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Active floating with buoyancy of pseudopodia *vs* passive floating by hydrodynamic drag force: A case study of the flat-shaped spumellarian radiolarian *Dictyocoryne*

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Abstract. It has been suggested that the pseudopodia of radiolarians play a role in controlling buoyancy for floating behaviour. To understand the function of pseudopodia in terms of planktonic capability, we performed culture experiments on the flat-shaped radiolarian *Dictyocoryne*. A glass cell, a stereomicroscope and an X-Y-Z stage were used to observe the behaviour of *Dictyocoryne* from a lateral view. Under static conditions, *Dictyocoryne* grounded on the bottom of the glass cell extended pseudopodia from both sides of the flat disc surface. Subsequently, these individuals rose slightly by a length equal to that of the extended pseudopodia but remained attached to the bottom. These results suggest that *Dictyocoryne* lacks the ability to surface by obtaining buoyancy through the emergence of pseudopodia. Under conditions of convection flow, *Dictyocoryne* moved in the downstream direction only when pseudopodia were completely extended. When the convection flow moved upward, the individuals moved with

the flow to just under the surface. In addition, convection flow changed the direction of a long, thick pseudopodium, called the axoflagellum, to be parallel with the flow. Consequently, the axoflagellum was always oriented towards the downstream side, being the disc face in the axoflagellum side on the upturn. Given that the flat-shaped spumellarians have symbiotic algae inside their cells, their unique planktonic capability leads to the stable efficiency of the algal photosynthesis.

Keywords: behaviour, holoplankton, hydrodynamics, protist, Spumellaria, symbiosis

Introduction

Holoplankton depend on the ambient seawater for feeding and respiration (Ruppert *et al.*, 2003). Because the seawater column differs in temperature, salinity and light intensity with depth (Collier, 1970), for each species of holoplankton, there should be a preferable habitat depth that enables essential biological activities.

Generally, holoplankton control their habitat depth by swimming or floating with sufficient control of gravity and buoyancy (Febvre-Chevalier and Febvre, 1994; Tsuda *et al.*, 2001; Hemleben *et al.*, 2012). In the case of immotile holoplankton including radiolarians, adaptation to a preferable depth may occur through a change in body density using light materials such as bubbles or oil droplets and through the hydrostatic and hydrodynamic effects of morphology (Febvre-Chevalier and Febvre, 1994; Suzuki and Not, 2015). With the exception of a study regarding the solitary collodarian radiolarian *Thalassicolla*, which has bubble-like extracapsulum structures that may provide buoyancy (Anderson, 1983), studies suggest that the pseudopodia play a role in generating positive buoyancy or producing drag, but this possibility has not been examined.

Polycystine radiolarians are marine holoplanktonic protists with no swimming organs (Suzuki and Aita, 2011). Based on the morphological features of their siliceous shells, 800 to 1000 species are known in the recent ocean (Suzuki and Aita, 2011), and their habitat depths differ depending on the species (e.g., Itaki, 2003; Kurihara *et al*., 2008; Boltovskoy and Correa, 2016; Matsuzaki *et al*., 2016; Boltovskoy, 2017; Zhang *et al*., 2018). Sinking, floating and drifting in seawater are feasible movements by which these organisms can change their habitat (e.g., Febvre-Chevalier and Febvre, 1994; Welling and Pisias, 1998; Suzuki and Not, 2015; Boltovskoy, 2017; Ichinohe *et al*., 2018). In sinking experiments for living and skeletal individuals of radiolarians, radiolarians with no extension of pseudopodia were found to be unable to float; thus, sinking was proposed as their dominant type of movement (Ichinohe *et al*., 2018). Radiolarian pseudopodia have long been believed to play a role in floating without effort (e.g., Anderson, 1983; Suzuki and Not, 2015), but their exact functions have not previously been analysed.

