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House formation and feeding behaviour of *Fritillaria borealis* (Appendicularia: Tunicata)

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Abstract Numerous marine animals use elaborate filtration mechanisms to feed on particles suspended in the sea. Video-microscopy reveals that the common appendicularian *Fritillaria borealis* do so in a unique way. They live inside acellular, mucous houses, where their tail undulations act like a peristaltic pump in a close-fitting tail chamber to force water through a complex set of filters. Suspended particles, between ~0.2 and 30 µm in diameter, are retained in this process and propagated towards the mouth of the organism to be ingested. Coarser particles are back-washed out of the house during brief intervals of tail arrest, when the elastic recoil of the house walls reduces its volume to one-eighth of its inflated state. At the same time, the bifurcated tip of the animal's tail slides into a sleeve-like extension of the house. This sleeve acts like a flipper to propel the animal and collapsed house several millimetres to a few centimetres through the sea as soon as muscular activity of the tail is resumed. After a second tail arrest, a special muscular twist brings the tail out of the sleeve, whereupon undulatory pumping movements are resumed to reinflate and process particle-laden water through the house. The complete behavioural cycle lasts ~30 s. The repetitive inflation and deflation cycles of the house are probably of importance for unclogging of the coarse "inlet" filters downstream to the tail pump, as well as for agglutination of the smallest food particles trapped in the house to ease their recapture in the endostylar pharyngeal filter during the ingestion process. The unique tail sleeve and flipper at the same time enable the animal to move away from the previously filtered water and rejected coarse particles, before the house is reinflated for resumed food filtration.

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Introduction

All species of Appendicularia are believed to produce external filtration devices by a complex secretory process of an epidermal glandular epithelium, known as the oikoblastic (i.e. house-forming) epithelium, covering some of their trunk. However, whereas the structural organisation of the external filter house of several species of *Oikopleura* has been worked out in great detail, the structural organisation of the feeding structures found in the genera *Fritillaria* and *Kowalevskia* are still poorly understood (Flood and Deibel 1998). In fact, up till recently, Fol's drawings from 1872 were as accurate and informative as any later drawing of these structures.

Fol (1872) described the external feeding structure of *Fritillaria megachile* as an extremely delicate, hollow vesicle, attached to the mouth of the organism. This structure was hardly visible unless the organism's tail undulated to inflate the structure by forcing water into the vesicle through an opening in its wall.

Lohmann (1903, 1909, 1933), who presented drawings of the feeding structure of an unidentified species of *Fritillaria*, as well as Bone et al. (1979), who studied the behaviour of *Fritillaria pellucida*, added some details to this view, but maintained that the organisms did not live *inside* their feeding structures, but only were *attached* to these by their mouth. In other words, the undulating tail caused a water jet to inflate the feeding structure from a distance. However, it has also been stated (Fol 1872; Lohmann 1909; Bone et al. 1979) that the animal and its feeding vesicle do not move appreciably through the water while the tail is beating. I find it difficult to understand, in hydrodynamic terms, how undulating tail-beats outside a feeding structure should push water into a vesicle from a distance, rather than propel the animal through the sea.

Twenty-six species of *Fritillaria* are recognised worldwide (Fenaux 1993, 1998; Fenaux et al. 1998) and several of them are important constituents of the marine zooplankton. Gran (1929) identified up to

240 individuals of *Fritillaria borealis* l⁻¹ seawater in centrifuged samples from outside Romsdalsfjorden, western Norway! There is also evidence from mesocosm experiments in western Norwegian fjords that the abundance of *F. borealis* may be regulated by predation rather than by food availability (Skjoldal et al. 1993). With a generation time counted in days rather than weeks, a high growth rate and fecundity (Fenaux 1976) and a grazing impact on micrometre-sized particles (this communication), the importance of *F. borealis* in the marine ecosystem has probably been underestimated for a very long time. A detailed description of the feeding biology and behaviour of this species, therefore, seems worthwhile. (Part of this study has previously been summarised in Flood and Deibel 1998).

Materials and methods

Fritillaria borealis (forma typica) (Lohmann 1896a, 1896b), with their feeding structures attached, were carefully scooped out of the surface water at the floating dock of Friday Harbour Laboratories, University of Washington, during January–February for several years between 1986 and 1996. These samples were kept in 100 ml beakers and brought rapidly to the laboratory for examination.

Comparable samples of the same species were also isolated by pipette from dilute plankton samples from Rosslandsvågen, western Norway, during March and April, 1997–2001. These samples were derived from vertical hauls (10–0 m depth) of a WP-2 net (Fraser 1968) with a pore size of 95 µm.

Likewise, several specimens of *Fritillaria pellucida*, with newly expanded feeding structures, were collected in the bay of Villefranche sur Mer, France, during the summer 2000, and studied after transfer to a bowl of filtered seawater.

