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Authors: Shiino, Yuta, and Suzuki, Yutaro

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# A rectifying effect by internal structures for passive feeding flows in a concavo-convex productide brachiopod

YUTA SHIINO<sup>1</sup> AND YUTARO SUZUKI<sup>2</sup>

<sup>1</sup>Institute of Science and Technology, Academic Assembly, Niigata University, 8050, Ikarashi 2-no-cho, Nishi-ku, Niigata 950-2181, Japan  
(e-mail: y-shiino@geo.sc.niigata-u.ac.jp)

<sup>2</sup>Institute of Geosciences, Shizuoka University, 836 Ohya, Suruga-ku, Shizuoka 422-8529, Japan

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**Abstract.** It has been experimentally shown that the shell morphology of concavo-convex productide brachiopods has the potential to generate passive flows for feeding. However, there still remains the problem of how the presence of internal soft parts influences the course and pattern of the flows. To clarify the effect of soft parts, we performed additional experiments of fluid visualisation using a flow tank and a transparent, polyhedral model with supposed soft parts in a postero-median region. Regardless of the ambient flow directions, the experimental results showed that inflows through ear gapes turned into symmetrical vortices inside the model. The soft parts altered the course of internal flows and interfered with the vortices entering the median region. Therefore, stepwise inflows pushed the precedent vortices forward as the rotational speed decreased. As a result, the slower vortices aligned with the brachial ridges on which the lophophore was arranged. Morphologically, productide brachial ridges tend to lie in the antero-lateral corners of the dorsal disc. The rectifying effect by means of soft parts, though consequential, would enable productides to sieve food particles from gentle vortices rather than from swift vortices just after the inflow through the ear gapes.

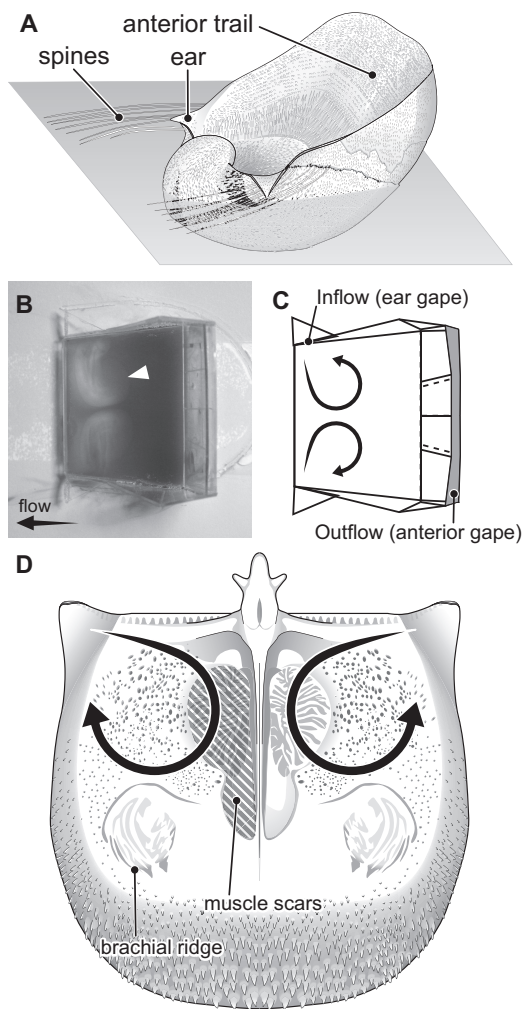
**Key words:** biophysiology, Echinoconchoidea, functionality, hydrodynamics, Strophomenata, suspension feeder

## Introduction

One of the morphological innovations in brachiopods is exploring the possibilities of the concavo-convex shell as seen in strophomenides and productides. Of these brachiopods, the productide shell forms played a role in allowing them to live freely reclining on the sea bottom, and enabled adaptations to a wide variety of benthic conditions (Figure 1A; Grant, 1968, 1976; Rudwick, 1970; Leighton, 2000). Moreover, a shell form that maintains its life posture on the sea bottom has a hydrodynamic advantage arising from the generation of passive feeding flows (Shiino and Suzuki, 2011). The shape of the concavo-convex shell could contain only a small amount of soft parts internally, thereby lowering the metabolic rate of the organism. Consequently, the morphology and function of the productide shell provided a robust adaptation to benthic life by means of lower energetic and oxygenic costs, possibly leading to their great diversity (e.g. Carlson and Leighton, 2001; Curry and Brunton, 2007).