Through culture experiments, the aim of this study was to examine the spatial behaviours of flat-shaped spumellarian radiolarians and determine whether they can surface under static and flowing seawater. Based on the experimental results, we discuss how these organisms utilise the seawater column to maintain a planktonic lifestyle.

Material and methods

Material for experiments

Living flat-shaped spumellarian radiolarian *Dictyocoryne* spp. were used for the culture experiments. The individuals were collected offshore of Sesoko Island, Okinawa, on 28 November 2016 and 1 November 2017 (Figure 1) with the research vessel “Euphoria 3” of the University of the Ryukyus (Matsuoka *et al*., 2017). At the sampling locality, a custom-made No. 3 Matsuoka hand net (Matsuoka, 2002; square mouth opening with 50 cm length, 44 μm mesh size) was used to sieve plankton, including *Dictyocoryne*, at a 5 m depth. Detailed sampling methods were described in our previous study (Ichinohe *et al*., 2018).

The flat-shaped spumellarian radiolarian *Dictyocoryne* spp. herein includes *Dictyocoryne profunda* Ehrenberg and *Dictyocoryne truncata* (Ehrenberg). Both species of *Dictyocoryne* are characterised by a flat triangular shell with three arms and a single long, thick pseudopodium called an axoflagellum. Motional capability of pseudopodia including the axoflagellum, are limited to extending and retracting (Suzuki and Sugiyama, 2001). The morphological features of *Dictyocoryne* are shown in Figure 2.

Experimental protocol

To observe radiolarian behaviour, a microscopic experimental system was constructed using a custom-made X-Y-Z stage (Sho-densha, Japan), a white LED light, an observational stage, a glass cell and a stereomicroscope (Figure 3). There were two types of glass cells for the experiments; one with a cylindrical shape, a 5 mm external diameter and a 30 mm height and another with a square-pole shape, a 10 mm width and a 40 mm height. The glass cell was placed on an independent observational stage, and the position was adjusted using the X-Y-Z stage. The glass cell was divided into a bottom part and a middle part (Figure 3). An HC-W870M the digital video camera (Panasonic, Japan) was connected to the stereomicroscope with an HD-TV1C attachment (Sho-densha, Japan; with a 10× conversion lens). The glass cell was illuminated from the underside by a white LED light. To avoid the potential effects of seawater density, the seawater temperature was fixed at 27°C.

The movie data were edited with video editing software (Microsoft Windows Live Movie Maker version 2011, USA and Kenkun Aviutl version 1.00, Japan) and converted into ordered sequential data as an Audio Video Interleaved (AVI) file type. The AVI file was analysed with image analysis software (ImageJ version 1.49, The National Institutes of Health, USA), and the movie (frame sequence: ca. 0.034 s time interval = 30 frames per second) was also analysed.

Evaluation of the results of culture experiments

The floating mode of life for radiolarians is enabled by the extension of pseudopodia (Matsuoka, 1992, 2007; Sugiyama *et al.*, 2008; Suzuki and Not, 2015). Except for the solitary case of a spherical radiolarian (Suzuki and Sugiyama, 2001), there are two hypothetical explanations of the mechanisms of this floating behaviour:

1) the density of the radiolarian with extended pseudopodia is lower than that of the seawater, and/or 2) the pseudopodia experience drag or lift sufficient to exceed the gravity force, resulting in flow drift. Both assumptions were evaluated to test how a radiolarian on the bottom of a glass cell floats, with special attention given to the degree of pseudopodial extension. If a radiolarian floats by acquiring a lower density, an individual in static water conditions will move upward as the pseudopodia gradually extend as observed in a previous study (Suzuki and Sugiyama, 2001), and should ultimately detach from the bottom of the water tank. In addition to the lower density hypothesis (1), the drift hypothesis was also evaluated on the basis of the relationship between the movement of the individual and the surrounding convection flows. However, no previous papers have objectively examined the effects of surrounding convection flows. Hence, the present study examined the degree and direction of pseudopodial extension, and the moving speed and direction of radiolarians and floating small particles were representative of the ambient flow.