The samples, still in beakers containing approximately 100 ml of either seawater directly from the field, or seawater filtered through a 0.45 µm pore size membrane filter, were mounted on a microscope stand with bright-field or dark-field illumination from below. Several brands of dissection microscope were used throughout this study, and most video recordings were made through a Wild model M5A dissecting microscope, equipped with a Sony HVM-200 B&W CCD video camera and mounted on a movable lever arm that allowed it to be adjusted rapidly in all directions to keep the freely swimming animals and their feeding structures within the field of view and at the correct focal level. The recordings were made on Panasonic video tape recorders (models AG 2510 and AG 7300, NTSC format) with frame numbers added through a Thalner Electronics model VC-405 frame counter. The water temperature during most of these experiments ranged between 12°C and 15°C.

For analytical purposes the live video sequences, run at distinct frame rates, proved most useful. Frozen frames from the same sequences had inferior resolution, but will nevertheless be used throughout this article as documentation. Frozen frames of the same house and animal complex, taken at short intervals, could also be mounted as stereo pairs for three-dimensional viewing, provided that the pair showed a suitable parallax shift.

Frame-by-frame analysis for timing of distinct phases of behaviour was made on an Apple MacIntosh IICI computer, equipped with a QuickCapture videoboard (Data Translations) and the NIH Image 1.43 public domain software package.

Small amounts of washed and repeatedly centrifuged melanin particles from the ink of *Sepia officinalis* were sometimes added to the water to increase the visibility of the delicate and transparent feeding structures (Flood et al. 1990). These melanin particles had a diameter of 0.13 ± 0.23 µm (mean \pm SD, Flood et al. 1992) and formed a stable, non-agglutinating suspension in seawater.

Attempts were also made to mount abandoned houses of both *F. borealis* and *F. pellucida* on Formvar and carbon-coated grids for electron microscopy to establish the physical parameters of their “inlet” as well as food-concentrating filters. These specimens were stained by uranyl acetate and lead hydroxide before examination in a Hitachi H-600 transmission electron microscope operated at 60 and 80 kV.

Results

Both live video sequences and still frames of such videos showed that most of the *Fritillaria borealis* organism was located within an acellular, mucous-like feeding structure, about 2 mm wide and of very complex organisation (Figs. 1, 2, 3). Only the posterior (gonadal) part of the animal trunk and the anterior “shoulders” of the tail were exposed to the outside of this feeding structure, which therefore may appropriately be called a “house”.

Houses expanded in non-filtered water from the field were generally decorated with numerous particles of variable size that obscured much of their internal construction (Fig. 1). Such details were far easier to see in houses expanded in filtered seawater to which slight amounts of melanin particles from *Sepia* ink had been added. These particles resulted in quite even “staining” of the house walls, filters and septae (Figs. 2, 3). To ease the readers understanding of the description and videographic illustrations (Figs. 1, 2, 3, 4, 5) below, the author’s interpretation of the architecture of the *F. borealis* house and its water circulation pattern is presented as a line drawing (Fig. 6).

The house consisted of three main compartments: (1) a midline tail chamber that surrounded most of the muscular tail of the animal, (2) a wide midline food reservoir that surrounded the mouth and circum-oral

Fig. 1a–c *Fritillaria borealis*. Frozen video-frames of *F. borealis* in its house in non-filtered seawater direct from the field. **a** Dark-field side view of animal (*A*) resting inside its deflated house (*H*). **b** Dark-field view of the same animal actively pumping in the same house. **c** Dark-field side view of the same animal (motion blurred), just after it has jettisoned its house

Fig. 2a–c *Fritillaria borealis*. Frozen video-frames of *F. borealis* in its house expanded in *Sepia*-melanin-containing filtered seawater. **a** Dark-field side view of animal (*A*) resting inside its deflated house (*H*). Note the sleeve-like flipper (*F*) projecting from the lower aspect of the house. **b, c** Stereoscopic picture-pair of animal in its inflated house as seen from the side. (The undulating tail of the organism has been erased so it does not interfere with proper stereovision.) Note the flaccid sleeve (*F*) projecting from the bottom of the tail chamber