The feeding model, as exemplified by the productide *Waagenoconcha*, hypothesises that inflows are produced

through the ear gapes at the postero-lateral corners, while outflows occur through an anterior gape (Figure 1B, C). The flow inside the shell is characterised by a pair of flat-vortex movements that align with a pair of coiling brachial ridges. Because a food-capturing tentaculate organ, the so-called lophophore, is attached along the ridges (Brunton *et al.*, 2000), the characteristics of the vortices could enable them to serve as a sieve for food particles (Shiino and Suzuki, 2011). However, the visualised vortices inside the hollow model (Figure 1B–D; see also Type-1 model in Shiino and Suzuki, 2011) were not aligned with the lophophore. This finding is not concordant with an effective feeding model that has its internal flow patterns aligned with the shape of the lophophore (fig. 11a in Shiino and Suzuki, 2011). In addition, the passive internal flow patterns in the hollow model show a broad distribution of vortices at the posterior end of the model, which would normally be occupied by the soft parts, such as the muscles and the digestive tract (Figure 1D). Given that internal body parts should alter the course of the internal flow (Shiino, 2010), the effect of the internal structures on the passive generation of inter-



**Figure 1.** Life posture and feeding model of *Waagenoconcha*. **A**, Life posture with the ventral valve partially buried in the underlying sediment; **B**, Visualised flow pattern using the hollow model without the simulated soft parts. The vortices were posteriorly generated inside the model (white arrowhead); **C**, Schematic illustration of **B**; **D**, Schematic illustration of the dorsal interior, showing the courses of the vortices along the surface of the internal dorsal disc. Note that the vortices demonstrated previously in the hollow model passed over the body cavity area and never reached the brachial ridges (Shiino and Suzuki, 2011).

nal flow patterns is worthy of consideration.

The aim of this study was to conduct flow experiments with the principal soft parts in a body cavity using an experimental model.

### Materials and methods

Flow experiments using a water tank and a polyhedral model were conducted to visualise the flow behaviour. The method used for the present study was described in