The degree of visible pseudopodial extension under normal optical microscopic conditions was divided into 3 phases: phase I (no visible extension of pseudopodia), phase II (extension of pseudopodia but less than the length of body size) and phase III (extending pseudopodia more than the length of the body) (Figure 4). By comparing the position of an individual in a movie frame with that of the individual in the subsequent frame, it was possible to calculate the moving speed of the individual. Weak convection occurred frequently, and the same procedure was adopted to calculate the flow velocities by tracing the movement of small *in situ* particles in the seawater. For the calculation, only particles smaller than 30 μm in diameter were used because large, heavy particles may move slowly, resulting in the underestimation of actual flow velocities.

Results

Radiolarian behaviour in the bottom part of the glass cell

Radiolarian behaviour was observed and analysed four times using four individuals. Throughout the observations, all individuals showed a similar pattern, as described below. After settlement onto the bottom of glass cell, the individuals started to extend their pseudopodia, including the axoflagellum (Figure 4). For one individual, the pseudopodia remained in the phase I for 191 seconds after settlement onto the bottom (Figure 4A). Subsequently, the pseudopodia gradually extended from the equatorial plane to phase II, while the lesser pseudopodia extended from the lateral margin of the plane (Figure 4B, C). Approximately 10 minutes later, the degree of pseudopodial extension reached phase III (Figure 4D‑F). As a result, the individuals rose slightly but remained attached to the bottom, with the pseudopodia at the lower side of the equatorial plane (Figure 4D, E). Under static water conditions, individuals never surfaced. The axoflagellum extended oblique to the equatorial plane of the shell and was aligned with the extended pseudopodia (Figure 4C‑E).

When a convection flow of more than 3.0 μm/s occurred parallel to the bottom surface, individuals with phase III of pseudopodia moved in the same direction as the flow. The moving speed of the individuals was approximately 2.0 μm/s, which was slower than that of the convection flow (Figure 5). During parallel water movements, because the pseudopodia of the radiolarians touched the bottom of the cell, friction forces would have occurred between pseudopodia and the bottom. Thus, the moving speeds of the radiolarian individuals might show underestimated value. When the convection flow moved upward, the individuals moved with the flow to reach under the surface (hereafter called "surfacing"; Figure 6). The convection flow whereby the axoflagellum oriented toward downstream (Figure 4F).

These results definitively proved that the pseudopodia of *Dictyocoryne* are ineffective in providing buoyancy. Furthermore, a buoyancy hypothesis for the axoflagellum ruled out by downstream orientation of the axoflagellum in ambient flow conditions.

Radiolarian behaviour in the middle part of the glass cell

A *Dictyocoryne* individual with a 270.6 μm shell length and phase III pseudopodia showed an upward and downward movements in upward and downward convection flows, respectively (Figure 7).

In the case of upward movement with upward convection flow, the moving speeds of the individuals increased monotonically as the convection flow speed increased (Figure 8). All cases showed that the convection flow velocities were higher than the moving speeds of the individuals, with a slope of 0.82 (Figures 7A, 8). During upward movement, the axoflagellum always oriented in an upward direction (i.e., in the downstream direction); thus, the equatorial plane was slightly oblique to the bottom of the glass cell.

In the case of its downward movement with downward convection flow, the moving speeds of the individuals were higher than the convection flow velocities, with a slope of 1.53 (Figures 7B, 8). During downward movement, the axoflagellum oriented in the upward direction (= downstream direction) (Figure 7B).