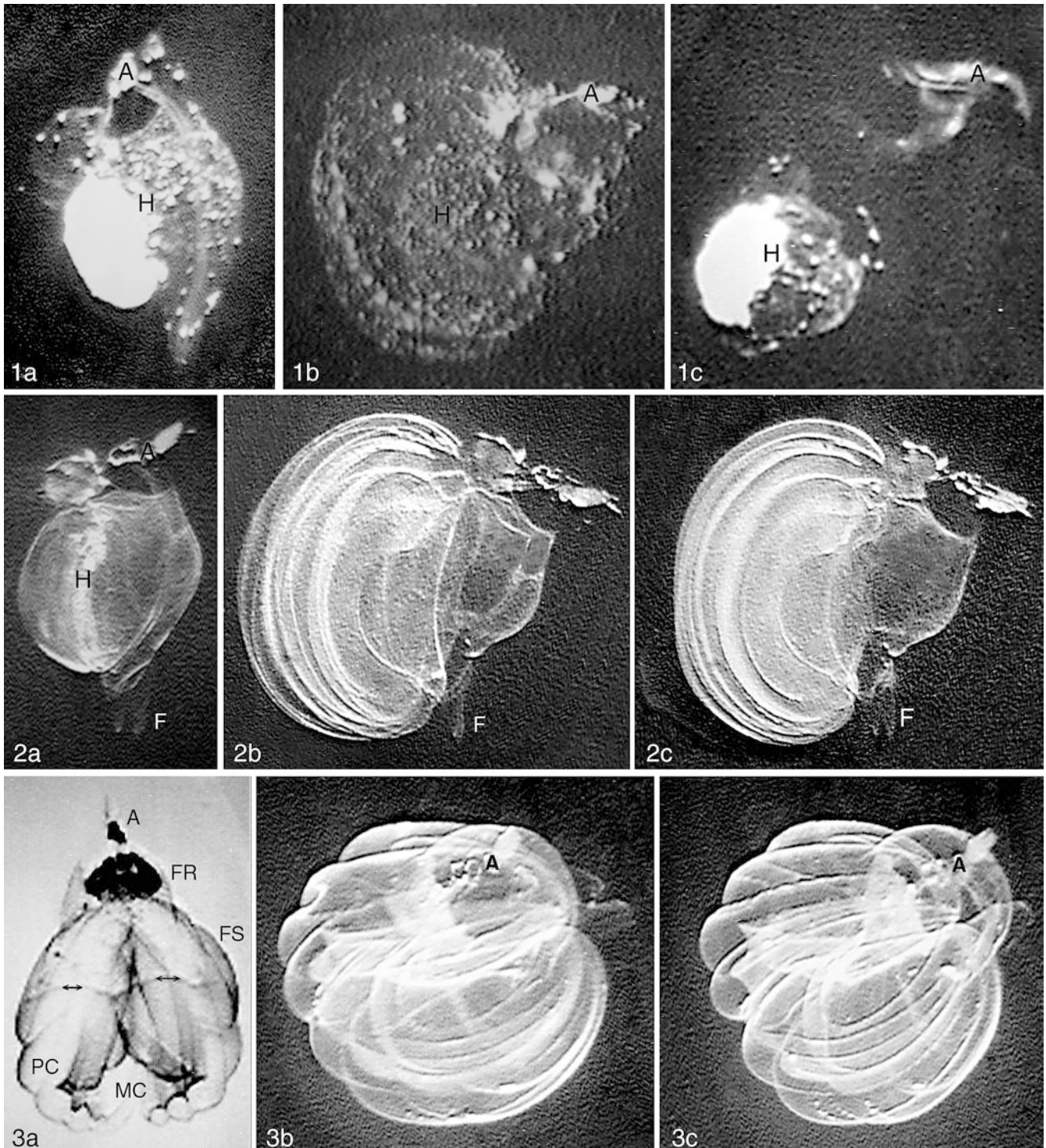
Fig. 3a–c *Fritillaria borealis*. Frozen video-frames of *F. borealis* in its house expanded in *Sepia*-melanin-containing filtered seawater. **a** Bright-field frontal view of animal (*A*) in its inflated house. Note the heavily stained food reservoir (*FR*) and the less heavily stained filter section (*FS*) of the house. The food-concentrating filters are probably made up of the external and internal walls of the fluted peripheral chambers (*PC*), and water is probably drained to both the exterior and the corrugated midline chamber (*MC*). The lines marked by double-headed arrows probably represent a coarse inlet filter, downstream to the tail chamber. **b, c** Stereoscopic picture-pair of animal in its inflated house. Oblique frontal view

hood of the animal, and (3) an extremely elastic filter section of bilateral symmetry that filled the gap between the tail chamber and the food reservoir. All of them responded to undulating movements of the tail with a pronounced inflation (Figs. 1b, 2b, c) and to tail arrests with a pronounced deflation (Figs. 1a, 2a).

The organism was attached to its house at three points: the mouth and circum-oral hood were deeply

embedded and fixed to the food reservoir, and two slender filaments connected the tips of the bilateral cuticular processes at the posterior end of the trunk (Fenaux 1965) to the upper, posterior and lateral margins of the tail chamber (Figs. 1a, 2).

The *tail chamber* was just wide and high enough to give room for the undulatory movements of the tail. The wave-fronts of the tail-beats evidently acted like a