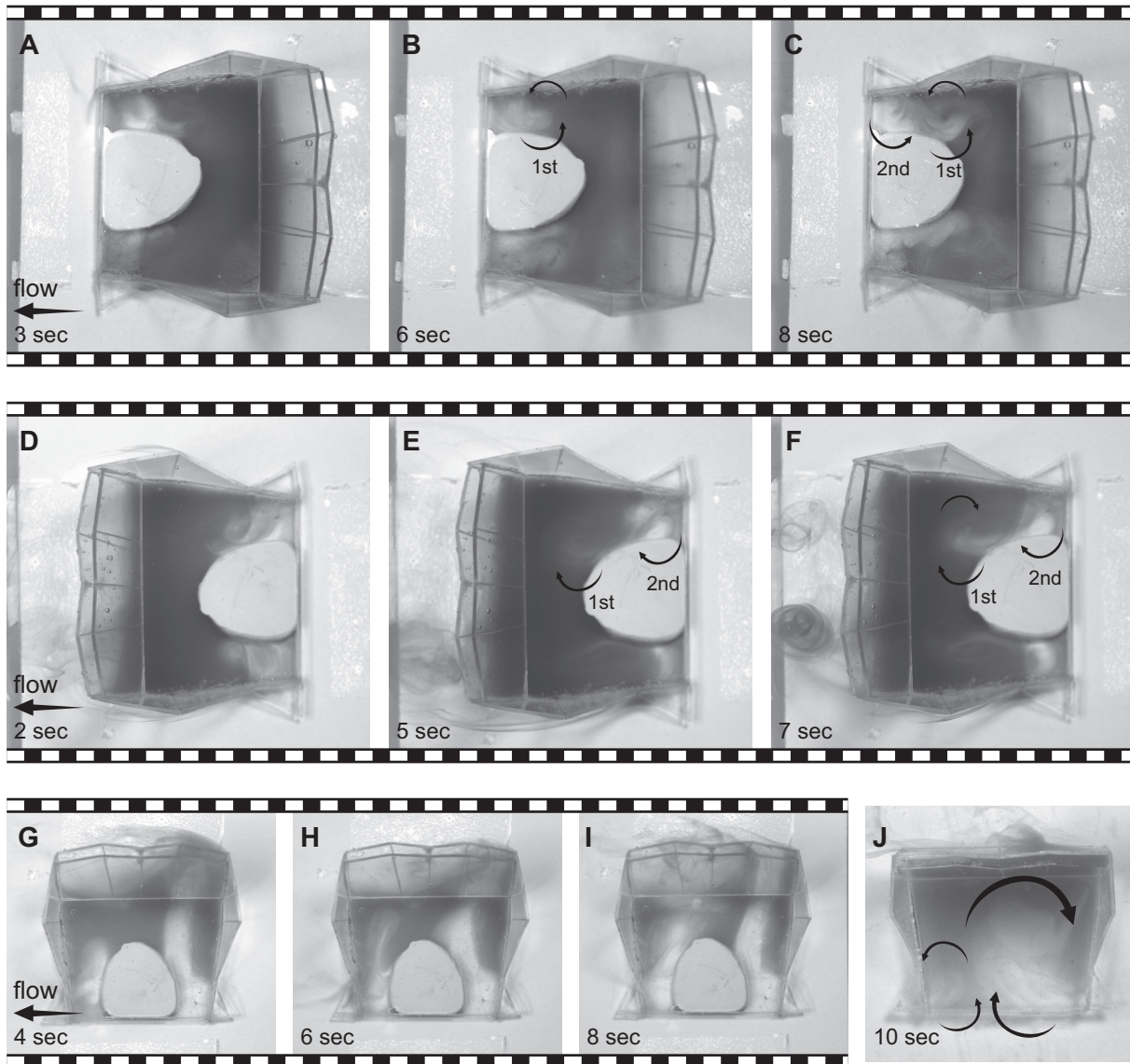
previous reports from our group (Shiino, 2010; Shiino and Suzuki, 2011).

**Fossil specimen.**—For the construction of the experimental model, we used a specimen of the middle Permian productide brachiopod *Waagenoconcha imperfecta* Prendergast (1935) from the Kamiyasse area, Southern Kitakami Terrane, Japan, as a reference (Shiino and Suzuki, 2007; Shiino *et al.*, 2011). The specimen is housed in the National Museum of Nature and Science, Tsukuba (NMNS PA15660).

**Flow in the water tank.**—The water tank was constructed from acrylic plates that were 1800 mm long, 200 mm wide and 150 mm deep (Shiino and Suzuki, 2011). Fresh water was supplied through a water hose at the upstream side of the tank, while a simple water gate at the downstream side discharged the flowing water. The stream velocity was calibrated at 0.081 m/s when the water gate opened to 15 mm. This velocity represents the threshold velocity for sand erosion (Hjulström, 1935) and is the most likely environmental condition under which the species lived (Shiino and Suzuki, 2007). The ambient flow was transitional between a laminar and a turbulent flow; the Reynolds number, calculated as  $Re = Lu/\nu$  (where  $L$  is the model height,  $u$  is the velocity and  $\nu$  is the kinematic viscosity), was less than 2500.

**Construction of the experimental model.**—To visualise the flow behaviour, a transparent polyhedral model was made by the same method as described in Shiino and Suzuki (2011). This model simulated the Permian productide brachiopod *Waagenoconcha* (Figure 1; Shiino and Suzuki, 2007, 2011). To ensure that the ventral side of the model adhered to the tank bottom, the valve resting on the sediment-water interface was partially flattened. Based on morphological observation, the anterior and ear gapes were designed to simulate the open-valve state of *Waagenoconcha*. The blueprint for the model was adapted from the Type-1 (imitation) model of Shiino and Suzuki (2011).