Discussion

Feasibility of buoyancy-based planktonic life

Typically, radiolarian cells and shells are denser than seawater, and the radiolarians therefore sink (e.g., Takahashi, 1983; Takahashi and Honjo, 1983; Ichinohe *et al.*, 2018). To compensate, pseudopodia function to adjust and control buoyancy in the seawater column; effortless sinking can occur by shedding the pseudopodia (e.g., Suzuki and Sugiyama, 2001; Suzuki and Not, 2015). However, in the present study, all of the individuals with extended pseudopodia remained settled on the bottom without the aid of the convection flows. To better explain for the planktonic lifestyle of radiolarians, the feasibility of buoyancy-based floating of an individual is worth considering.

When an object is in a fluid, its surface experiences pressure from the fluid. Because higher pressures act on the deeper parts of the object, upward force is exerted on the object as buoyancy. The buoyancy, F, is defined as $F = \rho V g$ (where ρ is the density of ambient fluids, V is the volume of the object and g is the acceleration due to gravity). Therefore, if the net density of the object decreases to less than that of the fluid, the object could move upward, as observed in the case of a floating ring in swimming pool.

In general, the materials inside the cells of plankton are denser than the seawater (Milo and Phillips, 2013). Lipid droplets are one candidate material to decrease the density of radiolarians, but they do not appear to be present in sufficient amounts inside the cell (Anderson, 1983). Therefore, if radiolarians need to obtain positive buoyancy, they must generate or take in light materials along with extending their pseudopodia. It has been taken for granted that the air bubbles generated by extending the pseudopodia can help to confer buoyancy (Matsuoka, 1993, 2006); however, the conjecture remains problematic with no supporting evidence. Ambient seawater may cross the cell membrane when pseudopodia extended, but this does not reduce the density of individual to that of the seawater in the case of the present *Dictyocoryne*. In light of the law of conservation of mass, *Dictyocoryne* would be forced to release the seawater when the pseudopodia contracted, a mechanism for control of buoyancy that seems to be physiologically and functionally unreasonable. Apart from the generation of light materials or their absorption from the seawater, histological evidence suggests another possibility: extension of the pseudopodia without broad modification of the cell body. The outermost ectoplasmic layer consists of a folded cell membrane that creates vacuoles inside (Cachon and Cachon, 1976). Locally retracting and unfolding the cell membrane could result in the extension of pseudopodia, possibly maintaining the quasi-outline of the cell body without changing its weight and volume. Although it is not clear at the present study, this volume dilation mechanism of radiolarians could explain how extending pseudopodia seems to simply increase their volume without changing the original outline of the cell (Suzuki and Sugiyama, 2001).

According to the morphological analyses of *Dictyocoryne*, the estimated total density of individuals without pseudopodia was 1.2 g/cm^3, much higher than the density of seawater at 1.02 to 1.03 g/cm^3 (Shiino *et al.*, *submitted to this special issue of InterRad XV*). With these facts in mind, many polycystine radiolarians, except the collodarians, may be unable to surface by intrinsic buoyancy under static fluid conditions, even with their pseudopodia fully extended. Instead, the radiolarians may move with the flow whenever they extend pseudopodia.

Hydrodynamic properties of pseudopodia

The present study revealed that the planktonic mode of life in *Dictyocoryne* is attributed to the movement of the individual with that of the ambient fluid but not to the buoyancy-based floating of the individual. Because this passive movement occurs when the pseudopodia are in phase III, further explanation of the relationship between the pseudopodia and flow is needed.

Typically, an object under flowing conditions suffers a drag force on the upstream side, that acts in the downstream direction. The drag force from the flows becomes larger than the frictional force due to settlement on the bottom. The object then detaches from the bottom, moving in the downstream direction. A larger surface area for an object increases the drag force. In the case of the present *Dictyocoryne*, innumerable fine pseudopodia were extended from the cell membrane (Figures 2, 4). An individual with well-extended pseudopodia would experience a greater drag force than an individual without pseudopodia or whose pseudopodia are retracted. As a result, the present radiolarians were able to adopt the planktonic mode of life by drifting in the seawater flow, as discussed previously (Ichinohe *et al.*, 2018). In this experiment, during upward convection flow, the individuals were forced to move slower than the convection flow, as seen in the bottom part and the middle part of the glass cell. In contrast, in the case of downward convection flow, the speed of *Dictyocoryne* along with the flow was faster than the speed of the convection flow. This movement indicated that the gravitational force overcame the drag force, causing the individual to sink through the downward flow.