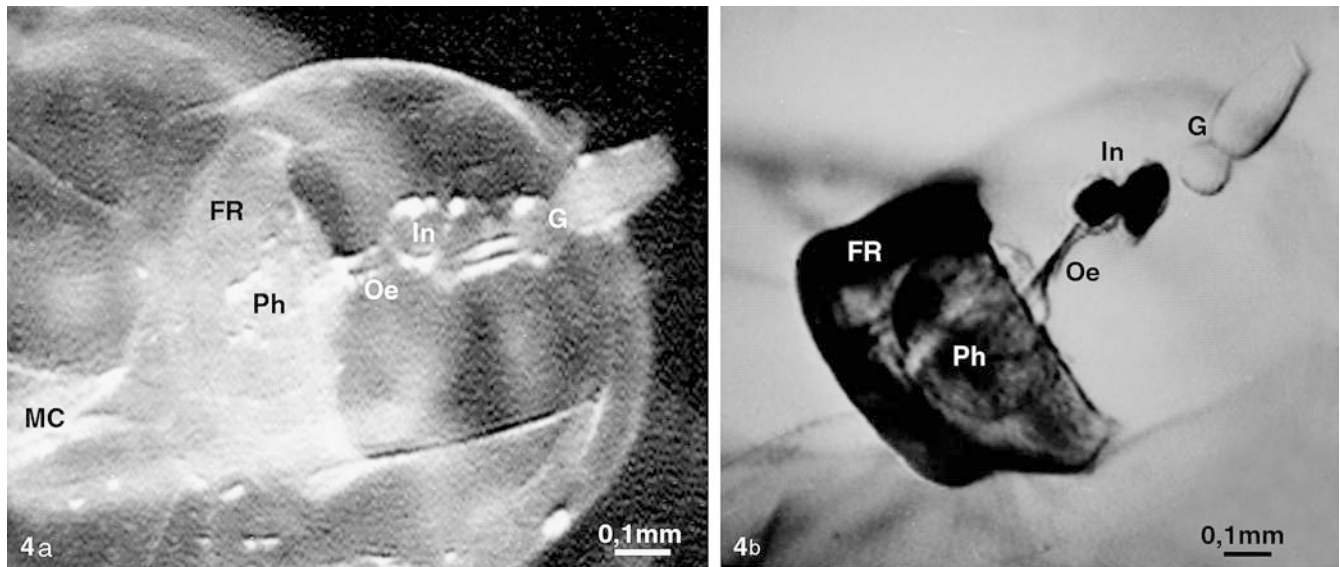


Fig. 4a, b *Fritillaria borealis*. Frozen video-frames of *F. borealis* in its house expanded in *Sepia*-melanin-containing filtered seawater. **a** Dark-field dorsal view of the three trunk segments: gonads (*G*), intestinal globule (*In*) and pharynx (*Ph*) and their relation to the food reservoir (*FR*) and upper part of the midline chamber (*MC*) of the house. **b** Bright-field dorsal view of the same animal to show the extent of the food reservoir (*FR*) in relation to the pharyngeal (*Ph*), intestinal (*In*) and gonadal (*G*) trunk segments. Note also the *Sepia*-melanin-laden pharyngeal filter passing down the oesophagus (*Oe*)

piston- or peristaltic pump to suck water from the exterior and push it down the tail chamber, into the house. Such a current of water could clearly be seen from the movement of suspended particles. It was also noted that particles $> 30 \mu\text{m}$ in diameter were arrested at the lower anterior wall of the tail chamber, whereas smaller particles, and water, continued into the filter section of the house to inflate this.

During tail arrests the wide, pumping portion of the tail chamber proved too short to give room for the entire stretched out tail. The distal one-third of the tail rather slipped into a *sleeve-like extension* of the tail chamber, pointing towards the exterior of the house. Together the flaccid sleeve and more rigid tail constituted a flipper (*F* in Fig. 2a), which acted to propel the house and animal complex several millimetres to a few centimetres through the water mass each time the animal resumed its tail movements, but before the house started to reinflate. During the reinflation process the tail slipped out of the flaccid sleeve (*F* in Fig. 2b, c) and the animal–house complex thereby lost its ability to move any further through the water mass.

The inflatable *filter section* (*FS* in Fig. 3a) was the widest part of the house. It was crescent-shaped in outline, with the convex surface pointing forward and ventrally. By using *Sepia* melanin particles suspended in the water, two membranes capable of trapping food and experimental particles above $\sim 0.15 \mu\text{m}$ in diameter were discerned in this section during its inflated state (Figs. 2b, c, 3). The outer membrane of this food-concentrating trap constituted the external wall of the

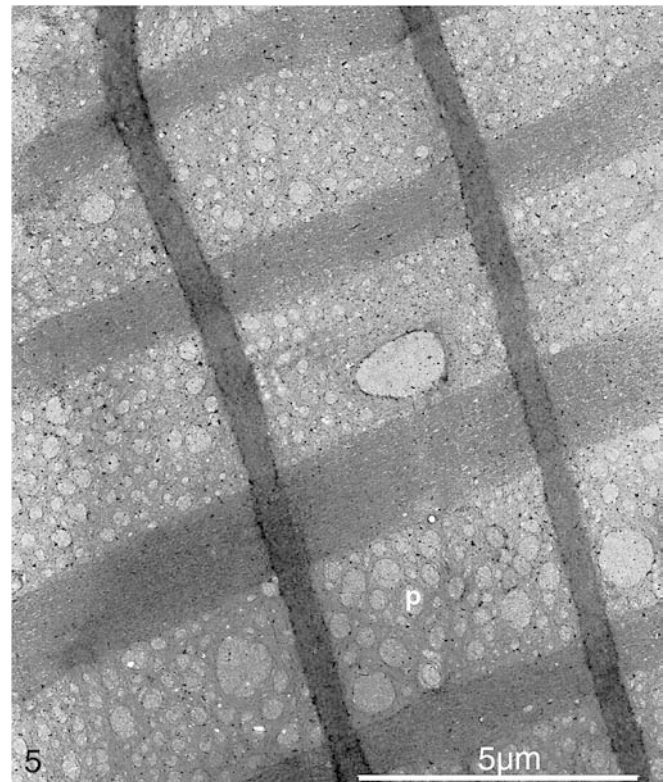


Fig. 5 *Fritillaria borealis*. Transmission electron micrograph of rectangular mesh structure found inside a house, micro-dissected and mounted on a supporting copper grid with Formvar and carbon film. Notice also the presence of minute oval pores (*p*) in a distinct layer

house and consisted of six outward-bulging bilateral flutes that ran from the lower end of the tail chamber to the food reservoir of the house. The diameter of these flutes (*PC* in Fig. 3a) appeared to increase gradually from the anterior sagittal plane to the more posterolateral border. In fully expanded houses, with actively pumping animals inside, water seeped slowly through