For comparison with the experimental results of the previous study using a hollow model (Shiino and Suzuki, 2011), reconstruction of the soft parts inside the experimental model was required. The candidates for the productide soft parts are a lophophore aligned on the brachial ridges and a portion of the body cavity encapsulating muscles and the digestive tract. Hydrodynamically, a portion of the body cavity could obstruct the flow path inside the shell, while the tentaculate organ of the lophophore could decrease the intensity of the flow behaviours due to its higher porosity. Because the lophophore, to some degree, enables water inside the shell to flow through it (Dhar *et al.*, 1997), we here reconstructed a portion of the body cavity to examine the effect of the main soft parts.



**Figure 2.** Experimental results of the meat (A–I) and the hollow models (J). A–C, Dorsal views with the anterior side facing upstream; D–F, Dorsal views with the posterior side facing upstream; G–I, Dorsal views with the lateral side facing upstream; J, Dorsal view with the lateral side facing upstream. The vortices moved anteriorly in the meat model, while they were broadly diffused inside the hollow model.

The body cavity is a space between the ventral and dorsal visceral area of the shell, which is separated from the mantle cavity by an inner mantle membrane (Rudwick, 1970; James *et al.*, 1992). Because the membrane is flexible, the muscle scars in extant brachiopods tend to be arranged at the outer visceral area, and thus the inner mantle membrane appears to occur along the lateral side of the muscle bundles, thereby forming a stable boundary between the body and mantle cavities (Williams *et al.*, 1997a, b). The body cavity should also be restricted posterior to the brachiopod mouth at the proximal end of the

lophophore. Given the brachiopod body organisation, the area of body cavity could be deduced from the positions of the muscles and the lophophore. Following the general rule of brachiopod internal structures, productides should have had their body cavity located between the dorsal and ventral visceral area surrounding the muscle scars (Brunton *et al.*, 2000). Pursuing the course of brachial ridges, the position of the mouth would be anterior to the anterior adductor scars, which appears to be concordant with the supposed body cavity. Taken together, simulated body parts of the supposed body cavity were included in



the model; this version is referred to as the meat model in this paper (Figure 2A). The simulated body parts were made of putty (Tamiya Epoxy Putty Smooth Surface, Tamiya Inc., Japan).

**Model settings and flow visualisation.**—The experimental model was adhered to the bottom of the water tank. The model was oriented in such a way that the anterior, posterior, or lateral side faced upstream. A water-soluble paint dye (Poster Color, Pentel Co., Japan) with a density slightly higher than that of fresh water was used to visualise the flow patterns. The visualised flow patterns were photographed three times per second using a digital camera (EOS Kiss, Canon Inc., Japan).

## Results and discussion

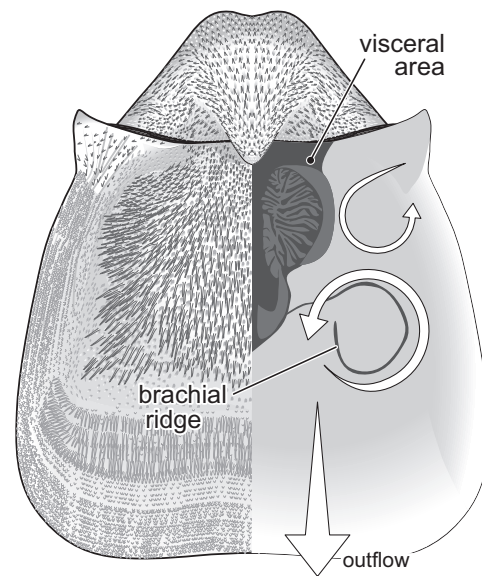
**Flow patterns.**—All experimental results for the anterior, posterior and lateral flow patterns showed an inflow through the ear gapes and an outflow through the anterior gape, with vortices occurring inside the meat model (Figure 2A–I). This flow pattern was also described in a previous study (Shiino and Suzuki, 2011).