The pseudopodia of all radiolarians extend from the surface of the cell (e.g., Cachon and Cachon, 1976; Anderson, 1983; De Wever *et al.* 2001; Suzuki, 2005; Suzuki and Aita, 2011). A larger surface area of a cell membrane is beneficial for extending numerous pseudopodia. However, enlarging the surface area for growth leads to an increase in cell volume, and a heavier weight results in immediate sinking, as demonstrated previously (Fig. 8 in Ichinohe *et al.*, 2018). To avoid the risk of sinking, a flat form best fits with the growth strategy of employing a large surface area to decrease the increase in volume (see also Shiino *et al.*, *submitted to this special issue of InterRad XV*).

Understanding the movement and orientation of *Dictyocoryne* requires further explanation of the mechanism by which the axoflagellum faced the downstream side in the horizontal and upwelling flows. Because the axoflagellum is a long, thick structure among the pseudopodia, it has unique hydrodynamic properties. The hydrodynamic function of the axoflagellum was discussed by Ichinohe *et al.* (2018) in the case of conical nassellarians. Based on extensive knowledge from aerodynamic studies (e.g., von Kármán, 1954; Yechout, 2003; Cook, 2013; Corda, 2017), an object in a fluid, such as a flying airplane or a badminton shuttlecock, flies in a stable manner with its axis parallel to ambient flow. In such trimmed rectilinear flow, the stability of a flying object relies on the degree of the yawing moment (von Kármán, 1954). This hydrodynamic effect, called the weathercock effect (Corda, 2017), has acted on the *Dictyocoryne* with axoflagellum, causing its direction to be downstream, similar to the case in nassellarian radiolarians (Ichinohe *et al.*, 2018). Following the same mechanism, sinking behaviour during flow of downward convection could change the direction of the axoflagellum upward, as also discussed in the case of nassellarian radiolarians (Ichinohe *et al.*, 2018).

The flat-shaped radiolarians have a tubular passway (tunnel) on the shell, which is an attachment trace of the axoflagellum within the patagial shell (Matsuoka, 1992, 1994). In the case of *Dictyocoryne*, the shell has a depression on one side of the equatorial plane (Matsuoka, 1992, 1994). Because the depression shows oblique elongated concavity, with the bottom close to a triple junction of arms (Shiino *et al.*, *submitted to this special issue of InterRad XV*: pylome), the axoflagellum has a tendency to extend oblique to the disc surface. As a result, the equatorial plane of the flat-shaped shell in *Dictyocoryne* could face the vertical direction to some extent, and this orientation appears to function in providing postural stability in fluids (Figure. 9). Suzuki and Sugiyama (2001) observed "rising movement" in a *Diposphaera hexagonalis* (Haeckel), when pseudopodia were elongated. This is also explained by the generation of lift with these radiated pseudopodia.

Adaptive strategy of *Dictyocoryne*

Living *Dictyocoryne* primarily inhabit a wide range of tropical regions in the Pacific Ocean (Lombari and Boden, 1985; Boltovskoy *et al.*, 2010) and are thus known as shallow warm water species (Matsuoka, 1993, 2009; Kurihara and Matsuoka, 2010; Ishitani and Takahashi, 2012). Among the species, *Dictyocoryne profunda* has a habitat depth shallower than 100 m (e.g., Matsuzaki *et al.*, 2016).