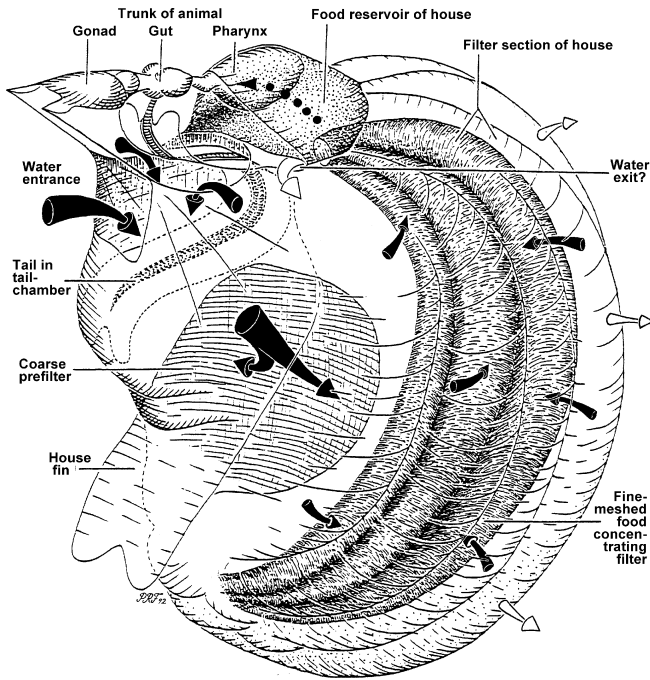


Fig. 6 *Fritillaria borealis*. Sketch of *F. borealis* in its inflated house as seen in oblique posterior view, with *black arrows* indicating the probable direction of flow of water and particles into the house, *white arrows* for water leaving the house, and *dotted arrow* for food particles accumulating in its food reservoir (reproduced from Fig. 6.6b in Flood and Deibel 1998)

this external wall over most of its surface. This was evident from the appearance of a layer of increasing thickness of clear water “lifting away” sepioid water from the external walls (S in Fig. 2c). Obviously, the external wall was also a food-concentrating filter that retained sepioid melanin particles, but allowed filtered water to pass.

The inner layer of the food-concentrating trap had similar flutes towards a midline cavity that extended like a corrugated, bent tube from the lower end of the tail chamber to the food reservoir (MC in Fig. 3a). Based on the direction of curvatures in the two membranes of the food-concentrating trap, it was obvious that the hydrostatic pressure was higher between these filters than in the outside environment and in the corrugated midline cavity. Water from the tail chamber, therefore, must enter between the two food-concentrating filters before being drained across the filter screens (with a concomitant drop in pressure) to the outside of the house, and to the corrugated midline chamber. Obviously, some filaments connected the outer and inner food-concentrating filters to each other along the borderlines between their convex flutes to prevent them from being blown further apart.

As soon as the animal stopped beating its tail, the elastic recoil of the filters caused the filter section of the house to deflate to a bean-shaped structure between the animal’s mouth and tail (Figs. 1a, 2a). The difference in volume between the inflated and deflated states of this filter section was about eightfold. Food particles

contained in the deflated filter section were probably coagulated to larger aggregates and gradually passed on to the food reservoir section of the house, whereas water was back-flushed through the tail chamber to the exterior of the house. The opaque mass of trapped particles in the deflated filter section of field houses was easily visible in the dissecting microscope (Fig. 1a) and probably constituted the structure misinterpreted by previous investigators (*vide supra*) as representing the entire feeding structure of fritillariids.

Particles arrested against the porous anterior wall of the tail chamber, as described above, were effectively washed out of the house during such tail arrest periods. From the video recordings these appeared to range in size from $\sim 30 \mu\text{m}$ upwards. In other words, the porous wall, downstream of the tail pump of the houses functioned similarly to the upstream inlet filters of oikopleurid houses, to prevent large (and potentially harmful?) particles from gaining access to the delicate filter section of the house (cp. Flood and Deibel 1998). Coarse net structures with rectangular meshes, possibly representing such an inlet filter, were identified in some of the specimens of *F. borealis* and *F. pellucida* processed for transmission electron microscopy (Fig. 5). However, the degree of stretching or elastic recoil of these specimens remains unknown, and the mesh parameters observed should be interpreted with great caution.








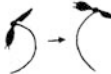

The *food reservoir* section of the house (FR in Fig. 3a) was about 1.5 times as wide and long as the embedded parts of the animal’s trunk and hood (Fig. 4a, b). Food particles from the filter section of the house were gradually passed on to this section of the house and gave this compartment a rather opaque appearance. From this reservoir a dense suspension of food particles was intermittently sucked into the mouth of the animal, re-trapped in its endostylar pharyngeal filter, and conveyed to the oesophagus and stomach (Fig. 4a). Activation of the spiracles seemed to be responsible for such ingestion.

