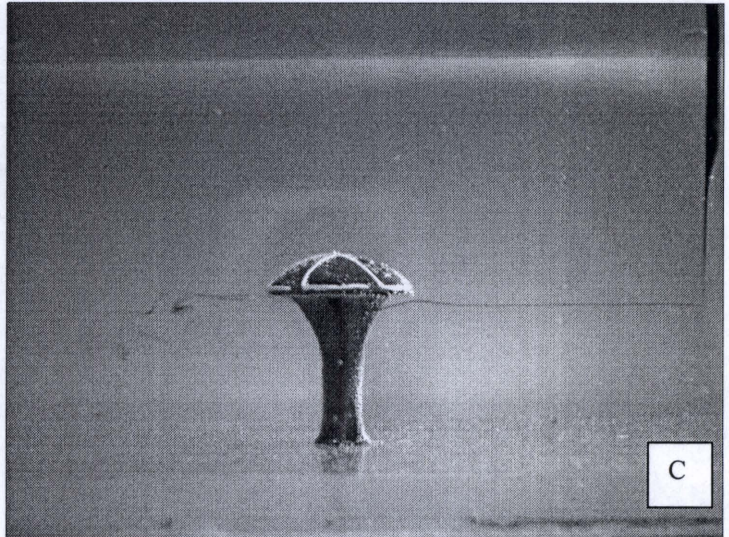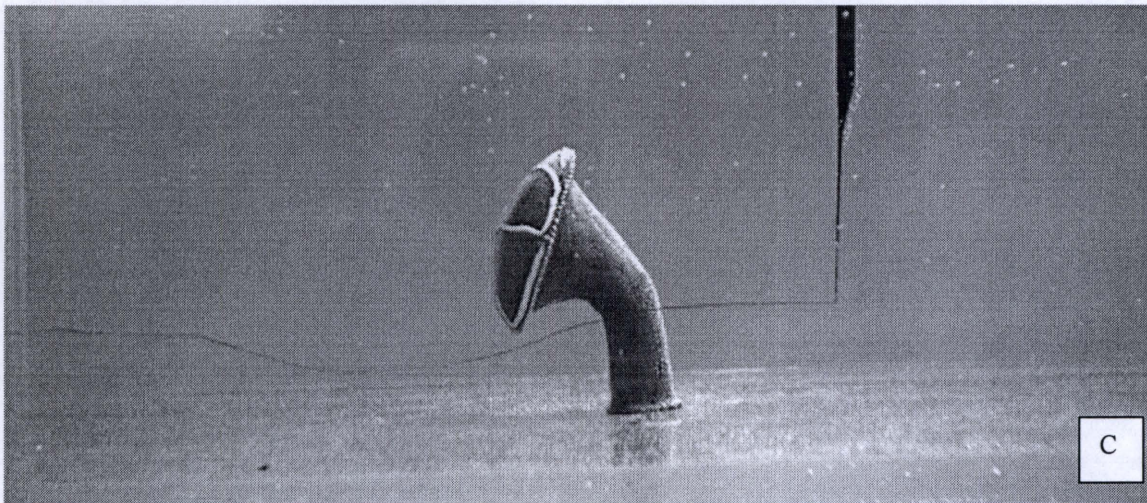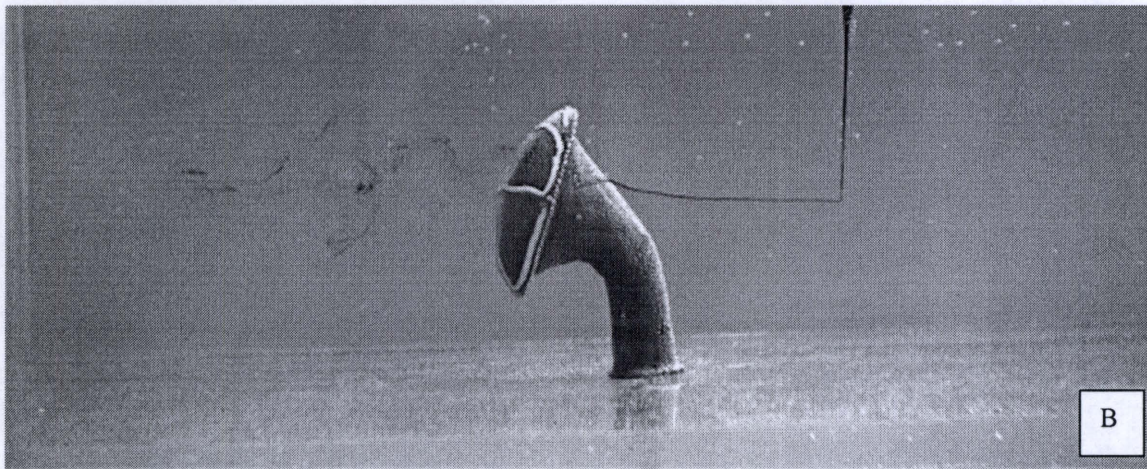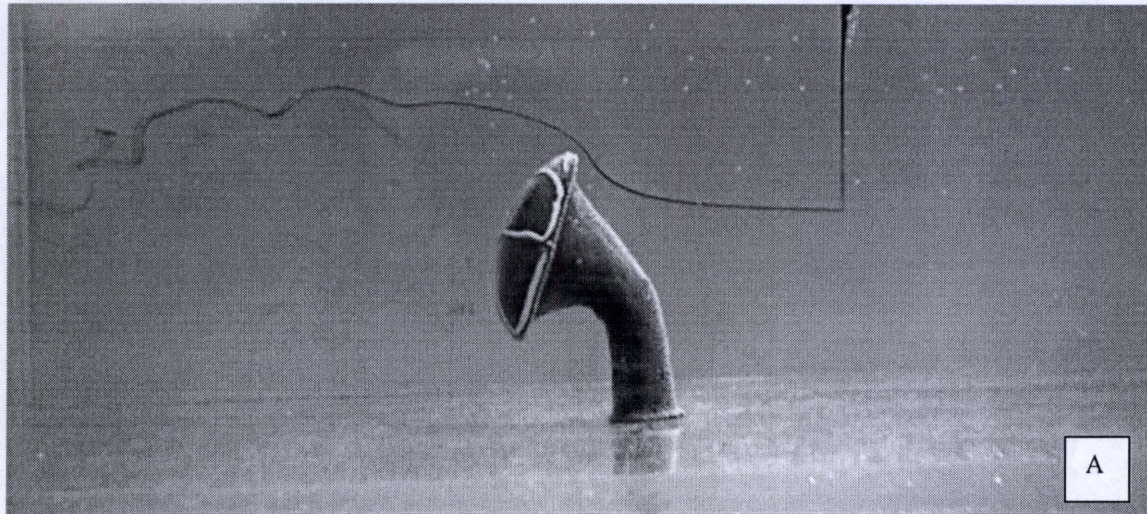
Figure 8: Pictures showing water behavior around the bent extended model with oral surface on lee side. **A**, dye injector aimed above bend in stem. **B**, dye stream aimed to one side of stem. **C**, dye stream pointed below lower edge of the oral surface.