According to Robert *et al*. (1996), flow speed offshore of the eastern Pacific Ocean drastically decreases at 40 m depth and decreases less than 5000 μm/s at 120 m depth (Robert *et al.*, 1996). In addition to the vertical disparity, the flow speed differs in horizontal marine realms, varying from almost zero to a few dozen cm/s (Talley, 2011). Such flow is enough to float *Dictyocoryne* with fully extended pseudopodia, preventing sudden sinking due to a large, heavy shell (Ichinohe *et al.*, 2018). Similarly, differences in planktonic capability in terms of passive spatial behaviour, as seen in the cases of foraminifers and radiolarians, may result the habitat differentiation.

The results of the present study suggest that, hydrodynamic disturbances constrain the habitat of the present *Dictyocoryne*. Flat-shaped radiolarians such as *Dictyocoryne*, *Spongodiscus* and *Spongaster* may take advantage of whole-body "sunbathing" to move effectively.

Conclusions and future perspectives

Using culture experiments, we determined that the radiolarians examined herein were unable to surface via buoyancy conferred by density lower than that of seawater. Instead, numerous fine pseudopodia could produce a drag force greater than the ambient flows, even at a speed of approximately a few micrometres per second. In movement with flow, the axoflagellum, a long and thick pseudopodium, can reorient the organism so that the axoflagellum faces in the downstream direction. The stable posture is that in which equatorial plane is slightly oblique to the horizontal direction, which may enhance the photosynthesis of symbiotic algae.

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Figure captions

Figure 1. Map of Sesoko Island, Okinawa, Japan, showing the sampling locality. The dashed line indicates the sampling area. TRBC: Tropical Biosphere Research Center, University of the Ryukyus.

Figure 2. Microscopic photograph of living *Dictyocoryne* under a normal optical microscope.

Figure 3. Schematic illustration of the experimental system and glass cell. A stereomicroscope with a 90-degree incline enabled observation from the lateral direction. The observation area of the glass cell was subdivided into a bottom part and middle part.

Figure 4. Radiolarian behaviour in the bottom part of the glass cell. **A,** phase I of the pseudopodia. **B,** phase II of the pseudopodia. **C,** phase II of the pseudopodia with axoflagellum. **D,** phase III of the pseudopodia with full extension of the axoflagellum. **E**, **F**. Axoflagellum reoriented to the downstream direction of convection flow.

Figure 5. Movements of individuals and particles in the bottom part of the glass cell. **A,** composite image of maximum brightness based on 3 photographs taken for 1 seconds each. **B,** history of speeds of the individual and particles. The solid and dashed lines show the average of 20 neighbouring points.

Figure 6. Composite image of maximum brightness based on 3 photographs taken for 1 second each showing surfacing movement in the bottom part of the glass cell.

Figure 7. Upward and downward movements of individuals and particles in the middle part of the glass cell. **A,** upward movement. Composite image of maximum brightness based on 8 photographs taken for 1 second each. **B**, history of speeds of

the individuals and particles in upward movement. The solid and dashed lines show the average of 20 neighbouring points. **C,** downward movement. Composite image of maximum brightness based on 8 photographs taken for 1 second each. **D**, history of speeds of individuals and particles in downward movement. The solid and dashed lines show the average of 20 neighbouring points.

Figure 8. Scatter plots of moving speeds with respect to flow velocities. All plots were calculated from one individual 270.6 μm in length.

Figure 9. Explanatory illustration of hydrodynamic stability in the flat-shaped spumellarian *Dictyocoryne*. Flows always alter the posture of *Dictyocoryne* with the axoflagellum facing in the downstream direction (weathercock effect; see Ichinohe *et al*., 2018).