Several abandoned and collapsed houses (cp. Fig. 1c), as well as cast off, unsuccessfully expanded rudiments to new houses, were usually found in vials left with seawater and fresh animals for a few hours. This indicated that at least some animals were capable of expanding new houses at frequent intervals, even in the enclosed environments of 100 and 200 ml beakers, but also that this process often failed and resulted in loss of house rudiments.

The *behaviour* of *F. borealis* in relation to its house could be divided into several phases: (1) the rudiment-expansion phase, (2) the normal feeding cycles and (3) the house-jettison phase. One animal also showed (4) a peculiar water outflow-obstruction-behaviour. In addition, most animals were observed in (5) a free-swimming phase (cp. Table 1).

Unfortunately, the conditions under which these behavioural aspects were observed, cannot be considered physiological; the animals were obviously stressed by the presence of container walls within a few

Table 1 Tabular survey of distinct motor behaviours shown by *Fritillaria borealis*

Name of phase	Appearance of animal	Tail movement	Tail beat frequency in Hz	Duration of phase in sec.	Function
Rudiment expansion		Wiping ventro-flexion	2-3	Highly variable	Deployment of new rudiment
Feeding cycle Active pumping		Propagated wave	~ 8	~ 20	Trapping of food particles
Feeding cycle Deflation		None	0	0,5	Backwashing of inlet filter
Feeding cycle Swimming with house		Whole tail flexions	~ 15	~ 1	Locomotion, Prevent re-clogging
Feeding cycle House re-inflation		Dorsi-flexion, Ventro-flexion, Propagated wave	once once ~ 8	0,1 0,1 2	Filling of tail-chamber Re-inflation
House jettison		Whole tail flexions	~ 15	10-600	Detachment from house
Water outflow obstruction		Constant ventro-flexion	once	5-10	Prolonged feeding?
Free swimming		Whole tail flexions	~ 15	Variable	Wait for rudiment synthesis
Free resting		None	0	Variable	Ditto

centimetre range and may also have reacted to turbulence, temperature and light conditions other than those experienced in their natural environment, as well as to the presence of the *Sepia* ink particles used to visualise the walls and filters of the houses. However, in spite of these limitations, the observed behaviour, or at least its qualitative components, is likely to reflect the normal functional capabilities of these animals.

1. The *rudiment-expansion phase* (after an animal had escaped from its old house) appeared to vary somewhat in duration, but could be as short as 30 s. It consisted primarily of special tail muscle contractions, whereby the tip of the tail wiped repeatedly against the ventral surface of the anterior trunk segment in an anterior direction, probably to grasp hold of the ventral part of the rudiment to stretch this out before the tail could be inserted into a rudimentary tail chamber to start the real house inflation process (data not shown).
2. The *normal feeding cycle* was the most typical behaviour observed (Fig. 7). It consisted of at least

four phases: (a) the active pumping phase, (b) the deflation phase, (c) the “swimming with house” phase and (d) the re-inflation phase.

- a. The *active pumping phase* lasted approximately 20 s at 12°C and consisted of prominent tail undulations travelling from the proximal to the distal part of the tail. Their frequency was about 8 Hz, and the amplitude probably high enough to occupy the entire height of the tail chamber. At any moment the tail constituted a curvature corresponding to about three-fourths of a wavelength, thus always touching the upper and lower walls of the tail chamber at some level. Hereby, the propagating tail wave-front acted like a piston to force water down the tail chamber. For this pump to act properly, it is also necessary for the tail fins to cover the entire width of the tail chamber to prevent water from passing to both sides and behind the advancing tail wave-front. Although this geometry could not be verified by direct observation, it seems reasonable to propose such a

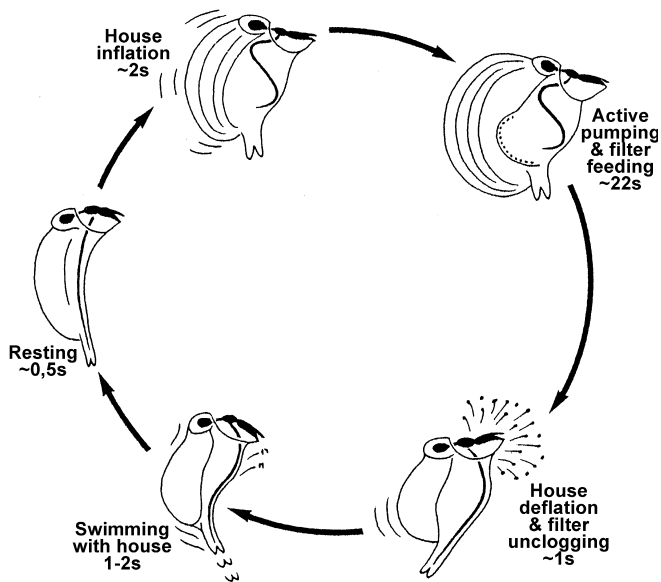


Fig. 7 *Fritillaria borealis*. Schematic representation of the typical feeding cycle in relation to the inflation/deflation process of its house

high-efficiency situation. Based on frame-by-frame analysis of a video-sequence, the speed of the tail wave-front down the tail chamber was determined. Together with measurements of tail width (determined on fixed samples), and tail chamber height (measured as tail beat amplitude in perfect lateral projection), the volume of water being processed through the house could be approximated (cp. Flood 1991). Assuming the pump to be non-leaky, a pumping rate of $3.8 \text{ mm}^3 \text{ s}^{-1}$ was derived for an adult animal with trunk length 0.9 mm. Allowing for frequent, but brief, periods of non-pumping behaviour, a water processing capacity of ~ 10 to 12 ml h^{-1} or $\sim 250 \text{ ml day}^{-1}$ therefore seems reasonable for an adult.