Under anterior or posterior flow conditions, the behaviour of the vortices inside the meat model differed from those reported for the hollow model (Shiino and Suzuki, 2011). For the hollow model, stepwise inflows generated a series of vortices, in which the first vortex moved towards the median region (Shiino and Suzuki, 2011, fig. 4E). However, it is apparent from the results of the present study that the soft parts hampered the movement of the vortices towards the median region; thus, the first vortex was pushed in an anterior direction. As it moved anteriorly, the vortex decreased in its rotational speed.

Under lateral flow conditions, the movement of the vortices differed dramatically from that seen in previous experiments (Figure 2J; Shiino and Suzuki, 2011). The soft parts prevented a vortex on the upstream side from infiltrating into the median region. Instead, a vortex through the ear gape on the downstream side emerged, resulting in nearly symmetrical vortices (Figure 2G–I). Stepwise inflows through the ear gapes pushed the vortices ahead of them, thus decreasing the rotational speed.

**A likely model of food capturing.**—The presence of the principal soft parts clearly altered the course of the vortex movement inside the model. Regardless of the ambient flow direction, the vortices aligned with the productide brachial ridges at the antero-lateral corners of the dorsal disc, which enabled the animal to sieve food particles effectively (Figure 3; Shiino and Suzuki, 2011). For lateral flow patterns, the soft parts have a rectifying function that produces symmetrical bilateral vortices, in contrast to those observed in the hollow model (Figure 2J).

The efficiency of food filtration depends on the reach



**Figure 3.** Schematic illustrations of the feeding model of productides. A stepwise inflow through the ear gape pushed the preceding vortex and then aligned with the course of the brachial ridge.

of the lophophore in capturing food particles, assuming that the animal was able to utilise the entire lophophore. Because asymmetrical internal flow behaviour causes an apparent deterioration of the filtering area, brachiopods may not prefer an ambient flow from the lateral sides. For the generation of a stable feeding flow inside the shell, the animals must adjust their life posture so that the ventral or dorsal valve faces upstream with respect to the ambient flow direction (e.g. Tomašových *et al.*, 2008; Shiino and Angiolini, 2014), or by otherwise exploiting the rectifying function of the internal flow.

In the case of spiriferides, the shell morphology functions to produce a spiral flow pattern surrounding the spiral lophophore (Shiino *et al.*, 2009; Shiino, 2010; Shiino and Kuwazuru, 2010, 2011). Although the spiral lophophore has a rectifying function, the spiral movement of the internal flow was not entirely symmetrical when the lateral side faced upstream (Shiino, 2010). This behaviour leads one to conclude that the spiriferides could employ the pedicle to mitigate this risk to some degree by changing their life posture to an appropriate orientation. Unlike the spiriferides, the productides lay on the sea bottom with their ventral valve facing down, with no pedicle attachment in mature individuals (Figure 1A). To maintain this life posture, productides usually had spines on the shell, anchoring themselves to soft substrates (Rudwick, 1970). In addition to such typical spines, large *Waagenoconcha* had thick bundles of spines at the ear extremities, which prevented them from turn-

ing upside down (Figure 1A). Unable to change their life posture, productides may have evolved to establish functional autonomy in their feeding system.

Apart from a better relationship between the lophophore shape and the characteristics of the vortex movement, the passive mechanism of food filtration would depend heavily on the flow speed surrounding the lophophore tentacles. Because rhynchonelliformean brachiopods seem to require a slower internal flow for feeding (e.g. Dhar *et al.*, 1997; Shiino, 2010; Shiino and Kuwazuru, 2011), it is likely that productide brachial ridges were arranged to circumvent swift and unstable vortices that occurred just after the inflow through the ear gapes. Development of brachial ridges at the antero-lateral corners of the dorsal disc might constitute an adaptation by which the vortex movement is kept as far away as possible from the ear gapes to slow down the rotational speed of the vortices.

Our results investigate a small part of the morpho-functional problem presented by the concavo-convex productide species. A great variety of morphological functions exists in brachiopods, in addition to the function of passive feeding flows. Further study of functional requirements may reveal why brachiopod morphology takes the forms it does.

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