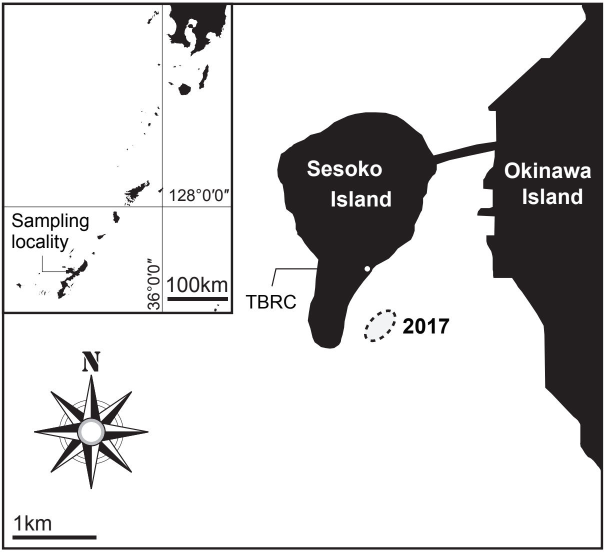


Figure 1 (Ichinohe et al.)

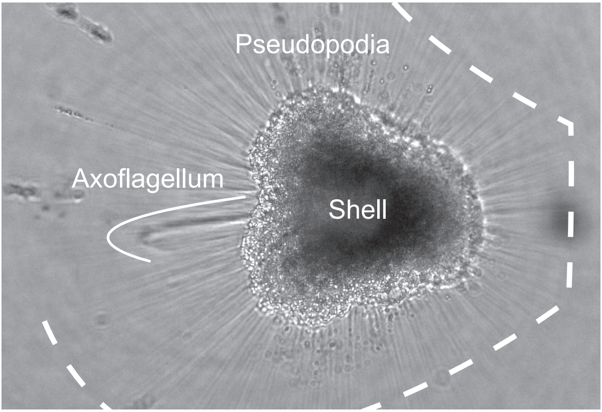
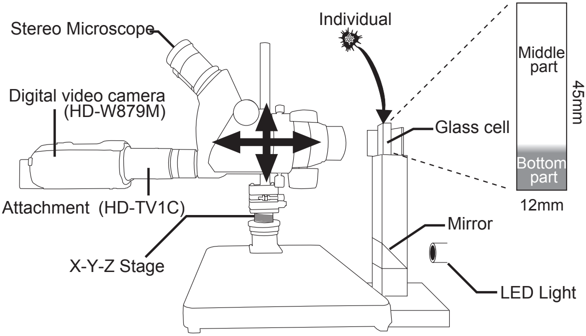


Figure 2 (Ichinohe et al.)



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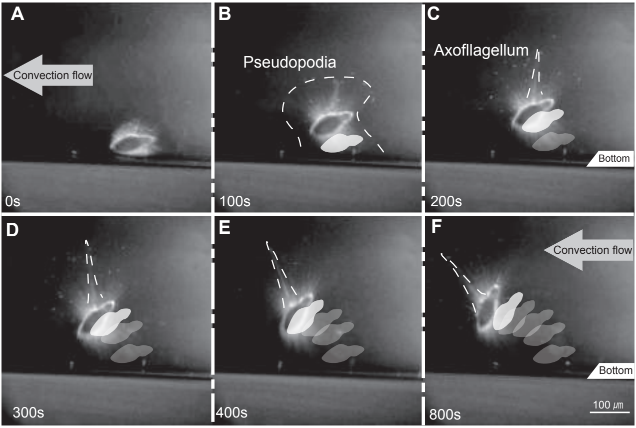

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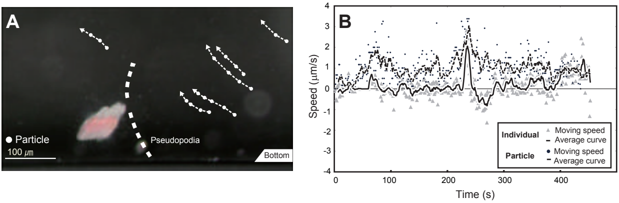