Experiment 3:

When the bent model is positioned with the oral surface on the stoss side, the water

displacement acts in a similar way as in the previous experiment. The water is deflected to either

side of the theca when the dye stream is directed at the center of the theca. Flow is diverted right

at the boundary of the oral surface, which would also allow the proximal ambulacra to catch food

(Figure 9 A, B). Eddies are created when the dye injector is aimed below the center of the oral
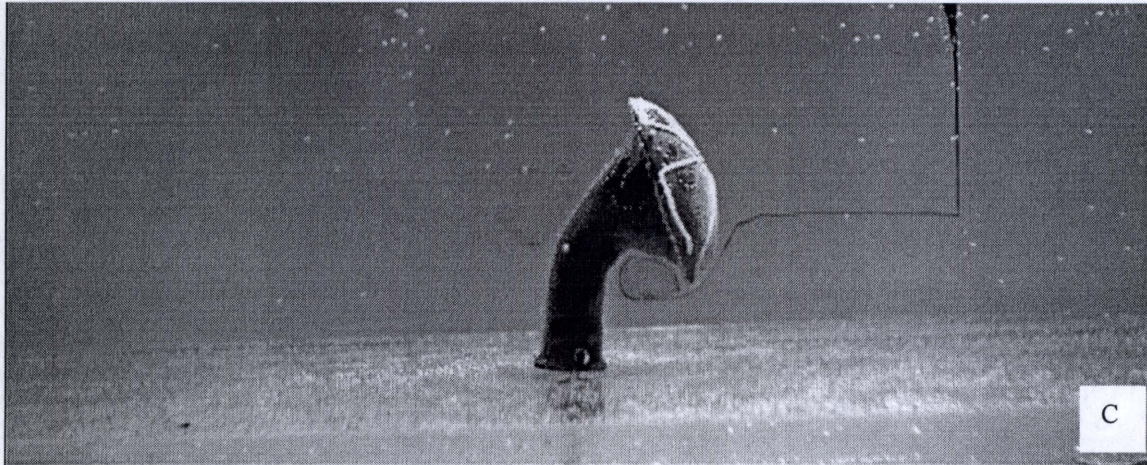
surface (Figure 9 C).

Figure 9: Water behavior around the bent extended model facing into the current. **A**, stream directed at center of oral surface. **B**, dye directed slightly above center of oral surface. **C**, stream pointed below center of oral surface.

Experiment 4:

The behavior of the fluid around the bent model that is positioned with its oral surface perpendicular to the direction of water flow shows similar characteristics as its behavior around the upright posture. Water is accelerated at the stoss side, but turbulence is generated on the lee side (Figure 10).
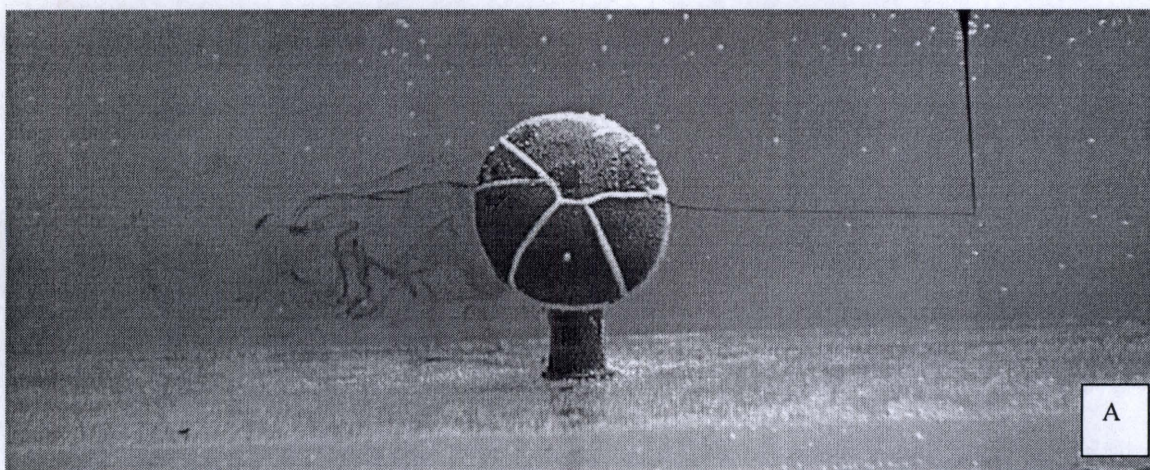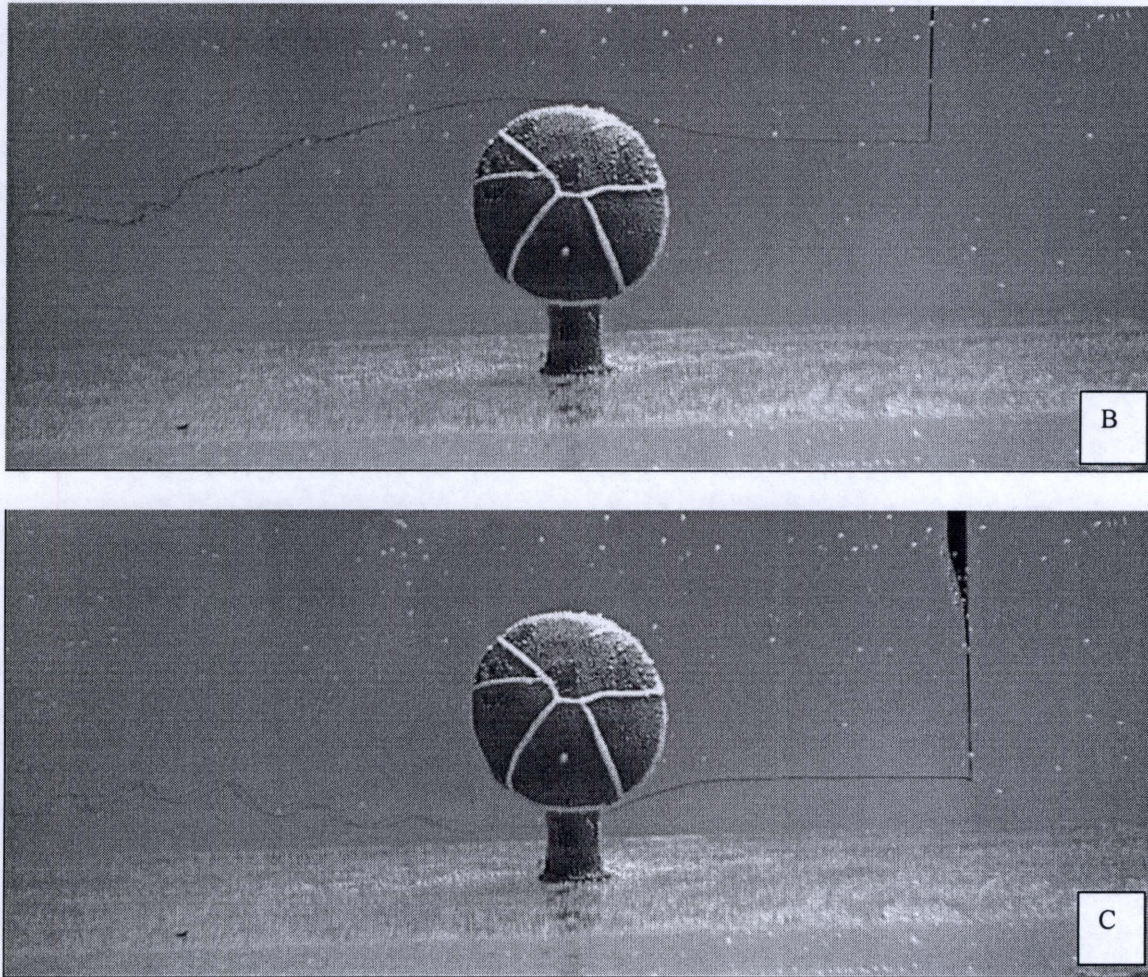
Figure 10: Pictures showing behavior of fluid around bent extended model facing sideways to direction of current flow. **A**, stream aimed at center of theca where stem attached to theca. **B**, dye directed above center of theca. **C**, dye injector aimed below center of theca.

Experiment 5:

The contracted posture causes the boundary layer to become extended. Flow gets accelerated over the top of the oral surface. Water becomes stagnant on the lee side, which is apparent due to a stagnant cloud of dye (Figure 11).
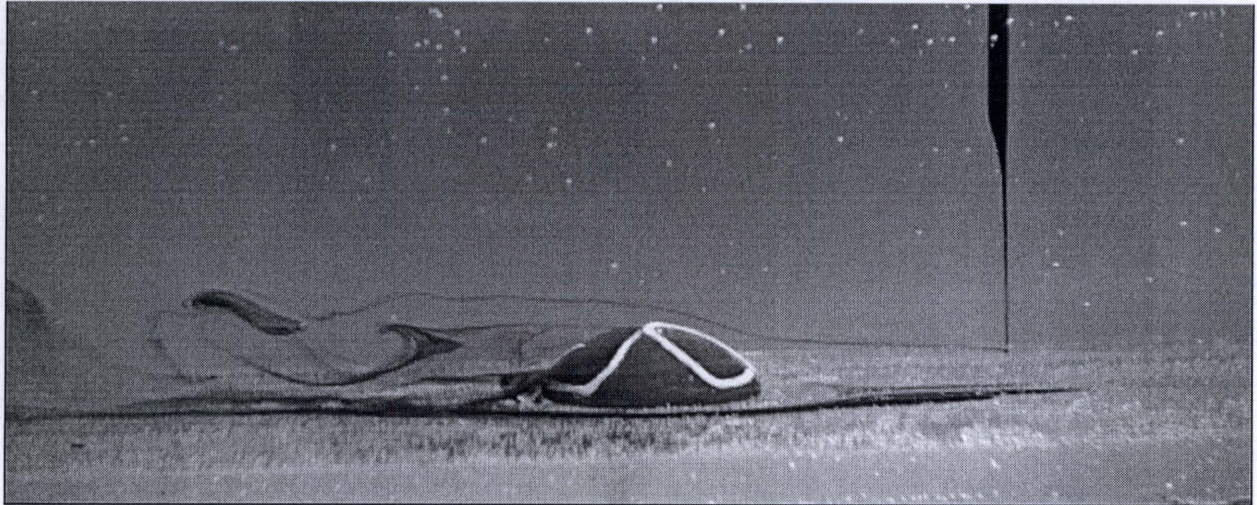
Figure 11: Fluid behavior around contracted model.

Discussion and Conclusions:

A feeding advantage for discocystinid edrioasteroids would be provided if the water velocity increases across the ambulacra. Acceleration of water will cause more food particles to pass per unit of time, which would allow the animal to capture more food. The edrioasteroid would have preferred a posture that maximized water acceleration around its ambulacra.

The extended upright posture only produces acceleration on the stoss side of the organism. Some turbulence is created on the lee side and thick boundary layer exists there. This suggests that the animals could only effectively obtain food on the stoss side ambulacra. Since this posture would not provide maximum food capture, it is unlikely that discocystinids used this position to acquire food from the water column.

The bent posture facing in the same direction as the water flow also does not appear to provide maximum acceleration across the ambulacra. Accelerated water is created at the ambitus, which would allow maximum food uptake, but the more proximal ambulacra would not

be able to capture food. Furthermore, some turbulence is generated on the lee side of the theca, which would not be beneficial to the organism.

If the organism were to be bent, but facing perpendicular to the direction of water flow, the feeding capability would also be less effective. There would be a possibility to catch food on the stoss side, since water is accelerated across the ambulacra. The lee side, however, would again not be able to collect food particles.

The least effective posture is the contracted position. If the organism used this posture for feeding, it would most likely not capture very much food. The boundary layer of the water would be extended to the height of the animal, which would create an area of almost static water around the theca, so that virtually not food could be obtained.

From this analysis it appears that the bent posture, which is facing into the current, provides the greatest feeding advantage for discocystinid edrioasteroids. The flow rate is increased around the edges of the theca, where the ambulacra are located. Furthermore, the water would be deflected right at the boundary of the organism, which minimizes the boundary layer of the water. This would be advantageous, because the tube feet need to extend beyond the boundary layer to maximize food capture. Another advantage of this posture would be that water is also accelerated along the center of the oral surface, so that the inner ambulacra could also obtain food. Water is only accelerated along the edges of the theca or only on one side of the theca in the other extended positions. Therefore, it can be concluded that the extended bent posture, which faces into the current, is the most effective for feeding purposes. Ambulacral capacity will be maximized, because the entire length of the ambulacra can catch food. Since the organism would try to maximize its food intake, it is conceivable that edrioasteroids took this position for feeding.

Even though, the mechanism of extension and contraction is related to feeding, this ability could also serve other functions. The mechanism could also function as a respiratory system, as Bell (1977) has suggested. However, this analysis has clearly shown that the ability to extend into the active water column provides the organism with increased feeding capacity. This analysis also suggests that podia were present within the ambulacra of the organism, even though there is no skeletal evidence. The results of the experiments show that a boundary layer exists, which indicates that podia are needed to extend beyond the boundary layer to catch food. This study supports the hypothesis that the mechanism of extension in discocystinids can serve feeding purposes.

Acknowledgments

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