- b. The *deflation phase* was characterised by a tail arrest of 0.5–1 s duration in a semi-flexed posture, resembling that of a quiescent animal without a house. During this tail arrest, the entire filter section of the house collapsed to an opaque, small ellipsoid body, located between the food reservoir in front of, and between, the mouth and the tip of the tail. This deflation probably resulted in a pronounced coagulation of small particles trapped between the filters, thus enabling the animal (at a later stage) to ingest larger aggregates of particles rather than to recapture individual small particles in the pharynx. The volume of the filter section was reduced to one-eighth of its inflated volume during the deflation phase, and most of the water contained was forced to back-flush out of the house through the tail chamber. The coarse particles trapped in the “inlet” filter, downstream of the tail, were then washed out of the house. Some water from the filter section, and the dense suspension of particles contained therein, were probably also forced into the food reservoir during the deflation process. Another important event of the deflation process was that the arrested tip of the tail slipped into the sleeve-like extension of the tail chamber.
- c. The “*swimming with house*” phase usually started as soon as the deflation process was completed. It consisted of repeated whole tail contractions, one side alternating with the other at a frequency of about 15 Hz. This phase lasted for only about 1 s, but, since the tip of the tail was still inserted in the sleeve-like extension of the tail chamber, this structure acted like a flipper, projecting from the collapsed house in such a way that both animal and house moved through the water for several body lengths, thus leaving the area of previously filtered water. This translocation, although at a millimetre scale, probably enhanced the animal’s chances of exploiting new food resources rather than to re-filter the same water mass several times.
- d. The *re-inflation phase* started after approximately 0.5 s of tail arrest at the end of the “swimming with house” phase. A single and particularly strong dorsi-flexion of the entire tail, lasting only 0.1 s, then stretched out the deflated house to some degree. This dorsi-flexion probably served to reinflate the tail chamber to some extent and was immediately succeeded by a prominent single ventro-flexion starting in the middle of the tail and travelling towards both of its ends. This also lasted for only 0.1 s and probably aimed at pulling the tip of the tail out of the sleeve-like extension of the tail chamber. By this single stroke the entire tail was free to move inside the tail chamber. The normal antero-posterior tail undulations then took over to propel water down the tail chamber. These contractions had a frequency of about 8 Hz, and were able to reinflate the entire house to its full size in a matter of 1.5–2 s. This phase then continued without any intermission in the active pumping phase described above.
3. The *house-jettison phase*. On several occasions animals partly detached from their houses were observed. This was evidenced by movements of the trunk relative to the inflated house, in synchrony with the tail-beats. In most cases, it was one of the suspensory ligaments from the upper end of the tail chamber to the posterior cuticular processes of the trunk that detached first. However, in a few cases it also seemed like the mouth of the animal was first to detach from the house. The animals of such partly detached houses soon switched from normal pumping rhythm to strong whole tail flexions. These alternating dorsal and ventral flexions had quite a high frequency (15 Hz) and sooner or later detached the animal completely from its house (Fig. 1c).

4. A *water-outflow-obstruction behaviour* was observed once: the animal in a fully inflated house suddenly curved the tip of its tail up in front of its mouth and kept it there for 5–10 s. Apparently, this behaviour prevented water from leaving the house at a normal speed. It remained more than half inflated even after 5 s. It is speculated that this behaviour enables the animal to ingest more of the food particles accumulated in the food reservoir before normal feeding is resumed.
5. A *free-swimming behaviour* was frequently observed, although it was impossible to decide if this was part of the normal behaviour, or a result of stressful *in vitro* conditions. In general this swimming behaviour consisted of whole tail flexions, alternating dorsal and ventral, at a frequency of about 15 Hz. The duration of this type of swimming varied extensively and could be interrupted by periods of complete tail arrest of variable duration. The tail always had a semi-flexed curvature, with the concavity ventral towards the pharynx, during these arrest periods. The observations reported above were all made on *F. borealis*. However, a few observations were also made on functional houses of *F. pellucida*. These revealed much the same architecture and inflation–deflation dynamics as reported for *F. borealis*. The only difference noticed so far was the presence of fewer filter ridges in the filter section when compared to that of *F. borealis* (data not shown).

Discussion

The vesicle-like feeding devices, previously described as attached to the mouth of *Fritillaria megachile* (Fol 1872), *F. pellucida* (Bone et al. 1979) and an unidentified fritillariid (Lohmann 1903, 1909, 1933), probably represent houses of a comparable construction. At least, my own observation of a real house verifies this for *F. pellucida*. It is also difficult to explain, in a hydrodynamic sense, how undulating tail-beats may push water into a remote vesicle of high elasticity rather than to propel the animal through the sea. The complete transparency, minute size and constant movement of these creatures make me believe that the walls of the tail chambers were too transparent to be noticed in the studies mentioned above.