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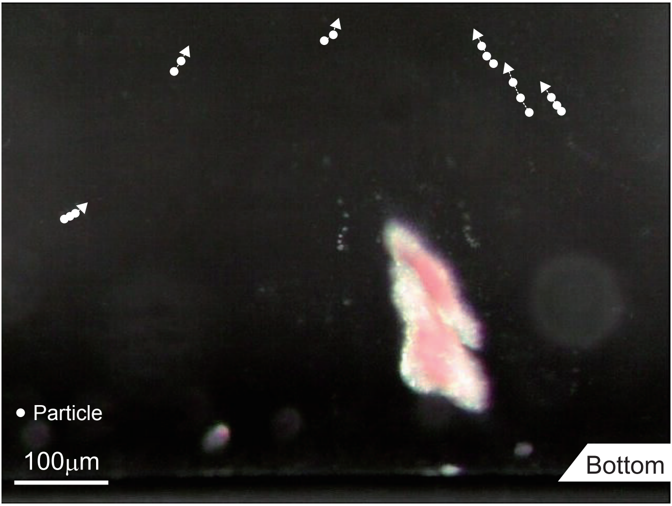

Figure 6 (Ichinohe et al.)

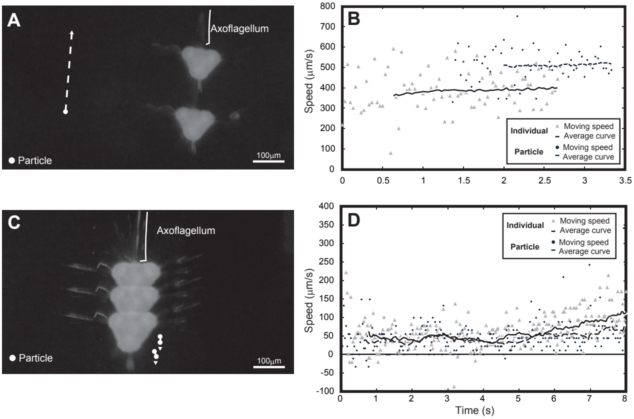

Figure 7 (Ichinohe et al.)

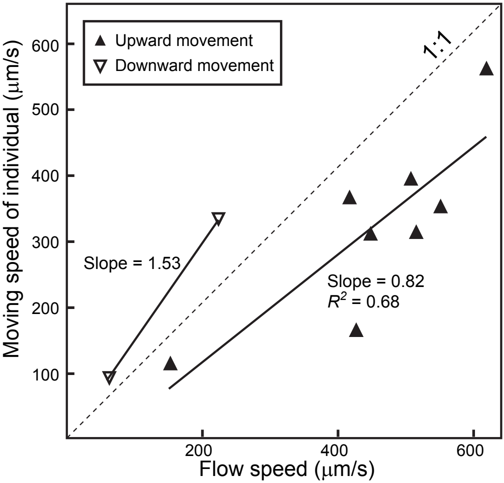

Figure 8 (Ichinohe et al.)

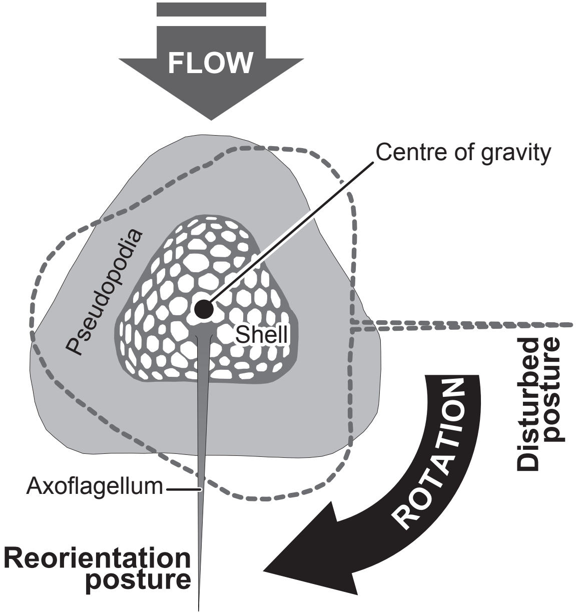

Figure 9 (Ichinohe et al.)