Houses of similar appearance to those described for *F. borealis*, but of about 4 cm diameter and belonging to a “giant” fritillariid, were also observed through a video camera attached to the R.O.V. “Ventana” of Monterey Bay Aquarium Research Institute at 250 m depth in the Monterey underwater canyon during the spring of 1992 (Silver and Flood, unpublished data). One of the >2 cm long animals that produced such houses was caught in a sampler during this cruise and was later found to correspond better to the original description of *F. magna* (Lohmann 1896a), than to its

re-description as included in the species *F. aberrans* by Tokioka (1958).

All the species of *Fritillaria* mentioned above belong to the subgenus *Eurycercus*, which is characterised by a bi-partitioned tip of the tail, as distinct from the subgenus *Acrocercus*, which is characterised by a pointed or acuminate tail tip (Lohmann 1933; Fenaux 1993, 1998). The general house morphology described above, therefore, should not be considered to be valid for the entire genus. In particular, the sophisticated sleeve-like extension of the tail chamber, enabling *F. borealis* to swim with its deflated house in position for later reinflation, needs verification in other species. It may represent a specialisation not present in other species, particularly within the subgenus *Acrocercus*.

Although there are numerous details still missing in our knowledge and understanding of the fritillariid house, it should be clear that it serves several complex functional requirements in very elegant and novel ways, different from those of all other filter-feeding animals (Jørgensen 1966), including the Oikopleuridae (Flood and Deibel 1998).

In fact, in certain ways the fritillariid house seems more sophisticated and advanced than the oikopleurid house: the pronounced elastic properties and the elegant sleeve-like extension of the tail chamber, enabling the animal to move around, with its deflated house ready to be reinflated, appear to represent a great energy-saving mechanism compared to the situation for the Oikopleuridae. This type of house may allow the fritillariid to exploit new micro-areas of the water mass for every feeding cycle. It also allows the fritillariid to escape from attacking predators with their house, whereas oikopleurids have to leave their houses behind when escaping. Likewise, the lack of supporting walls, external to the food-concentrating filters, appears to represent less synthetic investments in a fritillariid house than what is put into a typical oikopleurid house.

Similar to the Oikopleuridae, the rudiments of fritillariid houses are produced by a glandular oikoblastic epithelium. However, whereas the pattern of such oikoblastic cells has been examined in great detail in several oikopleurids (cp. Spriet 1997; Flood, submitted), only Lohmann (1903, 1933) has reported on the oikoblastic cell pattern of the Fritillariidae. At present it seems premature to relate architectural details of the fritillariid house to what is known of their oikoblastic cell pattern.

The calculated volume of water processed through the adult *F. borealis* house (~ 10 to 12 ml h^{-1}) is comparable to values reported for the smaller species of Oikopleuridae (Alldredge 1977; Flood and Deibel 1998; Acuña and Kiefer 2000). Likewise, the capacity of the *F. borealis* house to trap melanin particles down to $\sim 0.15 \mu\text{m}$ in diameter is comparable to the capacity reported for oikopleurid houses (Flood et al. 1990, 1992; Bedo et al. 1993; Flood and Deibel 1998). Accordingly, one may assume *F. borealis* to have a considerable impact on the microbial loop in their inhabited water mass. At a population density of about 4,000 adult individuals

m^{-3} *F. borealis* may sterile-filter the inhabited water mass on a daily basis. The occurrence of such densities of Fritillariidae is perhaps not entirely unrealistic, since densities of up to 240,000 individuals m^{-3} of *F. borealis* (non-specified individual size) have been reported (Gran 1929).

The characteristic patterns of behaviour observed for *F. borealis* are in good agreement with suction electrode recordings made on *F. pellucida* by Bone et al. (1979). According to Martini (1909) the brain consists of 52 cells, and the caudal ganglion, of 19–20 cells (not all of them neurons) in *F. pellucida*. Probably the numbers for *F. borealis* is much the same. The locomotor behaviour, which for *F. pellucida* has been shown to be governed by the tail ganglion alone (Bone et al. 1979), is therefore likely to be dominated by inherited rigid patterns (pacemaker neurons) rather than by plastic responses to a variety of inputs. One should rather be surprised by the number of distinct motor behaviours that so few nerve cells are responsible for, as has been disclosed by the present video recordings and previous suction electrode potential recordings (Bone et al. 1979). These behaviours include: (1) symmetrical tail undulations at two distinct frequencies, (a) a low one (5–8 Hz) associated with feeding and (b) a high one (10–15 Hz) associated with free swimming and swimming with a deflated house; (2) unilateral wiping flexures to deploy a new house rudiment; (3) single unilateral, whole tail flexures, (a) to start the reinflation of an existing house and (b) to remove the tip of the tail from its sleeve; and (4) constant ventro-flexion to obstruct water outflow from the house. This considerable range of behaviour, combined with (5) intervening pauses of (several) fixed durations, from such a limited number of neurons should be challenging to elucidate further.

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